Long-term Ecosystem Dynamics of Contrasting Grasslands in South Africa

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for my parents, Wenzile and Gabriel

"Do not go gentle into that good night,

Rage, rage against the dying of the light". - Dylan Thomas

Declaration

I, Abraham Nqabutho Dabengwa, hereby declare that the work on which this thesis is based is my original work and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university.

Signature: Signed by candidate

Date: June 2019

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Abstract

Rainfall, fire, and grazing all control changes in vegetation and soil in grassland and savanna ecosystems. In these ecosystems, wetlands are key resource areas because they keep moisture and collect nutrients that support grass production. The grass production supports high grazer densities in landscapes, especially during dry climatic periods. The equilibrium idea suggests that, at high densities, herbivores reduce grass production and damage soils. In contrast, the disequilibrium idea argues that unreliable rainfall and frequent droughts lower herbivore densities to levels rendering their effects negligible. Thus, grass production and grazer densities rarely stabilise. However, nonequilibrium theories suggest the relevance of both ideas in natural systems. Spatial and temporal scales used for looking at landscapes and the resilience of persistent soil and grass states control which idea wins. In turn, stability of vegetation states is related to traits of grass biomass including palatability, flammability, and tolerance to drought. At long timescales, we remain uncertain about how grass production in landscapes are affected by indigenous herbivores, and those managed with fires by pastoralists for livestock. In this thesis, I test nonequilibrium dynamics with stability domains of grass biomass, i.e., centres of stable vegetation states (tallgrass versus shortgrass), to assess the resilience of contrasting key resource areas. Long-term sediment proxy data offer the opportunity for assessing vegetation and soil dynamics over many centuries.

Grassland ecosystem dynamics were compared between two sediment cores from South African wetland grasslands. They were the productive montane grassland (Vryheid) controlled by fire and Hluhluwe-iMfolozi Park, a lowland savanna with grasses suppressed by indigenous herbivores. Vegetation change, grazing pressure, fire activity, nitrogen availability, grass biomass, soil stability, and age-depth models of sediments were studied respectively, with fossil grass phytoliths, fossil dung fungal spores, charcoal, stable isotopes, organic carbon (SOC), and x-ray fluorescence (XRF) spectrometry. Cluster and non-metric multidimensional scaling ordination methods were used to organise grass phytoliths, dung spores, and charcoal collections to uncover states of grass mosaics, grazing pressure, and fire activity, respectively. Also, grass states were evaluated by comparing changes in the relative intensity of fire and grazing with time. A long-term regional rainfall record provided a background for landscape scale changes in herbivore densities and local-scale interaction among moisture, grazing pressure, and grass biomass. Archaeological records suggested the presence of pastoralists in the region.

Changes in grass states at key resource areas were related to grass biomass, fire activity, and grazing pressure. At the grassland, the basal stable shortgrass state (from ca. 1 250-690 cal BP) was dominated by tallgrass Panicoideae and shortgrass Chloridoideae tribe phytoliths. Low charcoal records suggested fewer fires while the presence of spores indicated herbivores, supporting the presence of a shortgrass state. The gradual transition to a dynamic mixed tallgrass (unstable) state from ca. 690 cal BP was driven by increased rainfall and soil moisture. Therefore, fire activity and grazing pressure increased based on the rise in charcoal and spore concentrations. Nitrogen availability (δ15N) declined following an influx of Aristidoideae and an increase in Arundinoideae (*Phragmites*) phytoliths. However, from ca. 670-550 cal BP, soil salinity increased as suggested by the high Mg:Ca ratio. Fire and grazing alternated during the dry climate period starting from ca. 600 cal BP. The dry climate helped the gradual phase transition to the stable wetland tallgrass state dominated by *Phragmites* from ca. 410 cal BP to the present, associated with reduced fire and grazing. Basin infilling by unstable soils, suggested by an increase in the Zr:Rb ratio from ca. 590-490 cal BP, may have resulted in the spread of *Phragmites* that later eased soil erosion.

At the savanna, two persistent grass states were deduced from intensities of fire and grazing on grass biomass. Tallgrass state I with increasing charcoal and spore concentrations from ca. 2 140-2 020 cal BP, was followed by tallgrass state II from ca. 2 020 cal BP. The

regionally dry climate from ca. 1 900 cal BP was linked with more landscape fire and grazing pressure, suggested by high charcoal and spore concentrations. Surprisingly, tallgrasses remained as SOC stayed high. A major fire event at ca. 1 730 cal BP marked by peak charcoal was followed by the peak in spores at ca. 1 750 cal BP. An abrupt phase transition to a shortgrass state from ca. 1 610 cal BP represented by low SOC, coincided with lower rainfall from ca. 1 600-1 500 cal BP. The phase transition also coincided with a rise in local grazing pressure indicated by more *Sporormiella* spores and soil disturbance as indicated by the Zr:Rb ratio. Shortgrass state I was succeeded by shortgrass state II from ca. 1 340-960 cal BP with more grass biomass in the dry period from ca. 1 400-1 200 cal BP.

Large-scale drivers of vegetation and soil changes included rainfall, herbivore distributions, and pastoralists. At local-scales, grass states were maintained by relationships among fire activity, grazing pressure, and soil moisture. Thus, resilience within a stability domain depended on cross-scale relationships among drivers. In the savanna, positive feedback between high rainfall and soil moisture supported tallgrass states in the fire domain followed by a threshold/phase transition to shortgrass states ('grazing lawns'). The lawns in the grazer domain depended on positive feedback response between drought and grazing pressure that increased soil aridity. In contrast, an unstable tallgrass state in the fire domain followed the shortgrass state in the grazer domain at the mesic grassland. Pastoralists may have burned productive tallgrasses to feed their animals on palatable regrowth. *Phragmites* reed grass dominance associated with high soil moisture caused a phase transition to the low disturbance domain. Lawns in the grazer domain at the savanna suggested resilience. In comparison, tallgrass states in the fire domain and high grass biomass in grassland amounted to resistance.

Grazing effects on grass and soils in landscapes with reliable food increase the potential for many stable states of vegetation and soil. Surprisingly, key resources areas

studied were resilient because they either absorbed or recovered from heavy grazing and soil damage. Using the term 'degradation' to altered soils is misleading because some shortgrass states sustain grazers for decades. My findings suggest that grazer domains are natural features in some rangelands but that they are susceptible to degradation in semi-arid regions.

This study demonstrates the importance of scale-dependent feedback among climate, grassland productivity, hydrology, fire, and grazing in determining vegetation transitions and states. Stable states, and switches between them, are important for ecosystem dynamics and rangeland management. Also, new ways of using and evaluating multiple proxies are proposed to address instances when interpretations of ecological processes differ. The observations reported in this thesis highlight the contribution of palaeoecology in exploring nonequilibrium dynamics at long timescales.

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A journey of a thousand miles begins with a single step. My long journey entailed several years of peering down the barrel of a white Leica microscope conspicuously perched on old telephone directories. Thankfully, a dozen audiobooks made exceptional company as I took several steps forward. I learnt to value the largeness of small objects found in soil, the many people who supported me, my sponsors and you the readers of this work.

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Chapter One. **Introduction**

1.1 Background to study

Open grassland and savanna biomes support diverse grazers that affect ecosystem functioning. Grass production (i.e., growth) in these landscapes supplies grazers with food (Bonnet et al., 2010; McNaughton, 1984; Muthoni et al., 2014), promotes fires that limit closed woodlands (Bond, 2008b; Staver et al., 2011), and controls nutrient cycling (Blair, 1997; Hobbs, 1996; McNaughton et al., 1988). Since grass production depends on varying rainfall (Archibald and Hempson, 2016; Briggs and Knapp, 1995; O'Connor and Bredenkamp, 2004), landscapes are managed to limit adverse grazing effects on vegetation, soil nutrients, and other animals (Abel and Blaikie, 1989; Illius and O'Connor, 1999; Sinclair and Fryxell, 1985; van de Koppel et al., 1997). However, unreliable rainfall increases herbivore densities at productive grasslands (Fynn et al., 2015; Illius and O'Connor, 1999; Scoones, 1991), and may lead to the undesirable degradation effects outlined. But debates continue among ecologists, rangeland managers, and policymakers about suitable models for understanding dynamic grassy ecosystems.

1.1.1 Equilibrium and nonequilibrium models in rangelands

Models linking grass production to grazers' densities are challenged in rangelands (Abel, 1993a; Briske et al., 2003; Scoones, 1994; Sullivan and Rohde, 2002; Vetter, 2005). The equilibrium models rely on an idea of fixed stocking rates or animal densities for grazing systems based on annual grass growth (Dyksterhuis, 1949; Tainton et al., 1980; Tongway and Hindley, 2004; Vetter, 2005). In these systems, grazer numbers are controlled to minimise the risk of degradation that affects people's livelihoods, particularly in sub-Saharan Africa (Abel, 1993b; Ellis and Swift, 1988; Sinclair and Fryxell, 1985; Sullivan and Rohde, 2002).

However, alternative models are available for understanding ecosystem dynamics where density-dependence is unclear.

Unreliable rainfall, fires, and frequent grazing in semi-arid regions causes changes in grass production far from equilibrium (Derry and Boone, 2010; Ellis and Swift, 1988; Scoones, 1994; Vetter, 2005). The disequilibrium hypothesis argues that frequent droughts reduce grazer populations and causes unstable equilibrium dynamics (Ellis and Swift, 1988; Scoones, 1994). Also, fire and grazing feedback maintains variable levels of grass production (Archer, 1989; Downing, 1974; Perrings and Walker, 1997; Westoby et al., 1989). Thus, the multiple states or stages of grass production evidenced by aboveground plant biomass, suggests nonequilibrium theories that combine elements of equilibrium and disequilibrium (Briske et al., 2005; DeAngelis and Waterhouse, 1987; Illius and O’Connor, 1999; Noy-Meir, 1975; Rietkerk et al., 1996; Sullivan and Rohde, 2002; Westoby et al., 1989). Stocking rates, fixed carrying capacities, and range condition assessments are unnecessary in nonequilibrium systems (Abel, 1993a; Ellis and Swift, 1988; Sullivan and Rohde, 2002).

However, strict supporters of equilibrium ideas fear that failure to keep carrying capacities may cause irreversible ecosystem damage in rangelands (Bestelmeyer et al., 2015; Rietkerk et al., 1996, 1997; Sinclair and Fryxell, 1985). Nevertheless, there is overwhelming evidence of recovery (Allington and Valone, 2010; Ellis and Swift, 1988; Matchett, 2010; Prince et al., 2007; Scoones, 1994) and persistence of low grass cover (Muthoni et al., 2014; Sullivan and Rohde, 2002; Waldram et al., 2008).

1.1.2 Ecological resilience unites multiple stable states in rangelands

Multiple states of grass production caused by disturbance and climate have shifted debates from equilibrium (stability) to ecological resilience in grazing systems (Anderies et al., 2002; Briske et al., 2017; Illius and O’Connor, 1999; Vetter, 2009a). Resilience, described as the capacity of ecosystems to withstand disturbance without changing states (Folke et al., 2004; Gillson and Ekblom, 2009a; Holling, 1973), has become an important research paradigm.

Stability domains, i.e., describing centres or neighbourhoods of persistent grass biomass states in dynamic systems, are controlled by rainfall and consumers (Figure 1.1; Noy-Meir, 1975; Perrings and Walker, 1997). These stability domains and corresponding states are used in various forms for assessing desirable and unwanted rangeland conditions caused by fire and grazing effects in rangelands (Briske et al., 2005; May, 1977; Milton and Hoffman, 1994; Scheffer et al., 2001). Grass sward heights are convenient for describing persistent grass states within domains like the grazer short-statured grasses, shortgrass from here on, and tall bunchgrasses depending on fire, tallgrass from here on (Perrings and Walker, 1997). Changes or shifts to different domains or states may involve an ecological threshold (Gillson and Ekblom, 2009a; May, 1977), as in shifts from a mature tallgrass to a degraded grassland (Briske et al., 2005). Therefore, resilience is a powerful idea for understanding multiple stable states and thresholds.

Separating drivers of vegetation states in open ecosystems in constant flux is complex as there are ecological interactions among rainfall, disturbances, and people (Bond, 2005; Gillson, 2004a; Scholes and Archer, 1997; Walker et al., 1981). Overlaps between disturbances happen at multiple scales (Allred et al., 2011; Archibald and Hempson, 2016; Figure 1.2). This occurs more so in grass-dominated savannas and grasslands.

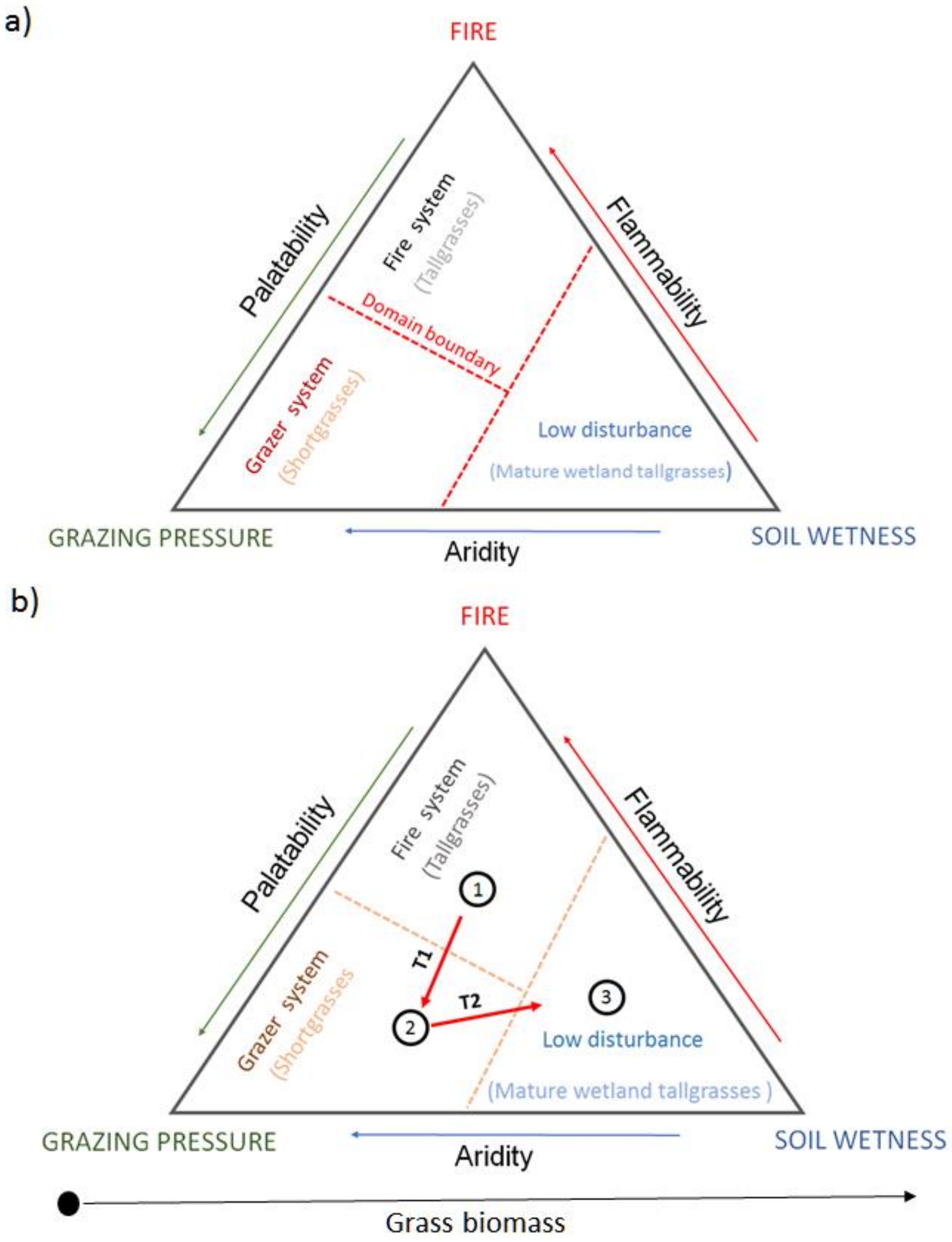

Figure 1.1. Stability domain phase space of grass biomass along disturbance gradients: (a) Drivers of vegetation persistence (stability) at key resource areas are aridity, flammability, and palatability of grasses; and b) Trace of vegetation states and transitions (T_i) of a wetland grass mosaic from a fire to a low disturbance domain.

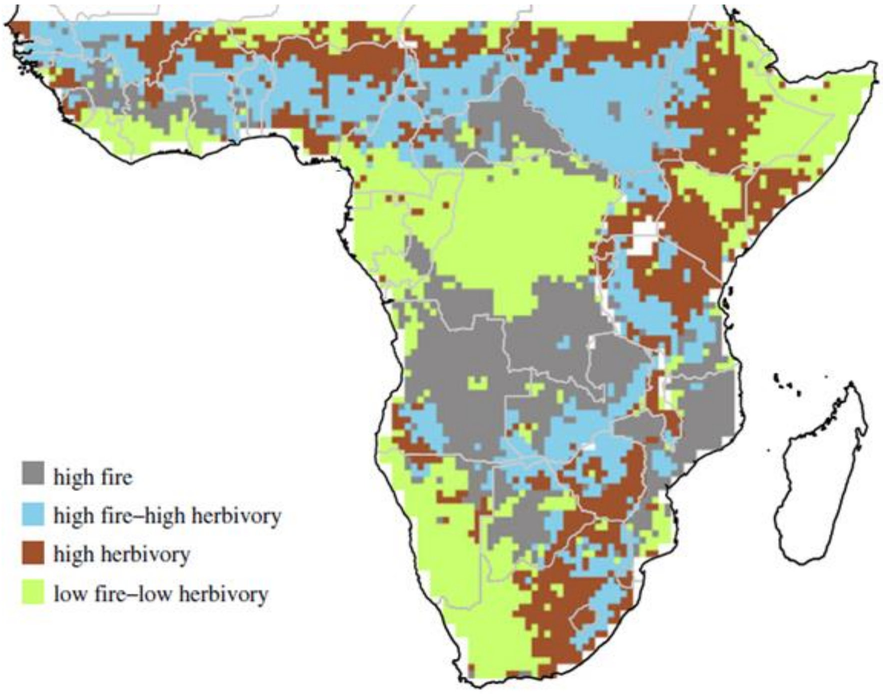

Figure 1.2. Distribution of fire and herbivore systems in Africa (figure from Archibald and Hempson 2016).

1.1.3 Factors controlling vegetation dynamics in grassland and savanna ecosystems

Open ecosystems depending on dynamic fire and herbivore disturbances occupy similar bioclimatic regions (Bond, 2005; Bond et al., 2002; Whittaker, 1975). These warm regions with long dry winters have peak plant growth during wet summers (Mucina and Rutherford, 2006; Vesey-Fitzgerald, 1963). Grasses using the C_4 photosynthetic pathway dominate in these tropical grassy biomes (Bond, 2008b; Bond and Parr, 2010; Parr, 2016). At regional to landscape scales (Figure 1.3), drought-tolerant savanna trees interrupt the dynamic grassy layer at fertile lowlands with deep soils (February et al., 2013; Huntley, 1982; Scholes and Archer, 1997; Walker, 1981). Because trees outcompete grasses for light, grass cover is lower in wooded areas compared with open savannas (Bond, 2008b; Greve, 2013; Scholes and Archer, 1997).

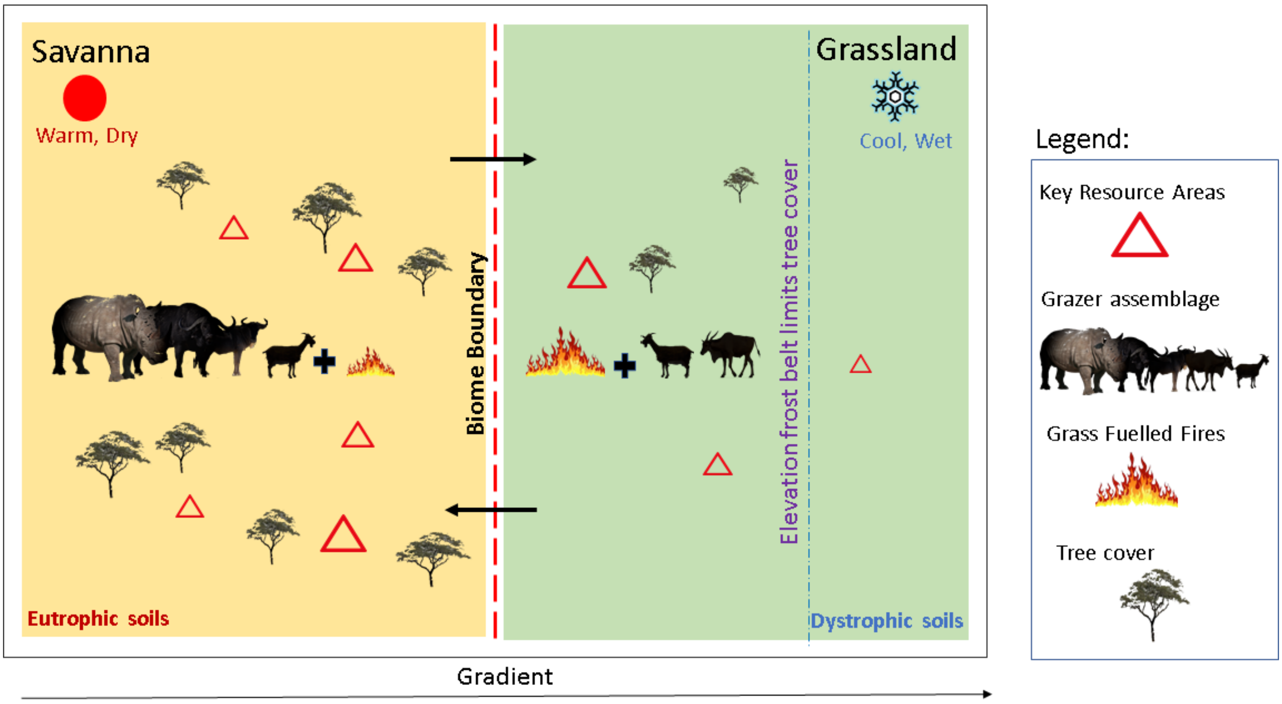

Figure 1.3. Drivers of vegetation changes in savanna and grassland ecosystems. Ecosystems are defined by sharp contrasts in climate, fire, herbivore densities, and soil fertility. Biome boundaries are shifted by climate, vegetation, herbivores, people, and fires.

Heavy grazing in savannas maintains patches with short-statured grasses in landscapes (McNaughton, 1983, 1984; Waldram et al., 2008). At high densities, unselective grazing checks tallgrasses which helps to increase less competitive shortgrasses (Augustine and McNaughton, 1998). Shortgrass dominated patches are known for stoloniferous, arid-adapted, and edible grasses whose productivity increases with grazing (Hempson, Archibald, Bond, et al., 2015; McNaughton, 1984; Veldhuis et al., 2014). Stable grazing lawns mostly occur at woodland openings, hillcrests, termite mounds, and wetland grasslands (Cromsigt et al., 2017; du Toit and Cumming, 1999; Grant and Scholes, 2006; Hempson, Archibald, Bond, et al., 2015; Waldram et al., 2008). Grazing lawn soils are often dry because of poor shading and reduced rainwater infiltration caused by trampling (Schrama et al., 2013; Snyman and Fouché, 1991; Veldhuis et al., 2014). However, soil and leaf nutrients are unusually high (Arnold et al., 2014; Craine et al., 2009; Cromsigt and Olff, 2008; Stock et al., 2010).

In contrast, nutrient-poor grasslands occur at higher elevations with cool moist conditions (Bond, 2008b; Scholes and Archer, 1997; Tinley, 1982; Vesey-Fitzgerald, 1963). The poorly drained shallow soils have limited nutrient pools partly because plant litter decomposition is slowed by low leaf nitrogen contents of mature plants (Anderson et al., 2007; Hobbs, 1996; Pastor and Naiman, 1992; Ruess and McNaughton, 1987; Ruess and Seagle, 1994). Frequent fires in these grasslands dominated by flammable C_4 tallgrass cause punctuated increases in soil nitrogen availability (Blair, 1997; Seastedt and Knapp, 1993). This counters the equilibrium decline in nitrogen availability with increased plant biomass or maturity (Tilman, 1985). Since grazers select palatable juveniles over mature plants, fire is the main consumer (Archibald and Hempson, 2016; Sinclair, 1975; Vesey-Fitzgerald, 1971). Still, productive montane grasslands provide important grazing reserves during winters and droughts (Hall, 1981; Ngugi and Conant, 2008; Vesey-Fitzgerald, 1971).

1.1.4 Key resource areas in rangelands

Productive wetlands providing critical dry season grazing reserves, at risk of degradation, feature in rangeland equilibrium debates (Gillson and Hoffman, 2007; Illius and O’Connor, 1999; Sullivan and Rohde, 2002). These key resource areas are found along drainage lines and lake margins and hold soil moisture and nutrients (Archibald et al., 2005a; Bell, 1971; Illius and O’Connor, 2000; Vesey-Fitzgerald, 1970), which support high herbivore densities in droughts (Illius and O’Connor, 1999; Owen-Smith, 1996; Redfern et al., 2003; Šmilauer et al., 2015). These areas serve as islands of equilibrium in oceans of disequilibrium landscapes. Herbivore densities, apparently unrelated to grass production in wider landscapes (Behnke and Scoones, 1992; Ellis and Swift, 1988), are strongly coupled to resources (Illius and O’Connor, 1999; Sinclair et al., 1985). As such, the link between water points and centres of degradation also supports these nonequilibrium dynamics (Brooks and Macdonald, 1983; Owen-Smith, 1996; Šmilauer et al., 2015).

Figure 1.4. White rhino eating near a wetland grazing lawn in Hluhluwe-iMfolozi Park, South Africa (*photograph taken by Lindsey Gillson*).

However, the persistence of wetland grasslands over long timescales, despite periodic heavy grazing and fires, suggests they are resilient (Fynn et al., 2015; Illius and O'Connor, 2000; Sullivan and Rohde, 2002; Vesey-Fitzgerald, 1970). For example, repeated burning of productive tallgrasses to promote grazing suggests resistance from vegetation (Fynn et al., 2015; Illius and O'Connor, 2000; Vesey-Fitzgerald, 1971). In comparison, grazing lawns that develop are resilient to grazing (Coller and Siebert, 2015; Lock, 1972; Waldram et al., 2008), increase soil aridity (Lock, 1972; Schrama et al., 2013; Veldhuis et al., 2014), and salinity (Arnold et al., 2014; Grant and Scholes, 2006; Seagle and McNaughton, 1992). Indigenous megaherbivores that are less bothered by predators include white rhino (*Ceratotherium simum*) and hippopotamuses (*Hippopotamus amphibius*) which are important resident grazers at African wetlands (Figure 1.4; Lock, 1972; Owen-Smith, 1988; Waldram et al., 2008). In these areas, grazers exert strong controls on grass biomass, which limits local fires and spread from surrounding landscapes (Waldram et al., 2008).

Stability domains of grass biomass may therefore help us learn about resilience of key resource areas under climate and consumer control (Figure 1.1). This could be done by examining grassland dynamics at centennial timescales, thereby widening the temporal scope of current debates about stability and resilience. Also, fire which is important for changing herbivore distributions by increasing palatability of grasses, has not been emphasised (Briske et al., 2017; Illius and O'Connor, 1999; Scoones, 1991; Sullivan and Rohde, 2002).

1.1.5 Long-term palaeoecological perspectives on ecosystem dynamics

Long-term studies of sedimentary fossil pollen, charcoal, and fossil dung fungus spores give insights into persistent grass states affected by herbivore densities at key resource areas (Figure 1.6; Gillson and Ekblom, 2009a; Lejju et al., 2005). For example, *Sporormiella* spores indicating herbivore biomass and local grazing pressure are linked to shortgrass states (Ekblom and Gillson, 2010a; Gill et al., 2012; Rule et al., 2012). Reconstructed grazing lawns are associated with high herbivore densities, aridity, and low nitrogen availability (Ekblom and Gillson, 2010b) and are similar to degraded wetlands (van de Koppel et al., 1997). In comparison, more charcoal signals tallgrass states suggesting high fire activity and mesic conditions (Breman et al., 2011; Ekblom et al., 2014; Ekblom and Gillson, 2010a; Gill et al., 2009; Lejju, 2009; Rule et al., 2012).

However, the low resolution of grass pollen limits the distinction between grass states in many studies. Hence, herbivores densities appear to increase with local moisture or following the arrival of pastoralists (Burney et al., 2003; Ekblom and Gillson, 2010a; Gill et al., 2012; Lejju et al., 2005). One reason for this is that pollen and spore preservation depends on local soil moisture (Moore et al., 1994), but moisture declines with local heavy grazing

(Pietola et al., 2005; Schrama et al., 2013; Wood and Wilmshurst, 2012). The reconstruction of herbivore biomass suffers because spores are rarely counted independent of pollen (Baker et al., 2013). An alternative interpretation of disturbances would be to assume that alternate stable fire and grazing mosaics have always been present in grasslands (Bond, 2005; McNaughton, 1984; Vesey-Fitzgerald, 1971). In the latter case, changing spore abundances may reflect temporary increases in grazing pressure around wetlands and not changes in herbivore densities, particularly in landscapes with megaherbivores (e.g., Cromsigt and Olff, 2008; Owen-Smith, 1987, 1988; Waldram et al., 2008).

Distinctive grass phytoliths are important for independently assessing grazing pressure from changes in taxonomic composition (e.g., Breman, 2010; Finné et al., 2010; Lejju et al., 2005; Novello et al., 2012). Phytoliths or ‘plant stones’ (e.g. Figure 1.5), form as resistant silica casts within grass leaf and inflorescences when silicates are taken up from soils (Piperno, 2006). Grass subfamilies indicated by phytoliths are important for interpreting climate-vegetation relationships used for reporting about aridity and grass sward heights (Barboni and Bremond, 2009; Bremond et al., 2005; Bremond, Alexandre, Peyron, et al., 2008). Productive wetland margins are demarcated by C_3 Pooideae and Arundinoideae subfamilies (Aleman et al., 2014; Kotze and O’Connor, 2000; Novello et al., 2012; Tieszen et al., 1979; Vesey-Fitzgerald, 1963, 1970). Importantly, dryland C_4 grasses represented by Chloridoideae and Panicoideae represent increased drought/grazing and fires, respectively.

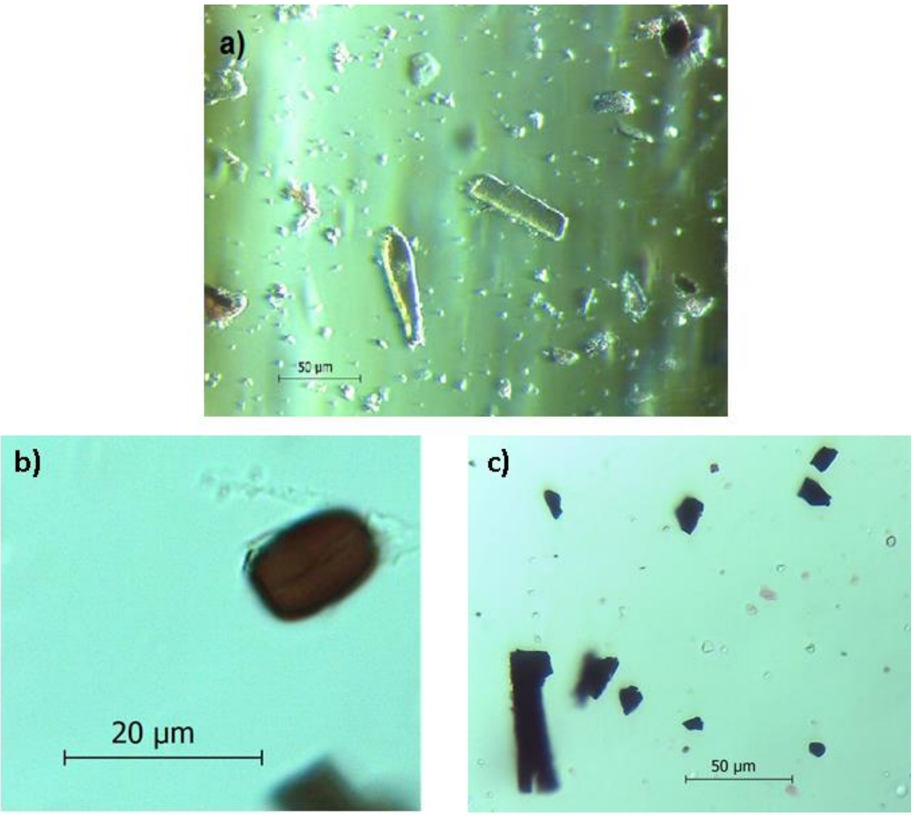

Figure 1.5. Sediment microfossil proxies a) grass phytoliths; b) *Sporormiella* dung spore; and c) charcoal [*images captured by A Dabengwa*].

Conflicting climate and grazing links to Chloridoideae suggests that phytolith explanations are also changeable. Positive responses between drought and grazing (Illius and O'Connor, 1999; Milchunas et al., 1988), and aridity and shortgrasses (Coughenour, 1985; McNaughton, 1984; Veldhuis et al., 2014), also compound problems. This suggests the aridity index based on the ratio of Chloridoideae shortgrasses to Panicoideae tallgrasses (Bremond et al., 2005; Novello et al., 2012) is for dry and wet conditions and is not reliable for key resource areas. Therefore, independent climate and disturbance proxies are necessary for exploring stability domains of wetland grass biomass, especially in landscapes used by indigenous herbivores and/or modified by people in the last millennium.

The Iron Age in South Africa from ca. 1 600-200 BP also changed fire and grazing regimes around key resource areas (Gillson and Ekblom, 2009a; Hall, 1981). The KwaZulu-

Natal Province with historically more indigenous herbivores (Baldwin, 1863; Coutu et al., 2016; McCracken, 2008; Voigt and von den Driesch, 1984), experienced an influx of livestock with the arrival of Nguni pastoralists from East Africa from ca. 1 000 BP (Huffman, 2004). Much later, pastoralists and farmers moved into the interior montane grasslands during the Little Ice Age droughts from ca. 450-150 BP (Huffman, 2004; Huffman and Woodborne, 2016). In the last century land management policies including: fire suppression, elimination of indigenous grazers and carnivores and concentration of pastoral communities in smaller areas may have increased the use and degradation of wetlands.

This study has two goals. The first goal is to use consumer stability domains to evaluate resilience of vegetation and soils states over centennial timescales at contrasting key resource areas. The study sites in KwaZulu-Natal (South Africa) are at opposing ends of rainfall, grass production, fire activity, and herbivore density gradients. The mesic montane grassland with more grass biomass is predicted to be controlled by fire. In contrast, grazers are expected to control biomass and soil processes in the semi-arid lowland savanna with many indigenous herbivores. Importantly, low regional rainfall in the past is expected to be associated with increased grazing pressure, low grass biomass, limited soil nitrogen, and soil losses at both sites. The second goal, an indirect one, was to evaluate how ecological proxies perform within stability domains as outlined in the research plan. The kaleidoscopic view of processes from many proxies is expected to faithfully represent patterns of change. The following questions guided the research:

1. Can grass mosaics be used to classify past landscapes into fire or grazer domains at centennial time scales?
2. How do grass traits separate consumer domains along productivity gradients at key resource areas?

3. How do wet and dry climatic periods change the importance of fire and grazing and ecological processes in landscapes?
4. At what spatial and temporal scales are consumer domains stable or resilient in landscapes?
5. What are the implications of this research for the long-term management of grasslands in disturbance-driven landscapes?

1.2 Research design

I selected two wetland systems for multiple proxy analyses in the KwaZulu-Natal Province, South Africa (Figure 1.7). There was a montane grassland and savanna site. The distant sites captured the regional rainfall, grass productivity, fire activity and herbivore density gradients (e.g., Archibald and Hempson, 2016; Hempson, Archibald and Bond, 2015; O'Connor et al., 2011; Waldram et al., 2008). The mesic grassland with more grass biomass was at the fire end of consumer control. At the herbivore extreme was the semi-arid savanna with less grass biomass. Stability domains of grass biomass around wetland systems were defined by the importance of consumers in space and time. Since key resource areas occupy small proportions of landscapes in mesic grasslands compared to large areas in arid environments (Cromsigt et al., 2017; Illius and O'Connor, 1999), negative effects on grass productivity and soil were expected to be low in the mesic grassland.

At landscape scales, wetland grass mosaic states (shortgrass *versus* tallgrass), were used to define consumer stability domains (e.g., Noy-Meir, 1975; Perrings and Walker, 1997). Grass states and respective biomass were deduced from relative intensities of fire activity and grazing. States were expected to differ in charcoal and dung spore profiles. Fire activity was expected to be high in relation to increased abundance of C_4 flammable tallgrass (Allred et al., 2011; Archibald and Hempson, 2016; Vesey-Fitzgerald, 1971). In comparison, shortgrass states are likely associated with heavy grazing and/or high herbivore densities, and may increase palatable shortgrasses (Hempson, Archibald, Bond, et al., 2015; McNaughton, 1984; Waldram et al., 2008).

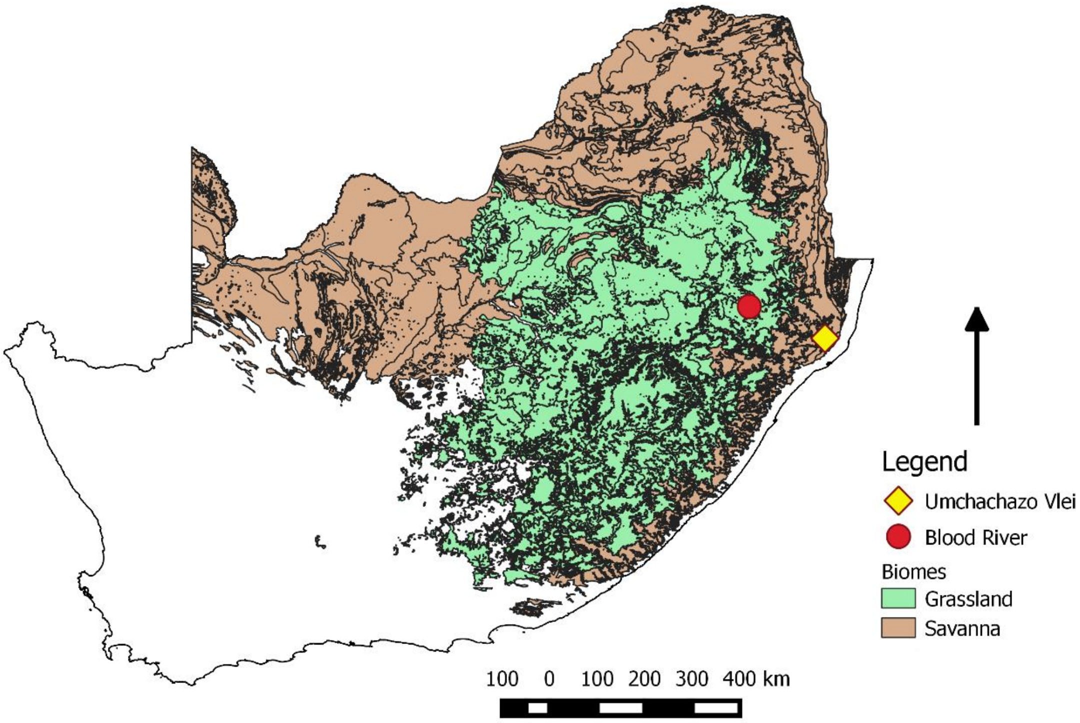

Figure 1.6. The location of study sites in the grassland and savanna biomes of South Africa.

However, the wetland soil moisture gradient affects stability domains deduced from charcoal and spores. For example, soil moisture conditions around wetlands may either enable or prevent landscapes fires at wetlands (Just et al., 2015; O'Connor et al., 2011; Vesey-Fitzgerald, 1970). Wetness also influences herbivore access to wetland margins and therefore controls grazing pressure (Fynn et al., 2015; Waldram et al., 2008). The resultant stability domains along the aridity gradient become the grazer, fire, and low disturbance (Figure 1.1). Hence, low charcoal or spore concentrations from sediments may each suggest grass states in two stability domains.

1.2.1 Multiple proxy assessment of grass stability domains

Since relationships between proxies and corresponding processes were expected to change in nonequilibrium rangelands, I combined multiple proxies to define and evaluate stability domains and soil ecosystem processes. Grass phytoliths from the grassland were used to define stability domains from plant responses independent of charcoal and spores. Persistent states were obtained from stratigraphic clusters of phytoliths representing grass subfamilies (Bennett, 1996; Finné et al., 2010). Shortgrass states maintained by grazers are expected to cause the codominance of Panicoideae and Chloridoideae C_4 grass subfamilies associated with dryland taxa (Coller and Siebert, 2015; Sieben, Collins, et al., 2016; Waldram et al., 2008).

In comparison, Panicoideae abundance suggested dynamic tallgrass states (Allred et al., 2011; Archibald et al., 2005b; Knapp et al., 1998). Regular incursions by flammable C_4 tallgrasses were expected when landscape fire activity was high (e.g., Just et al., 2015). However, dominance of mature wetland C_3 tallgrasses with Arundinoideae and Pooideae found at wetland margins suggests infrequent disturbance by fire and herbivores (Fynn et al., 2015; Vesey-Fitzgerald, 1970).

Stability domains were also independently checked with soil organic carbon and stable isotope analysis. Organic matter along sedimentary sequences was used to evaluate changes in the amount of grass biomass around wetland margins. SOC accumulation in grasslands depends on productivity of aboveground biomass and stemminess of plant tissue (Grime, 1977; Ingram et al., 2008; Seastedt, 1995). SOC therefore increases across stability domains from shortgrasses, tallgrasses, to reed grasses. In comparison, the $\delta^{13}C$ signal from sediment was used to check the origin of SOC based on the dominant C_3/ C_4 photosynthetic signal (Fredlund and Tieszen, 1997; Michener and Lajtha, 2007), and the C:N ratio indicating structural fibre content of plant tissue (Engloner, 2009; Longhi et al., 2008). Tall C_3 reed grasses like *P. australis* (represented by Arundinoideae), will have more lignin compared with C_4 tallgrasses, while C_4 shortgrasses have the least.

However, grazing lawns are controlled by herbivore densities and aridity that reinforce each other (Veldhuis et al., 2014; Vesey-Fitzgerald, 1970). This suggests that wetland grass phytoliths give unreliable climate signals. Wetland grasses in grazing systems are therefore in equilibrium with herbivore densities or grazing pressure (Illius and O'Connor, 1999; Muthoni et al., 2014; Waldram et al., 2008). This suggests the Chloridoideae to Panicoideae aridity index (Iph%) has limited relevance beyond local-scales (Novello et al., 2012). Thus, fossil diatoms (algae) found alongside phytoliths give independent information about this local aridity gradient (e.g., Novello et al., 2015), and are useful for assessing stability domains (Figure 1.7).

1.2.2 Geochemical proxies for assessing soil function

Geochemical markers were important for assessing changes in soil nutrients, salinity, and erosion across consumer stability domains. Domains helped compare rival equilibrium theories of soil nitrogen that is essential for plant growth. Equilibrium between nitrogen availability and vegetation development (Tilman, 1985), was expected to reduce the natural abundance of nitrogen ($\delta^{15}N$) in stability domains with high grass biomass. In contrast, the nonequilibrium suggests that frequent disturbances of grass biomass increase nitrogen availability (Blair, 1997; Seastedt and Knapp, 1993), and is expected at intermediate grass biomass. Therefore, this theory either punctuated $\delta^{15}N$ equilibrium or disequilibrium.

An interesting observation is the association between nitrogen-rich grazing lawns and saline soils (e.g., Arnold et al., 2014; Grant and Scholes, 2006; Seagle and McNaughton, 1992; Stock et al., 2010). Herbivores promote and depend on mineral salts (Mg, Ca, Na) to supplement their diets (Arnold et al., 2014; Grant and Scholes, 2006; Jarman, 1972; Seagle and McNaughton, 1992). Chloridoideae shortgrasses are adept at collecting salts in their plant tissue (Bennett et al., 2013; Ceccoli et al., 2015). However, salty soils indicate degradation because they suggest low grass cover, compact soils, and reduced rain water infiltration (Illius and O'Connor, 1999; Snyman and Fouché, 1991; van de Koppel et al., 1997).

Salty soils are susceptible to erosion. Coupling between wetlands and herbivore densities links soil disturbance to heavy grazing (Ingram, 1991; Pietola et al., 2005). Sheet erosion around wetlands transports large soil grains into sediments because of increased momentum of water over bare and compacted soils (Schillereff et al., 2014; M Wang et al., 2011).

1.2.3 Multiple proxy summary for assessing ecosystem dynamics

Below is a summary of the multiple proxy plan for evaluating vegetation dynamics, stability domain phase-space, and soil processes at key resource areas (Figure 1.8). Descriptions of palaeoecological methods are found in the next chapter.

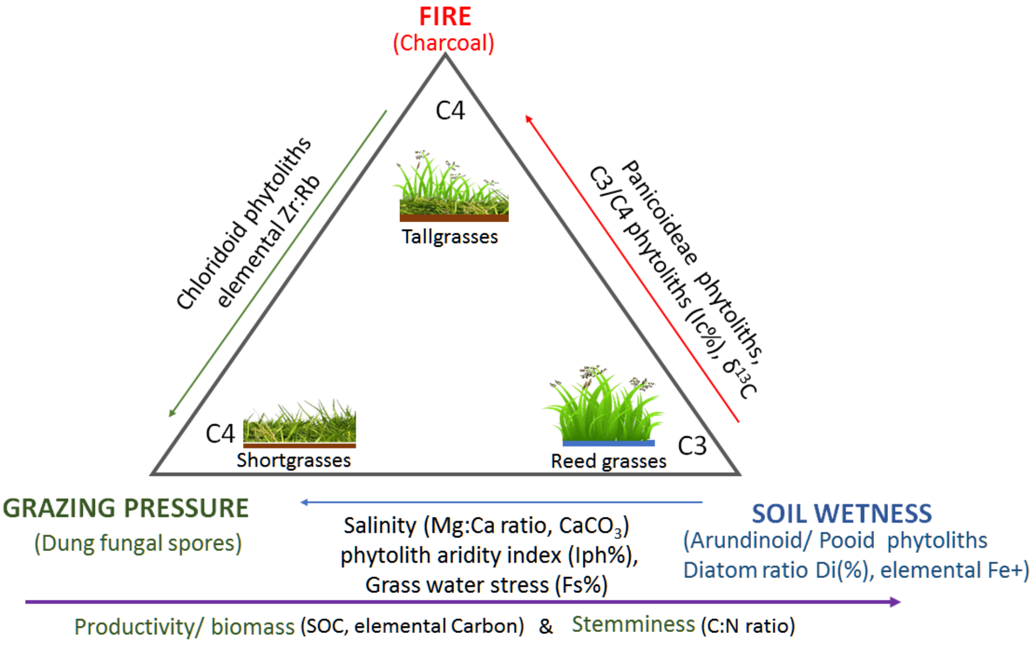

Figure 1.7. Multiple proxy research plan for assessing stability domain phase-space and soil processes at key resource areas.

1.3 Thesis outline

This thesis has six chapters outlined below:

Chapter One: Introduction. Presents a background to stability and resilience in key resource areas. Stability domains of grass biomass to disturbance and aridity are proposed for assessing vegetation and soil dynamics. I also state goals of the research.

Chapter Two: Literature Review. The chapter reviews key resource areas and their role in soil nutrient, palaeo-history of the study region, and interpreting consumer-driven systems at long timescales.

Chapter Three: Methods. An overview of field and laboratory methods used in this multiple proxy palaeoecological study are given, followed by statistical methods and analyses used.

Chapters Four: This chapter presents research findings from a montane grassland site (Blood River Vlei). The site may have been used by pastoralists in the last millennium. Rangeland stability paradigms are explored using the key resource area idea over long timescales. Grass dynamics related to climate and disturbances are discussed using vegetation state-and-transitions across stability domains. Stability domains are independently assessed with vegetation and disturbance proxies. Finally, soil nutrient dynamics were used alongside stability domains to discuss resilience.

Chapters Five: The chapter presents new discoveries from the Hluhluwe-iMfolozi Park savanna. Vegetation dynamics are discussed regarding state-phase transitions between fire and grazing stability domains of wetland grass mosaics. Grass states were defined in a new way from fire activity (charcoal) and grazing pressure (dung spores), and independently assessed with sediment organic carbon. Positive feedback between drought and grazing triggered state-transitions to low grass biomass and soil disturbance as predicted from theory.

Surprisingly, heavy grazing suppressed soil local moisture that reduced soil nutrient concentrations despite dung inputs from herbivores.

Chapter Six: Synthesis and Conclusion. Long-term ecological dynamics are compared between the grassland and savanna using stability domains. Resilience and hierarchy at the key resource areas are discussed. Theoretical contributions from this study are briefly outlined. The conclusion section discusses the implications of this study on rangeland management, methodological considerations, limitations, and directions for future research.

2.1 Role of key resource area in grassland stability and ecosystem functioning

Key resource areas are important for understanding ecosystem functioning in savanna and grasslands landscapes (Figure 2.1). These areas control herbivore populations (Illius and O'Connor, 1999; Owen-Smith, 1996; Sinclair et al., 1985; Vrba, 1987), moderate fire activity (Archibald et al., 2005a; Waldram et al., 2008), and affect soil nutrients and function (Arnold et al., 2014; Craine et al., 2009; Grant and Scholes, 2006; Ma et al., 2016; Seagle and McNaughton, 1992). As centres of high herbivore disturbances and potential ecological degradation, the areas contribute to overall stability and resilience of vegetation and soils in rangelands (Acocks, 1953; Illius and O'Connor, 1999; Owen-Smith, 1996; Rietkerk and van de Koppel, 1997; Sinclair and Fryxell, 1985). Therefore, management of key resource areas has tended to complement other methods of controlling herbivore densities (Sullivan and Rohde, 2002), but with mixed results.

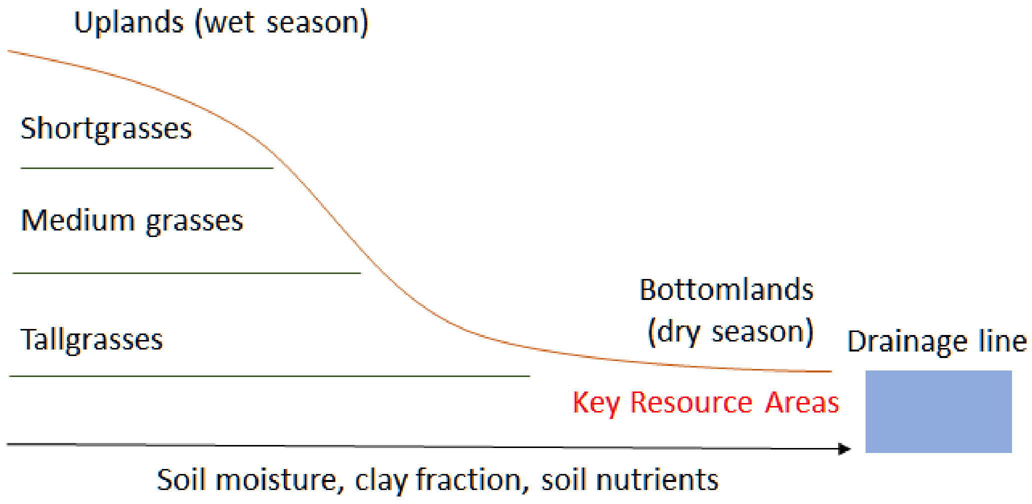

Figure 2.1. A general cross-section through a grazing landscape with relative seasonal grazing gradients (Bell, 1971) and location of wetland key resource areas with high soil nutrients (Anderson et al., 2010; Grant and Scholes, 2006; Seagle and McNaughton, 1992)

2.1.1 Key resource areas in rangeland ecology

Key resource areas intersect with two rangeland management strategies: water-point supplementation and population control. The strategies aimed at supporting herbivores (Coughenour, 1991; Derry and Dougill, 2008; Owen-Smith, 1996), and protecting landscapes from ecological degradation (Walker et al., 1987), assume density-dependent equilibrium. This suggests that wetlands controlling herbivore densities are important for understanding local and landscape level changes in vegetation, soil, and resilience (Illius and O'Connor, 1999; Western, 1975).

A better understanding of the role of key resource areas is responsible for changing rangeland water supplementation policies (Owen-Smith, 1996; Redfern et al., 2003). Initially, water supplementation was designed to alleviate herbivore thirst and extend their use of landscapes (Redfern et al., 2005; Thrash, 1998). This strategy depends on hierarchical patch dynamic (HPD) equilibrium (Coughenour, 1991; DeAngelis and Waterhouse, 1987; Senft et al., 1987), a nonequilibrium paradigm that predicts that the spread of herbivore effects on grass production and soils would be lower over a larger area because of multiple centres of disturbance (Brooks and Macdonald, 1983; Coughenour, 1991). Over the long-term, undesirable results from the policies were herbivore population increases, loss of grass cover, tree invasion, and soil damage (Brooks and Macdonald, 1983; Owen-Smith, 1996; Smit et al., 2007; Walker et al., 1987). Many water points have since been closed in and outside of protected areas (Hilbers et al., 2015; Redfern et al., 2005; van Wilgen and Biggs, 2011).

Piospheres, i.e., barren zones around wetland and water points, suggest grass mosaics disappear for brief periods in grazing catastrophes (Acocks, 1953; Noy-Meir, 1975; Owen-Smith, 1996; Rietkerk et al., 1997; Sinclair and Fryxell, 1985). Heavy grazing and trampling at first affects tallgrasses but even shortgrass succumb with time because of altered soil conditions (Graetz and Ludwig, 1978; Schrama et al., 2013). This suggests that density-dependent herbivory tolerance thresholds beyond grasses are vulnerable (Augustine and McNaughton, 1998; Briske, 1996; Graetz and Ludwig, 1978; McNaughton, 1983; Noy-Meir, 1975; Rietkerk and van de Koppel, 1997). Since piospheres mostly happen in drought in some rangelands (Derry and Boone, 2010; Illius and O'Connor, 1999; Matchett, 2010), this suggests multiple spatial and temporal scale processes controls resilience and stability of vegetation and soil.

In comparison, population control measures based on carrying capacities have also been reconsidered. The control methods of animals exceeding the 'carrying capacity' included forced removals (Brooks and Macdonald, 1983; Le Roux et al., 2017; Owen-Smith, 1988), movement of excess animals to underused areas (Brooks and Macdonald, 1983; Owen-Smith et al., 2017), and whole-sale slaughter or culling (van Wilgen and Biggs, 2011; Walker et al., 1987). Unlike the natural population regulation from resource constraints caused by droughts (Caughley, 1970; Ogutu and Owen-Smith, 2003; Sinclair et al., 1985; Walker et al., 1987), these methods are designed to prevent starvation and environmental degradation (Swemmer et al., 2018).

Drought fatigue from the 1960s, 1980s and 1990s forced a rethink of pre-emptive population control measures in parks and communal areas (Behnke and Scoones, 1992; Ellis and Swift, 1988; Scoones, 1991; Walker et al., 1987). First, state control of livestock densities had mixed success since some landscapes with key resource areas can support high stocking rates during droughts (Homewood, 1994; Scoones, 1991, 1992; Sullivan, 1996). Second, culling fell out of favour because of ethical concerns (van Wilgen and Biggs, 2011). Third, reintroduction of large carnivores in protected areas naturally controlled herbivore densities (Le Roux et al., 2017; Ogutu and Owen-Smith, 2003; Watson and MacDonald, 1983). Last, lifting of fences allowed natural dispersal of indigenous herbivores, and may have curtailed animal deaths during the recent drought at Kruger National Park (Swemmer et al., 2018).

2.1.2 Soil nitrogen dynamics in rangelands

Nitrogen is an essential nutrient for protein synthesis that controls plant and animal growth (Begon et al., 1996). Nitrogen supporting grass primary production in rangelands comes from the soil (Stock et al., 2010; Tilman, 1986b; Wedin, 1999). Grazers prefer to eat plants rich in protein compared with structural fibre (Georgiadis and McNaughton, 1990; Owen-Smith and Novellie, 1982). However, soil and plant nitrogen availability varies in space and time (Allred et al., 2011; Hobbs, 1996; Schrama et al., 2013; Tilman, 1986a). Factors controlling changes in nitrogen include rainfall and plant productivity (Allred et al., 2011; Coetsee et al., 2012; Tilman, 1985), fires (Allred et al., 2011; Anderson et al., 2007; Stock et al., 2010), and herbivore densities (Hobbs, 1996; Schrama et al., 2013; Stock et al., 2010).

There are two competing equilibrium ideas about soil nitrogen availability in grassy ecosystems. The equilibrium resource-ratio hypothesis assumes a fixed pool of nitrogen declines with plant development/maturity from patch to landscape scales (Tilman, 1985). Plant development represents the increase in grass biomass with time, from shortgrass to tallgrass states, locking nitrogen in plant tissue. Tallgrasses dominating later stages of plant development are superior competitors compared with shortgrasses for light, nitrogen, and eventually space (Grime, 1977; Tilman, 1985). In contrast, nonequilibrium ideas suggest open nitrogen pools driven by variability in rainfall, fire, and grazing (Blair, 1997; Coetsee et al., 2012; Hobbs et al., 1991; Seastedt and Knapp, 1993). Therefore, soil nitrogen may not be dependent on vegetation states in stages of plant development.

Nitrogen limitation is high in mature grasslands (Anderson et al., 2007; Ojima et al., 1994; Stock et al., 2010). The tallgrasses invest resources for growth in size and that results in more structural carbon compared with protein content in tissues (Griffiths, 1999; Milchunas et al., 1988). Grazers avoid mature plants because of their low food value suggested by high C:N ratios (Hobbs, 1996; McNaughton et al., 1988), and the resultant grass litter is also despised by microorganisms responsible for decomposition (Hobbs, 1996; Longhi et al., 2008; Pastor and Naiman, 1992; Ruess and McNaughton, 1987; Ruess and Seagle, 1994). Microorganism instead prefer to hold on to available nitrogen, whose natural abundance in soils is indicated by δ^{15}N, by limiting that availability to plants (Hobbs, 1996; Ruess and McNaughton, 1987). Disturbances by fire and grazing are therefore important for freeing up nitrogen and stimulating plant growth in grasslands.

Fires are important for nitrogen cycling because they free nutrients locked up in plants (Coetsee et al., 2012; Hobbs et al., 1991; Seastedt and Knapp, 1993). Grass productivity increases following fires as more growing resources become available (Knapp et al., 1999; Seastedt and Knapp, 1993). Burned patches attract grazers because they have plants at early growth stages rich in leaf protein (Allred et al., 2011; Hobbs et al., 1991). The fire and grazing interaction causes shifting patterns of disturbance in landscapes of productive grasslands causing nonequilibrium nitrogen supply (Allred et al., 2011; Hobbs, 1996; Knapp et al., 1998). However, suppression of grass productivity by herbivores can lead to different controls on soil and plant nitrogen.

Herbivores control nitrogen cycling through direct effects on plants and soils. Grazers transport nitrogen by eating grasses and depositing dung and urine to other parts of landscapes (Hobbs, 1996; Le Roux et al., 2018; McNaughton et al., 1988). At grazing lawns where herbivores are found at high densities, leaf nitrogen content is higher than that of tallgrass areas in the landscape matrix (Arnold et al., 2014; Coetsee et al., 2012;

McNaughton, 1984; Stock et al., 2010). Directly usable nitrogen from dung and urine is likely to be high in frequently used grazing lawns soils (Cromsigt and Olff, 2008; McNaughton, 1984). Key resource areas that draw herbivores also have an unusually high deposition of herbivore excrement (Rietkerk et al., 2000), and may skew nitrogen distributions in landscapes over long timescales.

However, fire and grazing may negatively affect nitrogen cycling in landscapes. Frequent fires used to promote grazing may instead increase tallgrasses with low leaf and litter nitrogen contents (Anderson et al., 2007; Ojima et al., 1994). Selective grazing can also increase unpalatable tallgrasses with low leaf nitrogen (Pastor and Naiman, 1992).

Negative effects on nitrogen cycling happen when herbivores at high densities modify soils. Loss of grass cover and trampling of soils caused by herbivores reduces soil pore sizes (Elschot et al., 2015; Pietola et al., 2005; Schrama et al., 2013). This results in low rain water infiltration of soils (Schrama et al., 2013; Snyman and Fouché, 1991), and stifles nitrogen cycling microorganisms needing oxygen (Bakker et al., 2009; Schrama et al., 2013). This suggests the trade-off between rain water-use efficiency and nitrogen availability in soils is mediated by herbivores (Gong et al., 2011; Schrama et al., 2013). However, nitrogen is not the only important nutrient sought after or controlled by herbivores in landscapes (Coughenour, 1991; Jarman, 1972; Seagle and McNaughton, 1992).

2.1.3 Mineral salt concentrations in rangeland soils

Areas in rangelands with unusually high soil nutrients, called ‘hotspots,’ are important for supporting herbivore diets (Arnold et al., 2014; Grant and Scholes, 2006; Seagle and McNaughton, 1992; Stock et al., 2010). Essential mineral salts include those of calcium, magnesium, potassium, and sodium. Herbivores are known for actively including salts in their diets (Jarman, 1972; Seagle and McNaughton, 1992). However, the importance of saline (salty) areas is also debated. Saline soils associated with low grass cover are often considered signs of degradation (Snyman and Fouché, 1991; Teuber et al., 2013; van de Koppel et al., 1997). Alternatively, they are natural features related to frequent use by indigenous herbivores (Coller and Siebert, 2015; Stock et al., 2010).

Saline patches in landscapes are linked to topography (Anderson et al., 2010; Arnold et al., 2014; Stock et al., 2010), water-holding clays (Anderson et al., 2010), herbivore pressure (Anderson et al., 2010; Coller and Siebert, 2015; Stock et al., 2010; Vesey-Fitzgerald, 1970), and fire-grazing interactions (Stock et al., 2010). However, there patches are associated low grass cover and dry compacted soils. Many natural salty patches are usually found at bottomland positions including key resource areas where nutrients collect (Anderson et al., 2010; Arnold et al., 2014; Grant and Scholes, 2006; Vesey-Fitzgerald, 1970; Yoganand and Owen-Smith, 2014).

However, there are no long-term studies available to judge between degradation versus natural origin of nutrient hotspots. Current studies suggest these features disappear when herbivore access is restricted around wetlands (Coller and Siebert, 2015), and when wet climatic conditions cause soil recovery because herbivores use more of the landscapes (Matchett, 2010).

2.2 Palaeoecological context of climate and disturbance in north-eastern grasslands of South Africa

2.2.1 Climate and land use changes over the last 2 000 years in the study region

The palaeoclimate records for South Africa suggest alternating wet and dry periods in the last 2 000 years (Chevalier and Chase, 2015; Holmgren et al., 1999; Stager et al., 2013). The regional multiple proxy rainfall reconstruction suggested coherent climate changed in a region including KwaZulu-Natal sites (Chevalier and Chase, 2015; Figure 2.2). At long timescales, rainfall was sensitive to the position of the intertropical convergence zone and southern Indian Ocean sea-surface temperatures (Chevalier and Chase, 2015; Stager et al., 2013; Sundqvist et al., 2013; Woodborne et al., 2015). The dynamic El Nino and La Nina cycles in the Southern Ocean circulations controlled rainfall at short timescales (Stringer et al., 2009; Tyson et al., 2002). Therefore, regional climate forms the backdrop of drought-related disturbances and land use patterns.

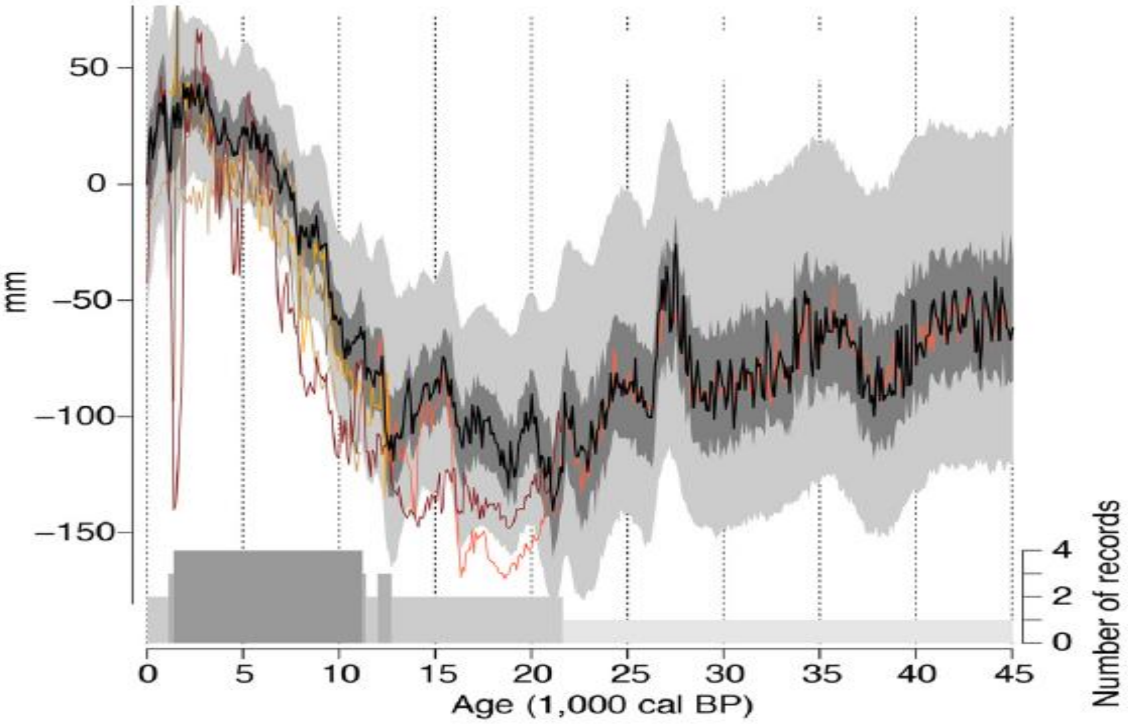

Figure 2.2. Reconstructed rainfall (mm) from pollen, diatom, and stalagmite records in the mesic north-eastern region of South Africa over the last 45 000 years. The black line shows reconstructed mean annual rainfall and shaded dark grey and light grey show the 20% and 50% uncertainty intervals about the mean (source caption Chevalier and Chase 2015).

Rainfall records from the region suggest the prevalence of long-lasting droughts in the last two millenniums (Chevalier and Chase, 2015; Stager et al., 2013; Stringer et al., 2009; Woodborne et al., 2015). The first occurred from ca. 1 900-1 700 BP (Chevalier and Chase, 2015; Holmgren et al., 1999). This was followed by another dry period from 1 400-1 200 BP (Chevalier and Chase, 2015; Ekblom and Stabell, 2008; Holmgren et al., 1999). However, dry conditions lasted longer in East Africa from ca. 1 550-950 BP (Verschuren et al., 2000).

They were controlled by the Indian Ocean dipole that causes alternating wet and dry conditions between the northern and southern hemispheres (Stager et al., 2013; Tyson et al., 2002; Verschuren et al., 2000).

Migrations by livestock rearing farmers and pastoralists from East Africa to Southern Africa from ca. 1 000 BP was caused by dry climatic conditions (Huffman, 2004; Tyson et al., 2002). The arrival of these peoples in Southern Africa is suggested by increased fire and grazing based on charcoal and dung spore concentrations in sediments (Ekblom et al., 2014; Ekblom and Gillson, 2010a; McWethy et al., 2016; Neumann et al., 2014; Thamm et al., 1996). And finally, a dry climate lasted from ca. 600-200 BP in south-east Africa (Chevalier and Chase, 2015; Gillson and Ekblom, 2009b; Holmgren et al., 1999; Stager et al., 2013; Sundqvist et al., 2013; Woodborne et al., 2015), prompting movements into the interior montane grasslands of South Africa where water and forage were plentiful. (Hall, 1981; Huffman, 2004).

Although climate encourages a top-down understanding of environmental change in landscapes (Ekblom and Gillson, 2010b), disturbances by fire and herbivores control vegetation and soil at multiple spatial scales (Coughenour, 1991; Cummings, 1982; Ekblom and Gillson, 2010b; Nicolson et al., 2002). Thus, ‘vegetation-climate equilibrium’ assumed for some proxies may fail to hold (e.g., Bremond et al., 2005; Bremond, Alexandre, Wooller, et al., 2008; Neumann et al., 2008; Truc et al., 2013). Wetland sedimentary proxy studies of grassland dynamics are affected because these plants may be in equilibrium with herbivores (Illius and O’Connor, 1999). Or remain at disequilibrium because of droughts (Ellis and Swift, 1988) and fires (Archibald et al., 2005a; Fuhlendorf et al., 2009; Vetter, 2005).

2.2.2 Grassland consumer stability domains from palaeo-landscapes

Multiple stabilities of grass production controlled by climate, fire, and grazing challenge conventional interpretations of sedimentary proxy data (e.g., Bond, 2005; Ellis and Swift, 1988; Illius and O'Connor, 1999; Vetter, 2005; Westoby et al., 1989). The conventional assumption of top-down control of ecosystems appears unsuitable in some landscapes since grasses remain stable although climate changes (Breman et al., 2011; Ekblom and Gillson, 2010b; Rule et al., 2012). Instead some studies suggest active key resource areas where herbivores support stable grazing lawns (Ekblom and Gillson, 2010b), and fire and grazing cause dynamic tallgrass states (Burney et al., 2003; Ekblom and Gillson, 2010a; Gill et al., 2009; Rule et al., 2012). Finding suitable stability domains in sediment records is hindered by the low taxonomic identity of grass fossils, type of models used for assessing stability, and challenges related to fire and grazing proxies.

2.2.2.1 Taxonomic constraints on identification of grass stability domains

Identifying multiple stability domains of grass biomass in rangeland that experience fire and grazing using grass fossils is complex. While some unique grasses demarcate wetland margins, many species are found elsewhere in landscapes (Kotze and O'Connor, 2000; Mucina and Rutherford, 2006; Vesey-Fitzgerald, 1970). Most sediment studies investigating disturbance rely on pollen that poorly resolves grasses to family level (Burney et al., 2003; Ekblom and Gillson, 2010a; Rule et al., 2012). For example, stability has been suggested for grass mosaics inferred from pollen despite variability in herbivore densities and fire activity from dung spores and charcoal proxies (Gillson and Ekblom, 2009a). Therefore, we may assume dynamic stability in tallgrass mosaics (Fuhlendorf et al., 2009; Hovick et al., 2015; Knapp et al., 1999), but remain uncertain about the fuel mixture.

In comparison, fossil grass phytoliths used for identifying assemblages to subfamily level give extra information about consumer control in reconstructed grass mosaics. The main grass subfamilies in African sediment records include Panicoideae, Chloridoideae and Pooideae (Barboni and Bremond, 2009; Bousman and Scott, 1994; Finné et al., 2010; Novello et al., 2012; Rossouw and Scott, 2011). For example, increased numbers of Panicoideae types are related to C_4 tallgrasses in landscapes with high fire activity and charcoal (Lejju et al., 2005). This contrasts with Chloridoideae whose peaks follow increases in spores, which suggests grazing promotes shortgrasses. Pooideae and Arundinoideae phytoliths represent C_3 grasses at wetland margins controlled by soil moisture (Finné et al., 2010; Novello et al., 2012). However, these C_3 grasses help with knowledge of vegetation stability at margins where fire and grazing are limited.

So, despite the dominance of grasses in pollen and phytolith records from grasslands, resolving consumer stability domains remains a challenge. Grass pollen can account for more than 70% of terrestrial grains in pollen records (Ekblom et al., 2014; Ekblom and Gillson, 2010a; Finch and Hill, 2008; Gillson and Ekblom, 2009a, 2009b; Neumann et al., 2008, 2010, 2014), and similar values are found with grass phytoliths (Breman, 2010; Finné et al., 2010; Lejju et al., 2005). Although there are differences in production rates of microfossils in ecosystems, they reflect vegetation structure surrounding wetlands. Lejju et al. (2005), for example, found matching vegetation patterns using stratigraphic units of vegetation in sedimentary sequences of pollen and phytoliths. This suggests vegetation patterns from sediment records broadly capture states of grass mosaics but not stability domains.

2.2.2.2 Models of vegetation stability

The idea that climate is the main driver of vegetation development with trees as the final stage hinders our understanding of grass stability domains in landscapes with key resource areas (Clements, 1916, 1936). This paradigm is imposed by the poor taxonomic resolution grass pollen compared with that of trees and forbs. Thus, few studies use nuanced nonequilibrium paradigms like HPD and resilience in grasslands and savannas (e.g., Ekblom and Gillson, 2010b; Gil-Romera et al., 2010; Gillson, 2004b). Still, functional distinctions between tree and grasses have been useful for both paradigms. However, relationships among large scale drivers of vegetation like rainfall and consumers (fire and herbivores) on local grass stable states at key resource areas are not well understood.

Tree recruitment in grasslands and savannas at large spatial scales is driven by rainfall (Sankaran et al., 2005; Tinley, 1982; Walker et al., 1981), fire (Archer et al., 1995; Bond, 2008b; O'Connor et al., 2014; Staver et al., 2011), and herbivory (Archer, 1989; Bond et al., 2001; Westoby et al., 1989). At small spatial scales, soil moisture (Huntley, 1982; Sankaran et al., 2005; Tinley, 1982; Walker et al., 1981), soil fertility (Bond et al., 2001; Huntley, 1982; Sankaran et al., 2005), and seed dispersal by herbivores (Olff and Ritchie, 1998) matters. Since trees are long-lived, their stability includes multiple spatial and temporal scales interaction with grasses that control fires and herbivory patterns. Using a pollen study, Gillson and Ekblom (2010b) argued that the stability of tree cover in landscapes depends on rainfall but that it was unstable at local scales. Interestingly, they suggested that stable grass states at local scales are driven by aridity. This proposition is counterintuitive because resilient edaphic wetland grasslands and mature tallgrasses in drylands are supported by drenched soils and rainfall (O'Connor and Bredenkamp, 2004; Vesey-Fitzgerald, 1963, 1970).

An interesting observation is that the anomalous conclusion is addressed by considering multiple grass states driven by soil moisture, fires, and grazers. Correctly, tree cover is variable in mesic grasslands where fires limits seedling recruitment (Bond, 2008b; Wakeling et al., 2011). High soil moisture around clay-rich wetlands upholds tallgrasses (Bell, 1971; Fynn et al., 2015; Kotze and O'Connor, 2000), and therefore controls tree cover by fuelling intense fires (Vesey-Fitzgerald, 1970).

On the other hand, heavy grazing by megaherbivores and other grazers can support grazing lawns around wetland margins (Lock, 1972; Owen-Smith, 1987; Waldram et al., 2008), as argued by Gillson and Ekblom (2010b). Interestingly, soil moisture losses from drought and heavy grazing (Illius and O'Connor, 1999; Sinclair and Fryxell, 1985), help trees establish following losses of grass cover (Brooks and Macdonald, 1983; O'Connor et al., 2014; Tinley, 1982).

Grass dynamics from Gillson and Ekblom (2010b) are reinterpretable with an alternative nonequilibrium theory (e.g., Illius and O'Connor, 1999). Stable grass production is expected at *local* key resource areas because of wet soils and heavy grazing, maintain mature tallgrass and grazing lawn stands. In comparison, (*global*) instability is the norm in wider landscapes owing to variable production caused by weak herbivore control, low soil moisture, and fires. The major challenge in applying this alternative theory are the multiple interpretations of fire and grazing proxies.

2.2.2.3 Challenges with interpreting fire and herbivore proxies

Our understanding of fire and herbivore control of grass stable states is complicated by nonlinear dynamics. The proxies used have multiple context-dependent interpretations (Figure 2.3). At bottom, several challenges stem from different dispersal ranges of charcoal and spores that define spatial extent of landscapes recorded in sediments.

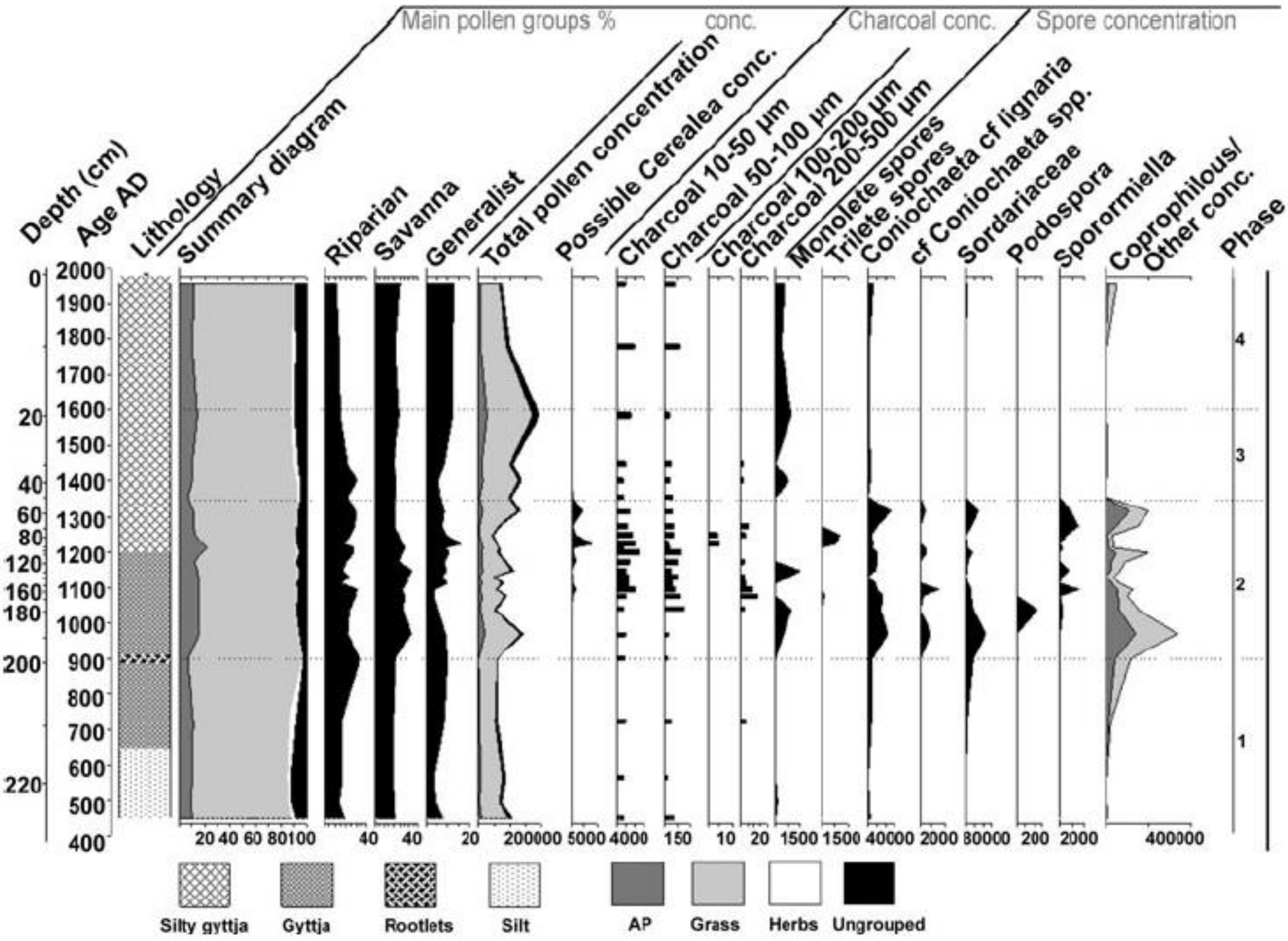

Figure 2.3. Pollen summary diagram of vegetation, fire, and herbivory sedimentary sequence from Lake Nhaucati, Mozambique (Image from Ekblom et al 2014).

There are several interpretations of sedimentary charcoal used for understanding historical fire-vegetation interactions. In grassy biomes, charcoal is a good indicator of fire activity (Leys et al., 2015; Power et al., 2008; Whitlock et al., 2010) and burned grass biomass (Daniau et al., 2013; Duffin et al., 2008; Leys et al., 2015). However, charcoal is also used to for fire intensity (Duffin et al., 2008). Dispersal models are the glue that bring together these explanations because they define charcoal source areas (Blackford, 2000; Duffin et al., 2008; Edward and Higuera, 2007; Leys et al., 2015; Oris et al., 2014; Patterson et al., 1987).

In general, particles larger than 150 µm (macrocharcoal) indicate local fires near wetland margins while those below 150 µm (microcharcoal) are from farther afield (Patterson et al., 1987). However, the arbitrary size classes imposed by methods are correlated even with other classes (Carcaillet et al., 2001; Pitkänen et al., 1999; Tinner and Hu, 2003; Whitlock et al., 1996). Therefore, the distinction between local and landscape fires imposed by methods is unsuitable on two counts.

First, trampling of vegetation and soils by herbivores around wetlands may cause the secondary breakdown of charcoal (Whitlock et al., 1996). Thus, less macrocharcoal may not signal the importance of landscape over local fires. Instead, it may suggest local heavy grazing and development of grazing lawns with time. Multiple proxies are therefore important for interpreting charcoal.

Second, fires are extinguished by tallgrasses in waterlogged soils around wetlands (Fynn et al., 2015; Just et al., 2015; O'Connor et al., 2011; Vesey-Fitzgerald, 1970). This situation may also result in the increase of charcoal deposition near wetlands from incompletely burned wet plant tissue (Simpson et al., 2016). Less flammable and resistant tallgrasses prevent the spread of fire between wider landscapes and wetlands (O'Connor et al., 2011; Vesey-Fitzgerald, 1970). Importantly, this explains the absence of large charcoal particles from grasslands with many lightning fires (e.g., Scott, 2002). Therefore, charcoal not only suggests burned grass biomass but also gives information about the structure of grass mosaics.

Reconstructing herbivory from spores also has challenges related to source area, multiple interpretations, and preservation issues. The spores used for reconstructing herbivore densities and grazing pressure have short dispersal distances. Dispersal in air is within 100m (Gill et al., 2013) and within 10m over soils around wetland margins (Baker et al., 2016).

These research findings suggest a stronger case for using spores to represent changes in local grazing pressure compared with herbivore densities in landscapes (Cugny et al., 2010; Ghosh et al., 2017; Graf and Chmura, 2006). For example, *Sporormiella* and other spores often increase following high fire activity (e.g., Burney et al., 2003; Ekblom and Gillson, 2010a; Gill et al., 2009; Rule et al., 2012; Wood and Wilmshurst, 2012). This suggests that tallgrass mosaics are lightly grazed compared with heavily grazed palatable post-fire shortgrasses (Allred et al., 2011; Archibald and Bond, 2004).

Herbivore densities and grazing pressure from proxy records are not interchangeable. This is an outcome of the nonequilibrium theory that suggests that while herbivore densities are coupled to wetland grasslands, control over grass production dwindles farther from wetlands (Illius and O'Connor, 1999). Therefore, an idea of herbivore density may not give much information about grass production in wider landscapes. Also affected are relationships between herbivory and tree cover.

Low spore concentrations in sediments from landscapes with many high herbivore densities is a contentious issue. When this happens, sampling bias is invoked since spores are often counted alongside pollen (e.g., Baker et al., 2013; Etienne and Jouffroy-Bapicot, 2014). However, herbivores themselves compromise spore preservation by exhausting grass cover, which leads to soil aridity around wetlands. As discussed earlier, heavy grazing compacts soils and lowers soil moisture around wetlands (Pietola et al., 2005; Rietkerk et al., 1997; Schrama et al., 2013). Ironically, low spore counts give better information about herbivore biomass compared with when spores are plentiful (Wood and Wilmshurst, 2012). Dependence on wetlands by grazers during long droughts and maintenance of grazing lawns may also result in few spores and local aridity (Ekblom and Gillson, 2010a, 2010b).

Chapter Three. **Palaeoecological Methods**

3.1 Collection of sedimentary cores

Sedimentary cores for the multiple proxy study were collected from November to December 2011 in KwaZulu-Natal using the vibracorer method (Baxter and Meadows, 1999). The grassland core was from Vryheid while the savanna one was from the Umfolozi section of the Hluhluwe-iMfolozi Park (Table 3.1). Cores were stored at 4 °C. The aluminium pipes containing cores had an internal diameter of 72mm. The analysis of grass subfamilies, grass biomass, fire activity, grazing pressure/herbivore biomass, nitrogen abundance/litter quality, soil stability/salinity was done with proxies from fossil grass phytoliths, loss on ignition, charcoal, fossil dung fungal spores, stable isotopes, and elemental analyses respectively, mentioned in the research design in the previous chapter.

Table 3.1. Lengths of sediment cores used in this study

Site	**Core (cm)**	**Biome**	**Elevation (m.a.s.l.)**	**Comments**
Umchachazo Vlei	233	Savanna	50	Riparian floodplain
Blood River Vlei	133	Grassland/ savanna boundary	1 200	Riparian floodplain

3.2 Laboratory methods

3.2.1 Subsampling of sedimentary cores

Cores were split, cleaned to remove surface contamination then subsampled. Two methods were used to collect samples along cores: syringe and razorblade (Moore et al., 1994). Syringes measuring three cubic centimetres volumes with a needle diameter of five millimetres were used to extract one cubic centimetre samples for microfossils (spores, charcoal, and phytoliths) and loss on ignition. Blades were used for isotopes with samples collected between two blades less than two millimetres apart and in this case a volume was measured with volumetric displacement.

3.2.2 Sediment description and age-depth modelling

A simplified Troels-Smith method was used to describe physical features, humus content, and detritus in sediment along the cores (Kershaw, 1997; Troels-Smith, 1955). A five-point scoring system (0-4) for each category was used with zero for absence and a maximum of four. Physical features scored included structure, degree of stratification and sharpness of boundary. Parts making up sediment were *Detritus* (plant material), *Argilla* (clay and silt), *Grana* (sand and gravel) and charcoal. Sediment colour was recorded using a Munsell soil colour chart (USDA Soil Conservation Service).

Samples from selected depths along cores were sent to accelerator mass spectrometry carbon-14 (AMS ^{14}C) dating laboratories for processing using standard protocols (Last and Smol, 2002). Organic material from the sediment was used for dating. Laboratories used were Poznan Radiocarbon laboratory (Poland), Beta Analytic Inc. (Florida), ^{14}CHRONO Centre (Belfast) and DirectAMS Radiocarbon Dating services (Seattle). Radiocarbon ages (BP) were calibrated using IntCal13 (Reimer et al., 2013) and the southern hemisphere SHCal13 calibration curves (Hogg et al., 2013). Age-depth models in calibrated years before present (cal BP) for the sedimentary sequences were estimated with calibrated radiocarbon dates using the ‘Clam’ package in R (Blaauw, 2010).

Bioturbation is a problem affecting the reliability of some age-depth models of sediments collected from areas with wild and domestic herbivores (Duffin et al., 2008; Ekblom and Gillson, 2010a). This causes shifts in the order of young and old dates along sediment cores. As a correction, some dates inconsistent with the order of time are excluded (Blaauw, 2010). However, sediment mixing by herbivores may lead to a long-term running average of ages, preserving the order of time (Ekblom and Gillson, 2010a).

3.2.3 Phytolith analysis of grazing mosaics and environmental change

Patch structure and composition of grazing mosaics plus associated environmental changes in landscapes were investigated with fossil phytoliths (Finné et al., 2010; Lejju et al., 2005). Phytoliths were obtained from sediments using Gayler’s (2011) modification of Lentfer and Boyd's (1998) heavy liquid flotation method. *Lycopodium* tablets were added to the one cubic centimetre samples. Carbonates were removed with a treatment of 7% HCl that also dissolved the tablets. Fine and coarse soil grains in samples were disaggregated using 5% sodium pyrophosphate ($Na_4P_2O_7$) and shaken for 48 hours (Katz et al., 2010). This was followed by sieving samples through 250 µm sieves into 500 ml beakers (Lentfer and Boyd, 1998). Macro-fossils (i.e., residue on sieves) were kept. ‘Still settling’ was used to remove fine clays in suspension from beakers every six hours by vacuum suction (Gayler, 2011; Lentfer and Boyd, 1999). The process was followed by refilling beakers with water, agitation of samples, still settling and vacuuming until the supernatant was clear. Phytoliths and other microfossils were recovered from remaining residue in beakers using heavy liquid flotation with sodium polytungstate ($Na_6(H_2W_{12}O_{40}).H_2O$) at specific gravity of 2.3-2.35 (Bremond, Alexandre, Wooller, et al., 2008). Samples were dehydrated with glacial acetic acid, then digested with an acetolysis mixture to remove starch and fibre grains except for phytoliths, pollen, spores and charcoal (Bennett and Willis, 2001; Lentfer and Boyd, 2000). Water was removed from samples using acetic anhydride and stained with safranin dye to mark organic microfossils for identification. A minimum of 300 diagnostic combined phytolith, spores and intact diatoms were counted per slide (Piperno, 2006), and expressed as percentages.

Grass silica short cells phytoliths from leaves and inflorescences were used to identify grasses to tribe level (Cordova, 2013; Finné et al., 2010; Fredlund and Tieszen, 1997; Madella et al., 2005; Mulholland, 1989), and trees at a coarse level (Bremond, Alexandre, Peyron, et al., 2008; Mercader et al., 2010; Novello et al., 2012; Piperno, 2006). There are many forms of grass short cell phytoliths that represent distinct grass subfamilies and tribes (Figure 3.1). However, sorting short cells into distinct tribes is affected by multiplicity because some forms are produced by several genera and by morphotype (i.e., shape) plasticity within forms (e.g., Barboni and Bremond, 2009; Cordova, 2013; Neumann et al., 2017). Nevertheless, Poaceae were grouped into tribes according to standard protocols (Barboni and Bremond, 2009; Cordova, 2013; Fredlund and Tieszen, 1994; Mulholland, 1989; Twiss et al., 1969).

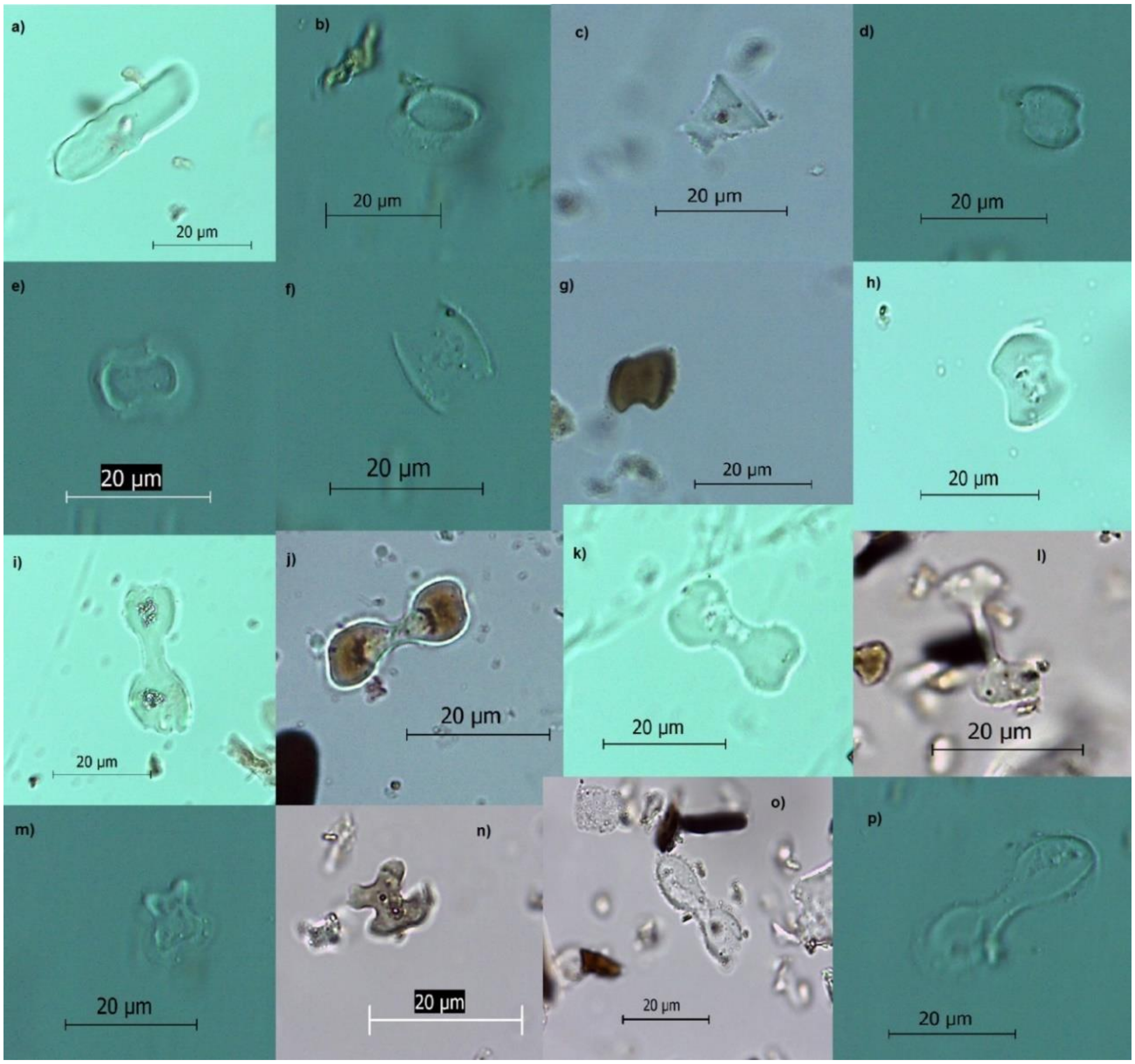

Figure 3.1. Examples of grass silica short cell phytoliths found at Blood River Vlei sediment. a). trapezoid; b-c). rondels; d-e) tall saddles; f-h). squat saddles; i-l). bilobate types; m-n). crosses (quadralobates); o-p). Stipa-type bilobates [*images captured by A Dabengwa*].

Diagnostic grass phytoliths of were used to identify grass subfamilies. *Lobates* (bilobates, crosses/quadralobates and polylobates) were used for the Panicoideae (Fahmy, 2008; Novello et al., 2012; Rossouw, 2009); *squat saddles* for Chloridoideae (Barboni and Bremond, 2009; Finné et al., 2010; Mercader et al., 2010; Novello et al., 2012); *trapeziform saddles* (tall-types) for Arundinoideae, Aristidoideae, Stipa and Pooideae (Barboni et al., 1999; Cordova, 2013; Neumann et al., 2017; Novello et al., 2012); *rondels* for Pooideae, Chloridoideae and Stipa

(Bamford et al., 2006; Cordova, 2013; Lu and Liu, 2003; Mercader et al., 2010; Novello et al., 2012; Rossouw, 2009); and *trapeziforms* for Pooideae (Barboni and Bremond, 2009; Lu et al., 2006; Lu and Liu, 2003; Madella et al., 2005; Rossouw, 2009). In general, mature tallgrass communities at soaked wetlands margin soils are dominated by Arundinoideae (*Phragmites australis*) and Panicoideae, with arid-adapted Chloridoideae representing shortgrasses marking dry soils at margins (Bremond, Alexandre, Wooller, et al., 2008; Lejju et al., 2005).

Tree phytoliths included globular forms (Lu et al., 2006; Mercader et al., 2009; Novello et al., 2012), sclereids (Lu et al., 2006; Mercader et al., 2009) and blocky forms and parallelipedals (Mercader et al., 2009). Other grass phytolith morphotypes/ shapes included bulliforms (for structure), elongate cells, and hairs (Bremond, Alexandre, Wooller, et al., 2008; Madella et al., 2005; Mercader et al., 2010; Novello et al., 2012; Piperno, 1988). These types are represented in Figure 3.2. Intact diatoms were considered indicators of moist local conditions (Figure 3.3).

Standard short cell phytolith indices were used to investigate environmental change. They included the aridity index (*I*ph%) measuring the Chloridoideae to Panicoideae ratio (Bremond et al. 2008); proportion of Pooideae (C_3) relative to abundance of Chloridoideae, Panicoideae and Pooideae (*I*c%) in short cell counts (Bremond et al. 2008); the dicotyledon to Poaceae phytolith (D/P^o) ratio (Bremond et al. 2008) and grass water stress *F*s (%) (Bremond et al. 2005). New indices developed for the multiple proxy phytolith dataset were the ratios of herbivore biomass/ grazing pressure to grass short cell sums using *Sporormiella* and *C. lignaria* spores (Equation 1 and 2). Local moisture was investigated with a ratio of intact diatoms to grass short cells sums (Equation 3; Figure 3.3).

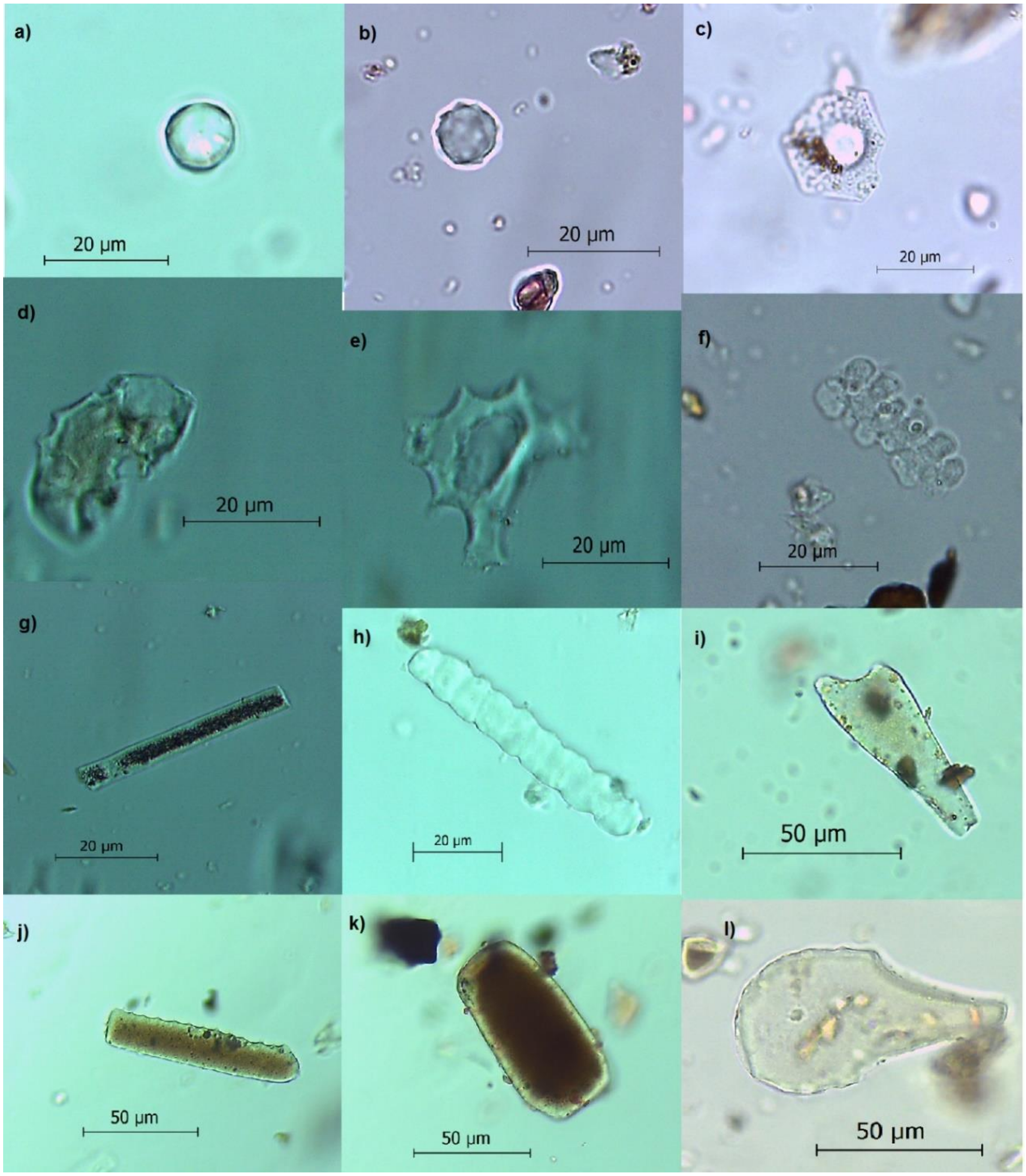

Figure 3.2. Sample of phytoliths types found in the Blood River Vlei sediment. a-b). spheroids/ globular phytoliths; c). Cyperaceae-papillae; d). angular vesicular; e). stellate; f-h). elongate forms; i) acicular/ hair; j). elongate wavy; k). parallelipedal blocky or bulliform; l). fan-shaped bulliform [*images captured by A Dabengwa*].

Equation (1)

$$Sporormiella\ to\ grasses\ (SP)\ (\%) = \frac{\text{Sporormiella spores}}{\text{Grass silica short cell sum}}$$

Equation (2)

$$C.lignaria\ to\ grasses\ (Clg)\ (\%) = \frac{\text{C. lignaria dung spores}}{\text{Grass silica short cell sum}}$$

Equation (3)

$$Diatom\ to\ grasses\ (Di)\ (\%) = \frac{\text{Fan} - \text{shaped Bulliforms}}{\text{Grass silica short cell sum}}$$

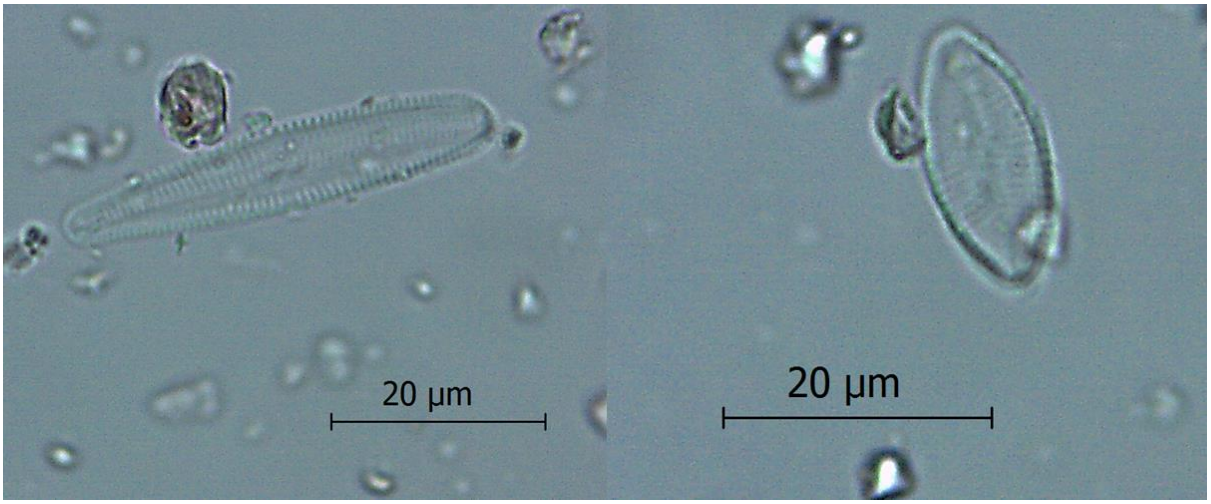

Figure 3.3. Intact diatoms found in the Blood River Vlei core [images captured by A Dabengwa].

3.2.4 Stable isotope analysis for assessing grazing mosaics and nutrient dynamics

Changes in the abundance of grasses using the C_3 and C_4 photosynthetic pathways in grazing mosaics and nutrient dynamics were assessed with stable isotopes of carbon and nitrogen, respectively. The discrimination of heavy and light isotopes of carbon dioxide by photosynthetic enzymes results in distinctive $\delta^{13}C$ range of values from plant tissues and soils (Fredlund and Tieszen, 1997; Hubick et al., 1989; Meyers, 1994; Tieszen, 1991). Plants using C_4 enzymes have higher $\delta^{13}C$ values compared to C_3 plants. However, $\delta^{13}C$ and the C:N ratio are also influenced by local inputs from aquatic and woody plants (Michener and Lajtha, 2007), leading to several interpretations when these are the sole proxies. Nitrogen cycling was based on the natural abundance of $\delta^{15}N$ in soils. Amounts depends on the discrimination of heavy and light isotopes of nitrogen based on their abundance in soil pools (Ekblom and Gillson, 2010b; Leng et al., 2005; Meyers, 1994). Nitrogen abundance is generally high in dry soils (Knapp et al., 1998) and areas dominated by shortgrass swards (Blair, 1997; Hobbs, 1996; Pastor and Naiman, 1992; Ruess and McNaughton, 1987). Wetland grazing lawns with arid-adapted grasses are considered to have high nitrogen availability in soils (Fox et al., 2015; Grant and Scholes, 2006; Veblen, 2012) compared to its low availability in fibrous mature tallgrass swards with slow decomposition (nitrogen mineralisation) rates (Hobbs, 1996; Pastor and Naiman, 1992; Ruess and McNaughton, 1987). The high structural carbon and low leaf nitrogen of tallgrasses increases soil organic carbon pools because this poor-quality litter is not favoured by soil microbes (Hobbs, 1996; Ingram et al., 2008; Longhi et al., 2008; Pastor and Naiman, 1992; Ruess and McNaughton, 1987). Heavy grazing and trampling also reduce the availability of nitrogen because grazers directly remove nitrogen in biomass while soil compaction dries soils and reduces its aeration (Schrama et al., 2013).

Samples for isotopic analysis were collected, treated and analysed using standard protocols (Ekblom and Gillson, 2010b; Walther and Neumann, 2011). The samples were sent to the University of Cape Town Stable Light Isotope Laboratory for determination of $\delta^{13}C$, $\delta^{15}N$, total carbon (TC), total nitrogen (TN), and C/N values using in-house references calibrated against International Atomic Energy (IAEA) standards. The measuring unit consisted of a Flash EA 1112 series elemental analyser and Finnigan DELTA plus XP continuous-flow stable isotope ratio mass spectrometer (Thermo Fisher Scientific, Massachusetts). Abundance of $\delta^{13}C$ and $\delta^{15}N$ were expressed with isotope ratios (‰), TC and TN were measured as percentage weight of the elements in samples, and C/N was a ratio of TC/ TN (Ekblom and Gillson, 2010b; Peterson and Fry, 1987).

3.2.5 Dung spore analysis of herbivore biomass and grazing mosaics

Dung spores were used as indicators of herbivore biomass (Baker et al., 2016; Burney et al., 2003; Davis and Shafer, 2006) and grazing pressure in landscapes (Cugny et al., 2010; Graf and Chmura, 2006). Fossil spores were obtained from the sediment samples using standard pollen methods (Bennett and Willis, 2001). Two *Lycopodium* marker tablets (~18 583 spores/ tablet) were added to each sample. Carbonates were eliminated using hot 7% hydrochloric acid (HCl) that dissolved marker grains. Samples were boiled in 10% sodium hydroxide and 10% sodium pyrophosphate was used to remove humic acids and disperse clays. Then samples were washed with seven percent HCl, treated with 60% hot hydrofluoric acid (HF), and washed again with hot HCl to remove colloidal silicates. Acetic acid was used to dry samples before cellulose digestion with an acetolysis mixture. Finally, samples were stained with safranin dye, dried using tert-Butanol ($C_4H_{10}O$) and mounted in silicon oil.

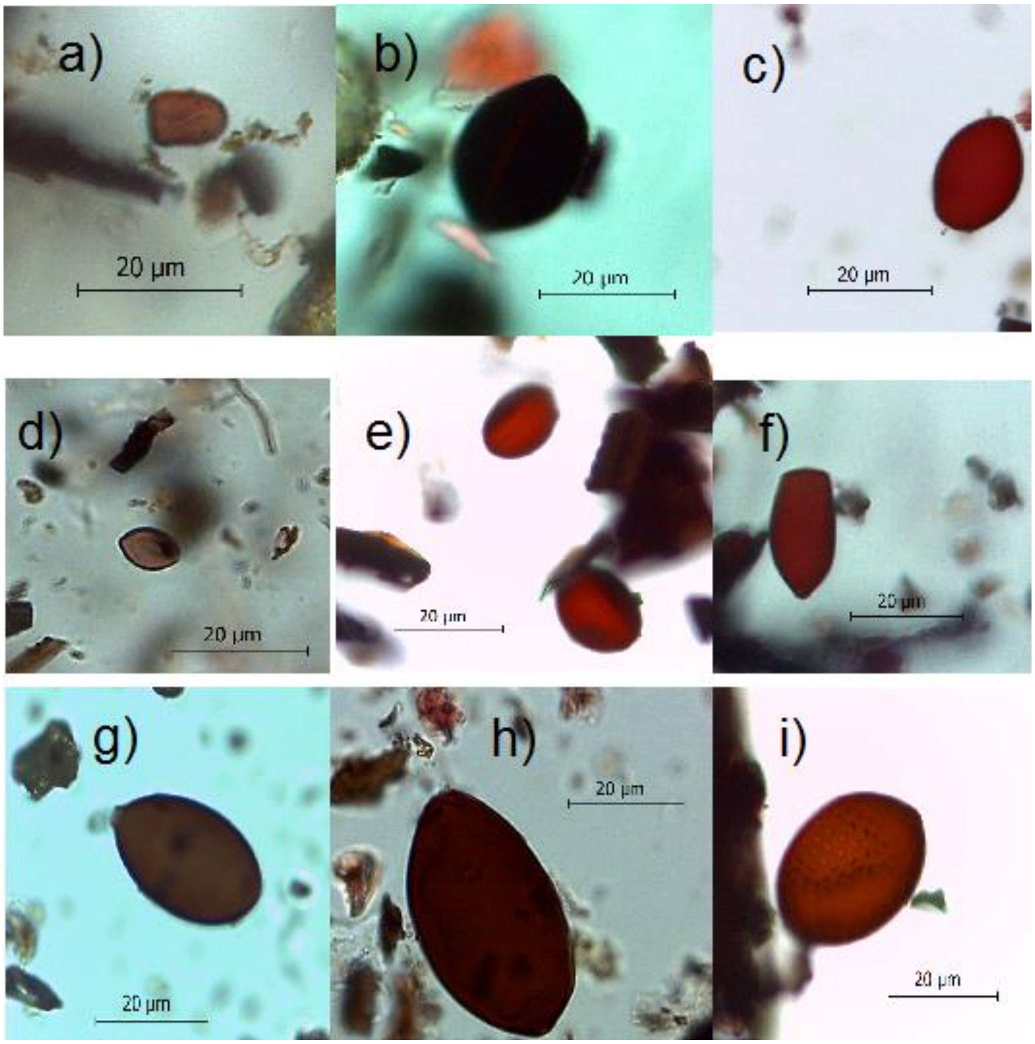

Figure 3.4. An illustration of dung spores used in palaeoecological reconstructions a). *Sporormiella*; b). *Coniochaeta gamsii*; c). *Cercophora*-type; d). *Chaetomium* type; e) *Coniochaeta lignaria*; f). *Cercophora*-type; g) *Sordaria*-type; h). *Podospora*; and i). *Gelasinospora*.

A minimum of 200 indicator spores (e.g. Figure 3.4) were counted per sample alongside other types (e.g., Figure 3.5) (Finsinger and Tinner, 2005). However, when the optimal indicator spore counts were not reached, counting was stopped at 250 *Lycopodium* that was considered adequate for sites with medium to heavy grazing (e.g., Etienne and Jouffroy-Bapicot, 2014; Finsinger and Tinner, 2005). The dung spore assemblage was compiled from published studies

(Burney et al., 2003; Carrión et al., 2000; Ekblom and Gillson, 2010a; Gelorini, 2011; Gelorini et al., 2011; van Geel and Aptroot, 2006). However, *Coniochaeta lignaria* (Figure 3.4e) are associated with herbivore dung and also signal moist local conditions at some African sites (Gelorini et al., 2012; Jarzen and Elsik, 1986). Therefore, they were expected to correspond with productive wetland margin tallgrasses. Independent spore concentrations were estimated with standard methods (Maher, 1981).

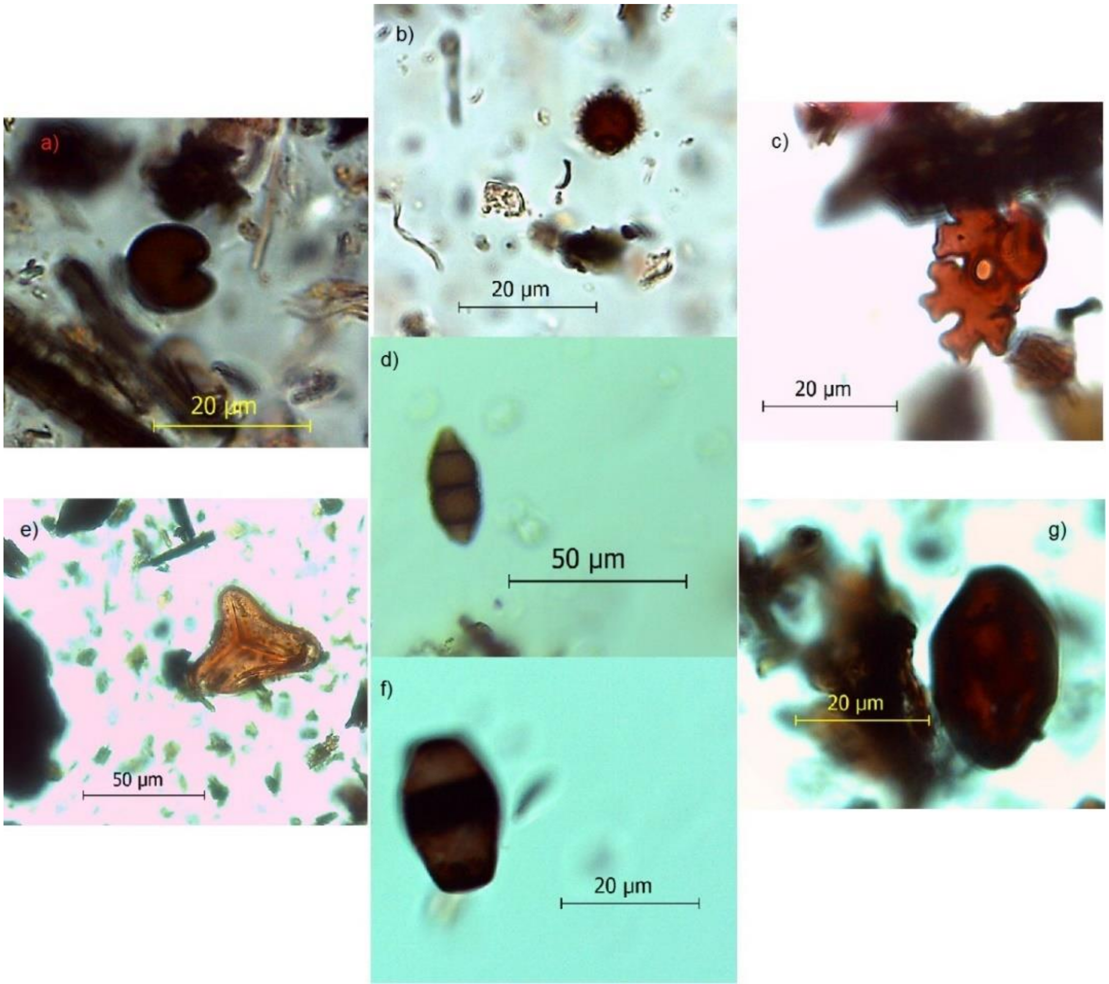

Figure 3.5. Other non-pollen types found in samples a). Form-E; b). Type 115/*Micrhystridium*; c). *Gaeumannomyces*/hyphopodia; d). unknown ascopsore; e). trilete spores; f). *Trichdochium*-type/IBB-26; g). *Diporotheca* T.1245.

3.2.5.1 Grazing mosaics from the dung spore assemblage

Changes in sward heights of grass mosaics with grazing pressure were investigated using indirect ordination of the dung spore assemblage. Heavy grazing around wetland margins was expected to reduce the proportion of tallgrasses but increase shortgrasses (Graetz and Ludwig, 1978; Rietkerk et al., 2000; Vesey-Fitzgerald, 1970; Waldram et al., 2008), as deduced from changes in frequencies and types of spores in sediments (e.g., Baker et al., 2016; Cugny et al., 2010; Etienne et al., 2013; Graf and Chmura, 2006). Spores are plentiful from heavily grazed wetland margins with short grasses compared with lightly grazed mature tallgrasses (Cugny et al., 2010; Graf and Chmura, 2006). Therefore, one of the ordination axes was expected to represent a grass biomass/productivity gradient from short to tall grass swards/mosaics, corresponding to local grazing pressure. However, this interpretation is complicated by fire that changes vegetation structure (see below).

3.2.6 Charcoal analyses for fire history

Fire history or activity in past landscapes was reconstructed from frequencies of charcoal fragments (Blackford, 2000; Duffin et al., 2008). Smaller charcoal particles < 150 µm (from here on referred to as microcharcoal) are thought to reflect landscape scale fire patterns because they disperse farther or come from great distances. In comparison, the larger charcoal particles > 150 µm (from here on referred to as macrocharcoal) are deposited locally (Clark, 1986; Patterson et al., 1987). Overall, charcoal frequency increases with grass biomass in burned areas (Leys et al., 2015; Marlon et al., 2015).

3.2.6.1 Microcharcoal

Microcharcoal fragments recovered alongside spores were counted from slide transects using a modification of Clark's point-count method (Clark, 1982), and concentrations estimated by comparison with *Lycopodium* markers (Finsinger and Tinner, 2005). At least 200 particles, the sum of charcoal fragments and *Lycopodium* markers, were counted per sample (Finsinger and Tinner, 2005). Lengths of charcoal fragments (Table 3.2), were estimated with a calibrated eyepiece graticule and categorised into size classes (e.g., Carcaillet et al., 2001; Duffin et al., 2008; Tinner and Hu, 2003).

Table 3.2. Microcharcoal particle size classes used in this study.

Class	A	B	C (	D	E
Size	<15µ	16-30µ	31-50µ	51-70µ	<71µ

3.2.6.2 Macrocharcoal

Macrocharcoal recovered from the pollen method were counted using standard protocols using a Leica EZ4 stereo microscope (Ekblom and Stabell, 2008). Only grey and black angular particles were counted because they correspond to charcoal (Blackford, 2000; Duffin et al., 2008).

3.2.6.3 Grazing mosaics from charcoal

Changing of grass heights with fire were deduced from indirectly ordinating charcoal size classes. The strong relationship usually found between microcharcoal and macrocharcoal size and abundance from sediments (Carcaillet et al., 2001; Pitkänen et al., 1999; Tinner and Hu, 2003; Whitlock et al., 1996), was used as a basis for combining the records. Since charcoal abundance is related to combustible biomass/burned area (Leys et al., 2015), wetlands with a high proportion of tallgrass swards were expected to yield more charcoal than ones with shortgrass swards. The ordination of charcoal particle sizes and abundance was expected to show a gradient of grass biomass/productivity reflecting an increase in the proportion of tallgrass patches.

Although secondary reworking of charcoal by herbivores occurs around sediment basins (Pitkänen et al., 1999; Whitlock et al., 1996), this was only expected to homogenise macrocharcoal in the less productive savanna where grazers can maintain stable grazing lawns. Of course, this violates the demarcation of microcharcoal and macrocharcoal as indicators of landscape and local fires respectively (Patterson et al., 1987). Thus, interpretations of charcoal that do not consider grazing effects are biased, especially when records are from grazing systems.

3.2.7 Weight loss on ignition of soil organic carbon for assessing grass biomass in grazing mosaics

Changes in grass biomass pointing to average sward heights at the wetland grassland mosaic were assessed with sediment organic carbon. Organic matter in soils depends on litter produced by herbaceous plants, and is proportional to both biomass and productivity (e.g., Grime, 1977). Biomass, therefore, increases with sward height and stemminess. Sediment organic carbon and inorganic carbon from sediment samples was determined using the organic weight loss on ignition (LOI) method (Heiri et al., 2001). An optimal sample weight of between 2-4 g of sediment (Q Wang et al., 2011), of measured volume was extracted using syringes to also determine dry bulk densities. Soils were weighed then oven-dried for 24 hours at 105 °C to remove water and volatile compounds to leave behind dry soil mass. Later, soils were baked at 550 °C for 4 hrs to remove organic carbon or LOI (Shulte and Hopkins, 1996). Finally, baking at 1 000 ºC for two hrs led to the measurement of inorganic carbon (IC) and calcium carbonate ($CaCO_{3)}$ contents by multiplying IC by 2.27 (Dean, 1974).

3.2.8 Elemental XRF analysis for assessing soil salts and disturbance

The activity of herbivores around wetland margins has effects on vegetation and soil factors: stability and salinity (Elschot et al., 2013; Grant and Scholes, 2006; Kuijper and Bakker, 2005; Matchett, 2010; Person et al., 2003; Pietola et al., 2005). Exploratory elemental analyses on cores was done to investigate changes in salinity and soil disturbance using an XRF analyser at 2-4 cm intervals.

An Innov-X Systems DELTA Standard handheld XRF Analyser (Innov-X Systems Europe, 2010) was used with the *Smart Shot 3-beam Soil Environmental mode* set at 15 kV and 200 µA with a dwell time of 30 seconds. Although residual moisture in sediments poses a measurement challenge, the machine had a correction mechanism. Cores were cleaned to create a smooth surface and covered with a thin polythene film. Scanning was done at 2-4 cm resolution because of the scanner's footprint. Detection limits of elements analysed were: Ti & Fe <10ppm; K & Ca <50ppm; Mg <1%; Rb, Sr, & Zr <5ppm. To measure consistency, the scanner was recalibrated every 20 readings and repeat spot measures taken at a minimum of five readings along cores (e.g., Czymzik et al., 2010; Kylander et al., 2011).

Elements associated with soil disturbance result in increased inputs of mineral components of soils including Ti, Fe, K, Rb, and Zr (Czymzik et al., 2010). However, high Fe concentrations are also indicative of waterlogged soils leading to the formation of clays or 'gley' soils at wetland margins (Acocks, 1953; Tinley, 1982). Other measured minerals of interest were Ca associated with changing soil moisture (Gill et al., 2009), and Mg that is enriched in dry grazing lawn soils (Anderson et al., 2010; Fox et al., 2015; Seagle and McNaughton, 1992; Stock et al., 2010).

Grazing lawn soils generally have higher salt concentrations compared to soils in matrix vegetation (Anderson et al., 2010; Coetsee et al., 2010; Fox et al., 2015; Grant and Scholes, 2006; Stock et al., 2010). Magnesium and calcium elements were used as proxies for soil salinity. Because these elements were difficult to measure with the spot beam, dry samples leftover from stable isotope analysis of nitrogen were analysed with a different machine. A Spectroscout energy dispersive XRF analyser was used (AMETEK Inc., 2013). The silicon drift detection limit was set at 30kV. Ratios of Mg/Ca signalling changes in soil moisture and salinity were obtained (e.g., Roy et al., 2009). Magnesium comes from mineral parts of the sediment. In contrast, carbonates ($CaCO_3$) depend on evaporation of water from soils and rely on variation in rainfall. Since grazers affect grass cover at wetland margins, changes in soil hydrology/moisture suggest varying levels of grazing (Di Bella et al., 2014; Ingram, 1991; Rietkerk et al., 1997; Veldhuis et al., 2014).

Trampling by herbivores at wetland margins compacts soils, and lowers water infiltration rates, may increase sheet erosion (Pietola et al., 2005). Coarse grained particles are carried into sediment basins because water has a higher energy along bare or sparsely vegetated soils with poor infiltration (Elschot et al., 2013; Pietola et al., 2005). The Zr:Rb ratio measures the variation in soil grain size, with coarser grains being enriched in Zr while fine grains have more Rb (Kylander et al., 2011; Liu et al., 2002). In sediment studies, peaks in the Zr:Rb ratio are used for detecting flood events (Schillereff et al., 2014), and they may represent grazing pressure and soil disturbance around small basins (Elschot et al., 2013).

3.3 Data analyses

Data analyses were conducted in R Statistical Programming (R Core Team, 2016). Datasets were assessed for normality and transformed with appropriate methods (Oksanen et al., 2015). Measures of spread for data used included sample means, ranges, standard deviations, and standard errors.

3.3.1 Grass mosaic states from cluster analysis and environmental gradients

Changes in environmental gradients and wetland grass mosaic states were found using cluster and gradient analyses Before analyses, phytolith and dung spore data were transformed using the Hellinger's distance matrix with the software package vegan v.2.4 (Oksanen et al., 2015). Hellinger's distances are appropriate for handling community ecology data with low values and many zeroes (Legendre and Legendre, 2003). The method lowers the weights of these samples in cluster and gradient analysis. However, natural logarithms were used to transform charcoal data following Tinner and Wu (2003).

Persistent grass mosaic states, i.e., stable vegetation states, were identified using the constrained incremental sum of squares (CONISS) method (Bennett, 1996; Grimm, 1987) with stratigraphic units of grass subfamilies from phytoliths. CONISS was also used to detect grass mosaic states (tallgrass vs shortgrass) from stratigraphic units of stable isotopes, charcoal, and spore sequences.

Non-metric multidimensional scaling (NMDS) and correspondence analysis (CA) were used to explore gradients of grass mosaic sward structure with microfossil assemblages. Sward height based on shortgrass to tallgrass states were deduced from relative intensities of fire and grazing in time using NMDS ordination gradients of charcoal and spore as discussed earlier. The NMDS method is an indirect gradient analysis obtained by running a search algorithm that compares dissimilarities among samples with rank-based ordering of objects to the best k dimensions fit data (Kruskal, 1964). The idea is to minimise stress values. Dissimilarity scores were based on Bray-Curtis distances among samples, producing stress values that range from 0 to 1. Stress values of < 0.05 are considered excellent, < 0.1 are good, values < 0.2 are usable while those between 0.2-0.3 or greater must be interpreted with caution (Clarke and Warwick, 2001). However, NMDS distances and axes were arbitrary means of summarising complex datasets and not directly interpretable (Legendre and Birks, 2012). Still, NMDS is valid for hypothesis testing and comparing multiple proxy data (Legendre and Birks, 2012). CA was used to explore the composition and structure of temporal grazing mosaics from the phytolith grass tribe dataset. CA preserves the chi-square chord distance of original data. Ordination units of CA are interpretable compared with those from NMDS (Legendre and Birks, 2012; Ter Braak, 1986).

3.3.2 Univariate and multivariate statistical methods

Comparisons of group and sample means were done using parametric Student's *t*-tests, one-way analysis of variance, and non-parametric Kruskall-Wallis tests (Legendre and Legendre, 2003). The *post-hoc* tests for the Kruskall-Wallis were pairwise comparisons with the Tukey and Kramer test using a Tukey distribution approximation for posterior probabilities. Pearson's correlations, linear regressions and nonlinear Poisson regressions were used to assess relationships between response and predictor variables (Legendre and Legendre, 2003).

Chapter Four. **Long-term climate, grazing, and fire controls on grass productivity at a South African montane grassland**

4.1 Introduction

Grass production at key resource areas in dynamic African rangelands is important for supporting grazers in crucial dry periods (Fynn et al., 2015; Scoones, 1992; Sinclair, 1985). Herbivore densities are in equilibrium with and controlled by the grass productivity around wetlands (Hempson, Illius, et al., 2015; Illius and O'Connor, 1999; Sinclair et al., 1985). Because these areas can support high densities of indigenous and domestic grazers, adverse effects include poor grass cover, dry soils, low nitrogen, and sheet erosion (Illius and O'Connor, 1999; Rietkerk et al., 1996; Sinclair and Fryxell, 1985; Wesuls et al., 2013). However, the relationship between grazer numbers and grass production is contested (Archer, 1989; Behnke and Scoones, 1992; Ellis and Swift, 1988; Westoby et al., 1989). Instead, the disequilibrium hypothesis argues that erratic rainfall and droughts decimate grazer populations, meaning they have no negative effect on grasses and soils (Ellis and Swift, 1988). Also, fire affects grass production by attracting grazers to burned areas, resulting in unstable grass biomass from the climate in mosaic landscapes (Allred et al., 2011; Archibald, 2008; Bond, 2005). Therefore, a long-term view is important for improving our understanding of ecological drivers of states of grass production before and after drought events.

Grass trait response to rainfall, fire, and grazing control the structure and behaviour of grazing mosaics (Milton and Hoffman, 1994; Walker et al., 1999; Westoby et al., 1989). Tallgrass mosaics dominate in open, high rainfall areas, and wet soils (Kotze and O'Connor, 2000; Sieben, Nyambeni, et al., 2016; Vesey-Fitzgerald, 1963). These fast growing grasses avoided by grazers when mature, can withstand grazing up to a certain point (Augustine and

McNaughton, 1998; Fynn et al., 2015; Illius and O'Connor, 1999). Their flammability fuels fires and is important for maintaining open landscapes (Anderson et al., 2007; Archibald and Bond, 2004). Also, burned tallgrass patches attract grazers to palatable post-fire regrowth after mineralisation of nitrogen (Allred et al., 2011; Archibald et al., 2005a; Waldram et al., 2008). However, unselective heavy grazing of post-fire regrowth lowers the resilience of tallgrasses past their threshold of tolerance, and supports the establishment of shortgrasses (Archibald and Bond, 2004; Augustine and McNaughton, 1998).

In comparison, continuous heavy grazing promotes stable shortgrass patches that tolerate heavy grazing and dry soil conditions (Lock, 1972; Sieben, Collins, et al., 2016; Waldram et al., 2008). Thus, proportions of shortgrasses and tallgrasses in mosaics are useful for describing stable states of grass biomass (Fuhlendorf and Engle, 2004; May, 1977; Perrings and Walker, 1997; Waldram et al., 2008). Ecological thresholds determined by grazing pressure and/or soil moisture separate stability domains of grass biomass (McNaughton, 1984; Rietkerk and van de Koppel, 1997; Veldhuis et al., 2014). Therefore, sediment studies are important for looking into resilience and stability because long timescales and fixed areas allow assessments of disturbance effects (Connell and Sousa, 1983).

Little is known about key resource areas in montane grasslands of South Africa over the last millennium. These areas with a milder climate may have been important for pastoralists and indigenous herbivores (Hall, 1981). Nguni pastoralists who moved into South Africa in the last 1 000 years (Hall, 1981; Huffman, 2004; Mitchell and Whitelaw, 2005), probably increased their use of wetlands with time, especially in the dry climatic periods (Hall, 1976; Holmgren et al., 1999; Woodborne et al., 2015). Effects of past peoples on vegetation are debated in South Africa (Acocks, 1953; Bousman and Scott, 1994; Feely, 1980; McKenzie, 1984; Meadows and Linder, 1993). Large herds supported by pastoralists who used fires are thought to have caused forest loss (Acocks, 1953). In comparison, the perceived overuse of grazing patches caused a rise in unpalatable grasses and trees in landscapes (Hall, 1981; McKenzie, 1984).

Palaeoecological proxies are available that reflect past climate, grass production, grazing pressure, and fire activity over long timescales. Grass communities around wetlands are distinguished with phytoliths that resolve taxa to subfamily level (Finné et al., 2010; Fredlund and Tieszen, 1997; Piperno, 2006). The siliceous phytoliths fossilised in plant tissues separate C_3 from C_4 vegetation (Alexandre et al., 1997; Finné et al., 2010; Fredlund and Tieszen, 1997), discriminate between C_4 shortgrasses (Chloridoideae) *versus* C_4 tallgrasses (Panicoideae) based on local hydrology (Barboni and Bremond, 2009; Bremond et al., 2005), and provide information on tree *versus* grass abundance (Barboni et al., 2007; Bremond, Alexandre, Peyron, et al., 2008). Phytoliths preserve well in dry soils (Alexandre et al., 1997; Piperno, 2006). Like spores used for reconstructing herbivore biomass and/or grazing pressure (Baker et al., 2016; Gill et al., 2013; Graf and Chmura, 2006), phytoliths are deposited near wetlands (e.g., Aleman et al., 2014; Novello et al., 2012), suggesting they are useful for studying changes in grass productivity/biomass at key resource areas.

However, interpretations of sedimentary proxies at key resource areas are affected by local factors. Although local moisture at wetland depends on climate (Chamaillé-Jammes et al., 2007; Nippert et al., 2013), local grass mosaics also influence it (Bremond et al., 2005; Bremond, Alexandre, Peyron, et al., 2008). Thus, counts of spores used to signal herbivore activity, e.g., *Sporormiella*, are affected by distance from wetland margins (Parker and Williams, 2011; Raper and Bush, 2009), and changes in wetland soil moisture (Wood and Wilmshurst, 2012). Chloridoideae shortgrasses linked with aridity (e.g., Bremond et al., 2005, 2008; Finné et al., 2010), also signal grazing lawns (Owen-Smith, 1987; Sullivan and Rohde, 2002; Vesey-Fitzgerald, 1970). Last, heavy grazing (Waldram et al., 2008) and wet grass fuel prevent fires from spreading (Just et al., 2015; O'Connor et al., 2011). Therefore, faithful reconstructions of compositional changes of grass states, fire, grazing, and local moisture, depend on using proxies in concert.

In this study, a floodplain grassland in the mesic montane grassland near Vryheid in KwaZulu-Natal, South Africa, is considered a key resource area. The region is dominated by tallgrasses suggests that fire is the dominant consumer of grass biomass. What is unknown is how climate, soil moisture, grazing, people, and fire interacted to maintain grass stable states in the last millennium. Interaction among local and landscape scale drivers may have been important for maintaining vegetation states and soil processes. Thus, equilibrium and disequilibrium ideas of stability domains of grass biomass/mosaics are explored to assess the resilience of the wetland grassland in the last 1 250 years.

To study ecosystem dynamics, the several local and landscape scale proxies used are indicated in parentheses. Local signals of grass subfamilies/mosaics (grass short cell phytoliths), tree to grass ratio (phytolith D/p° ratio), photosynthetic signal ($\delta^{13}C$), grass productivity/biomass (carbon loss on ignition), patch state (charcoal and dung spore gradients), aridity index or ratio of shortgrass (Chloridoideae) to tallgrass (Panicoideae) phytoliths (Iph% index), grazing intensity (dung spores), fire activity (charcoal), nitrogen availability ($\delta^{15}N$), grass fibre content (C:N ratio), and soil disturbance (Zr:Rb ratio), soil salinity (Mg:Ca ratio and $CaCO_3$), and additional proxies that are described in the next section. A regional multiple proxy palaeoclimate record (Chevalier and Chase, 2015) was used as a proxy for rainfall in the wider landscape to distinguish between local and regional drivers of hydrology.

Here I am interested in answering the following questions:

1. How does interaction among local moisture, fire, and grazing drive transitions between short and tallgrass states at the key resource area over long timescales?
2. How do stability domains of grass biomass used for organising grass states reflect traits related to fire activity, grazing pressure, and soil wetness?
3. Are vegetation states indicators of stability domains and resilience of grass biomass at the key resource area?
4. How does fire and grazing affect soil processes (i.e., erosion and nutrient cycling) at the key resource area?
5. What are the long-term effects of grazing on ecosystem management in mesic grasslands?

4.2 Methods

4.2.1 Description of study area

The study site is situated along the Blood River system of wetlands in Vryheid, South Africa (Figure 4.1). River flow was restricted and cut-off in many places along the meandering river c. 100-800 years ago, leaving behind many small basins along the river (Tooth et al., 2014). Mean annual temperature is c. 17 °C while average annual rainfall is c. 800 mm (Kotze and O'Connor, 2000). Infrequent frost conditions occur during winter months (Schulze and Maharaj, 1997). The shallow floodplain grassland with a small basin is flooded during the summer rainfall season (November-March). However, drying happens in the course of the dry winter season (May-August), leading up to the next rains (Kotze and O'Connor, 2000). The poorly drained duplex (clay-capped) soils around the floodplain are vulnerable to erosion when vegetation cover is low (Acocks, 1953).

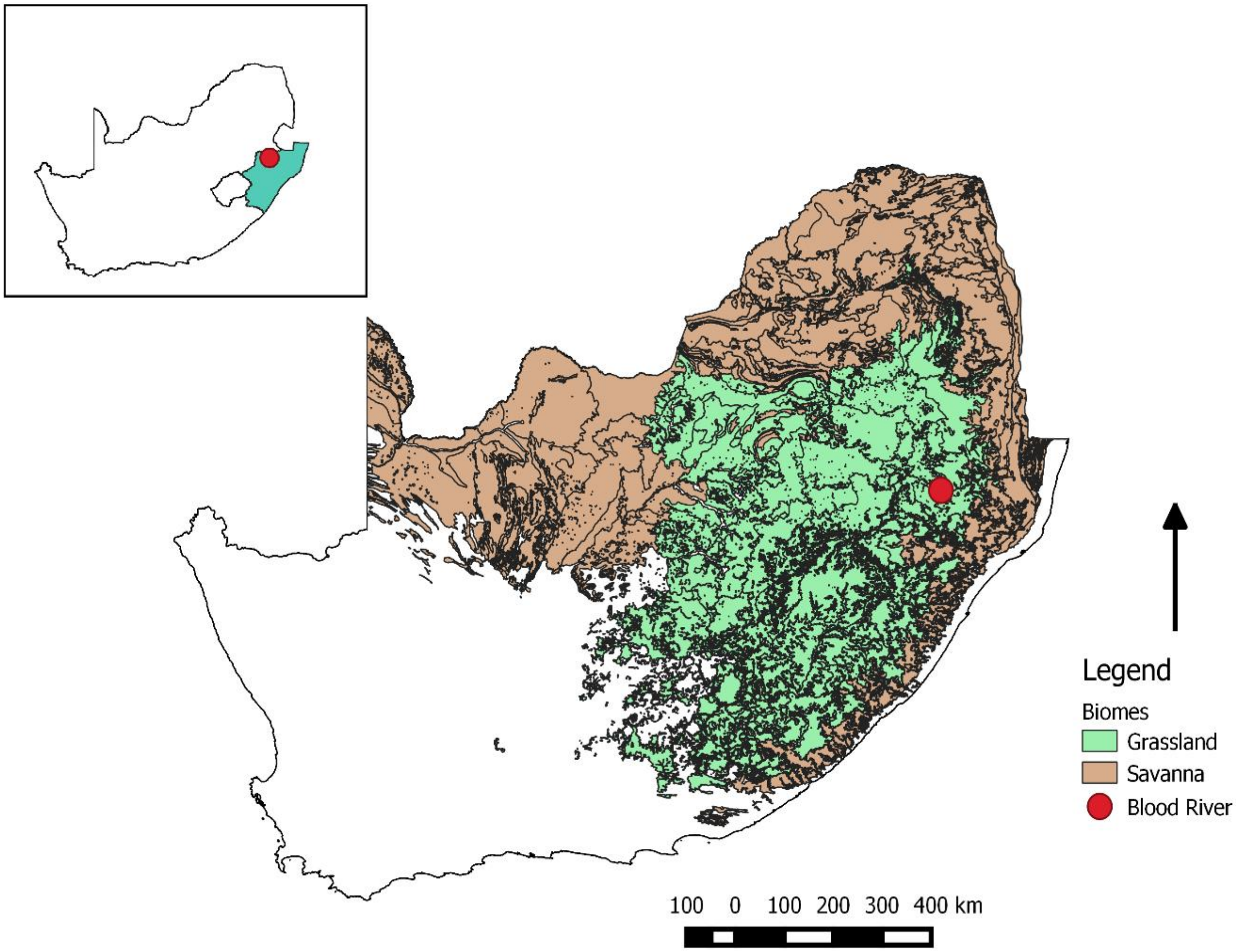

Figure 4.1. Montane grassland study site within the KwaZulu-Natal Province, South Africa. [Biome map from Mucina and Rutherford (2006)].

Vegetation around the floodplain grassland included trees and forbs (Figure 4.2). The main vegetation units in the landscape are classified as the KwaZulu-Natal Highveld Thornveld, Sandy Grassveld, and Paulpietersburg Moist Grassland (Figure 4.1; Mucina and Rutherford, 2006). The tallgrass mosaic in the dryland landscape was dominated by C_4 *T. triandra* and *Hyparrhenia hirta*, but other grasses and forbs included *Andropogon appendiculatus*, *A. junciformis*, *C. dactylon*, *Digitaria eriantha*, *Eragrostis spp.*, *H. hirta*, *Panicum maximum*, *Paspalum dilatum, Sporobolus africanus,* and the forbs *Crinum paludosum, Helichrysum* spp., *Bidens pilosa,* and *Solanum spp.* Flooded soils at the margin were dominated by *Phragmites australis* and C_4 *Cyperus cyperus*, but *Leersia hexandra* was found in the grass understorey. The tree layer was dominated by *Vachellia sieberiana woodii* extending from the riparian margin to the dryland, but other species were *Dombeya rotundifolia, Searsia dentata, Ziziphus mucronata, Euclea racemosa* and aloes. An interesting fact is that *Vachellia sieberiana* is thought to have invaded floodplain grasslands in the last century (Grellier et al., 2012; O'Connor et al., 2014).

Figure 4.2. Blood River Vlei floodplain showing contrast between short and tall grasses.

The site is found in commercial farmland with livestock but may have been previously used by pastoralists in the Zululand region. There was evidence of burning around wetlands in the region to control reed grasses (e.g., Kotze, 2013), and possibly to increase productivity of tallgrasses in fertile plains for grazers (e.g., Fynn et al., 2015; Vesey-Fitzgerald, 1971), or for riparian agriculture (Ingram, 1991; Kotze, 2013).

4.2.2 Palaeoecological methods

A 133cm sediment core was collected from the wettest area at a basin the size of a soccer field using a vibracorer to investigate ecosystem dynamics with proxy data. Standard methods for processing phytoliths (Lentfer and Boyd, 1998), pollen or spores (Bennett and Willis, 2001), charcoal (Carcaillet et al., 2001), stable isotopes (Gillson and Ekblom, 2009a), and LOI were used (Heiri et al., 2001). These methods are described in Chapter Three.

The core was analysed for multiple proxies including GSSCs, $\delta^{13}C/\delta^{15}N$/ C:N, LOI and $CaCO_3$, charcoal, dung fungal spores, Mg:Ca/ Zr:Rb ratios indicating, respectively, grass subfamilies/ grass sward height, photosynthetic signal/ nitrogen availability, grass biomass and salinity, fire activity, grazer pressure, patch structure, and salinity/erosion. A range of grass phytolith ratios were used: aridity index (Iph%), C_3-C_4 grass ratio (Ib%), and tree to grass ratio (Dp°) (Bremond, Alexandre, Wooller, et al., 2008), and grass water stress (Fs%) (Bremond et al., 2005). In addition, I tested indices: the diatom to grass ratio (Di%) for local moisture and the dung spores to grass ratios [*Coniochaeta lignaria* to grass (Clg%) and *Sporormiella* to grass (Sp%)].

4.2.3 Numerical analysis

Vegetation zones used for grass states deduced from phytoliths (Barboni and Bremond, 2009; Finné et al., 2010; Novello et al., 2012), were derived from CONISS (Bennett, 1996;

Grimm, 1987). The CONISS method was also used to signal changes in fire activity and grazing pressure from charcoal and dung spore clusters.

Non-metric multidimensional scaling, an indirect ordination method, was used to identify gradients of grass biomass (from vegetation states), grazing intensity from grass phytoliths, spores, and charcoal, respectively (Legendre and Birks, 2012). The grass biomass gradients from phytoliths was compared between CA and NMDS. Responses of grass biomass (tallgrass or shortgrass) around wetland margins to fire and grazing intensity were independently assessed using ordination gradients of spores and charcoal.

4.3 Results

4.3.1 Dating of sediment and age-depth model

Humin fractions of sediment from five subsamples were used for AMS ^{14}C radiocarbon dating (Table 4.1). The uncalibrated radiocarbon dates ranged from 1 640 ± 30 BP at 133cm base to 650 ± 41 BP at 41 cm depth. A smooth-spline age-depth model was generated from the highest posterior probabilities of the calibrated ages (cal BP) in Clam2.2 (Blaauw 2010; Figure 4.3), using 10 000 simulations with a smooth of 0.3. The average Akaike information criteria (AIC) fit was 43.36 and interpolated age estimates ranged from 5-259 years, with an average of 118 years. However, there were higher uncertainties in the interpolated estimates from 133cm to 65cm.

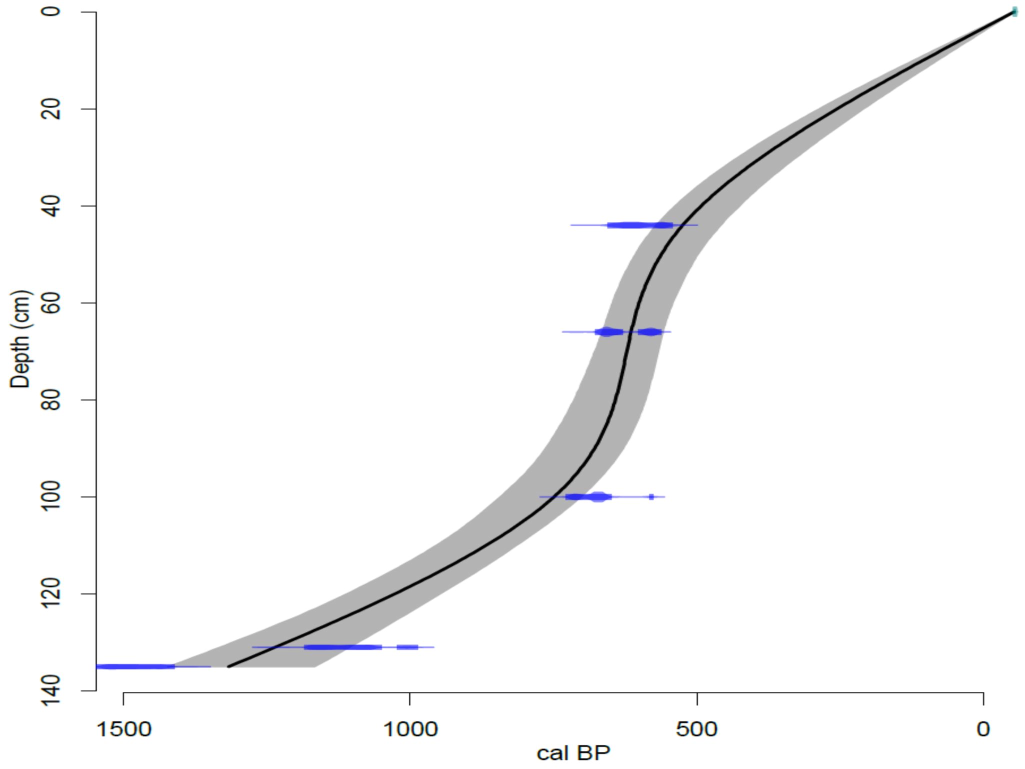

Figure 4.3. Blood River Vlei Age-depth model using the smooth-spline in Clam2.2 with 95% confidence intervals in grey and estimated ages represented by the solid black line.

Table 4.1. Blood River Vlei conventional radiocarbon ages and their equivalent southern hemisphere 13 (SHCal13.14C) calibrated calendar years using CALIB7.1 (Stuiver and Reimer, 1993)

Sample				**SHCal13 Southern Hemisphere Calibration in Calendar years (Hogg et al. 2003)**					
Lab	**Collection ID**	**Analysis ID**	**Depth (cm)**	**δ^{13}C (humin fraction)**	**Conventional Carbon Age BP**	**95% confidence interval calibrated radiocarbon dates**	**Probability (%)**	**95% confidence interval calibrated calendar dates**	**Probability (%)**
QUB	Blood River 44cm	UBA-26 947	44	-17.2	650 ± 41	cal BP 543-655	95	cal AD 1 269-1 407	95
Beta	BR66	Beta – 432 462	66	-20.2	730 ± 30	cal BP 563-601	38.3	cal AD 1 274-1 321	56.6
						cal BP 629-677	56.6	cal AD 1 349 -1387	38.3
Beta	BR100	Beta – 432 461	100	-15.2	780 ± 30	cal BP 577-583	1.6	cal AD 1 222-1 301	93.3
						cal BP 649-728	93.3	cal AD 1 367-1 373	1.6
Beta	BR131	Beta – 410 175	131	-11	1 240 ± 30	cal BP 988-1 022	5.4	cal AD 766-899	89.5
						cal BP 1 051-1 185	89.5	cal AD 928-963	5.4
Beta	BR BASAL	Beta – 379 492	135	-14.4	1 640 ± 30	cal BP 1 412-1 548	93	cal AD 390-402	2.5
						cal BP 1 551-1 560	1.9	cal AD 406-538	92.5

4.3.2 Sediment description

Nine stratigraphic units were found using a modified Troels-Smith protocol (Figure 4.4; Kershaw, 1997). Although the sediment was mostly gyjtta, there were variations in size, colour, and composition among stratigraphic units along the length of the core. Compositionally, the sediment units were made up of the following: Ld (*Limus detrituosus/*organic lake mud), Ag (*Argilla granosa/*silt), As (*Argilla steatodes/*clay), Th (*Turfa herbacea/*coarse roots of herbaceous origin > 5mm), Dh (*Detritus herbosus/*plant or animal fragments > 2mm), Dl (*D. lignosus*/plant or animal fragments > 2mm), Dg (*D. granosus/*plant or animal fragments ca. 0.1mm), Ga (*Grana arenosa*/fine sand). Plant size decreased with depth while there was limited variation in colour among neighbouring stratigraphic units except at LT-3 and LT-7. Sediment unit LT-5 had visible charcoal fragments. The recent stratigraphic units LT-7 to LT-9 had more visible plant fragments and less mineral content.

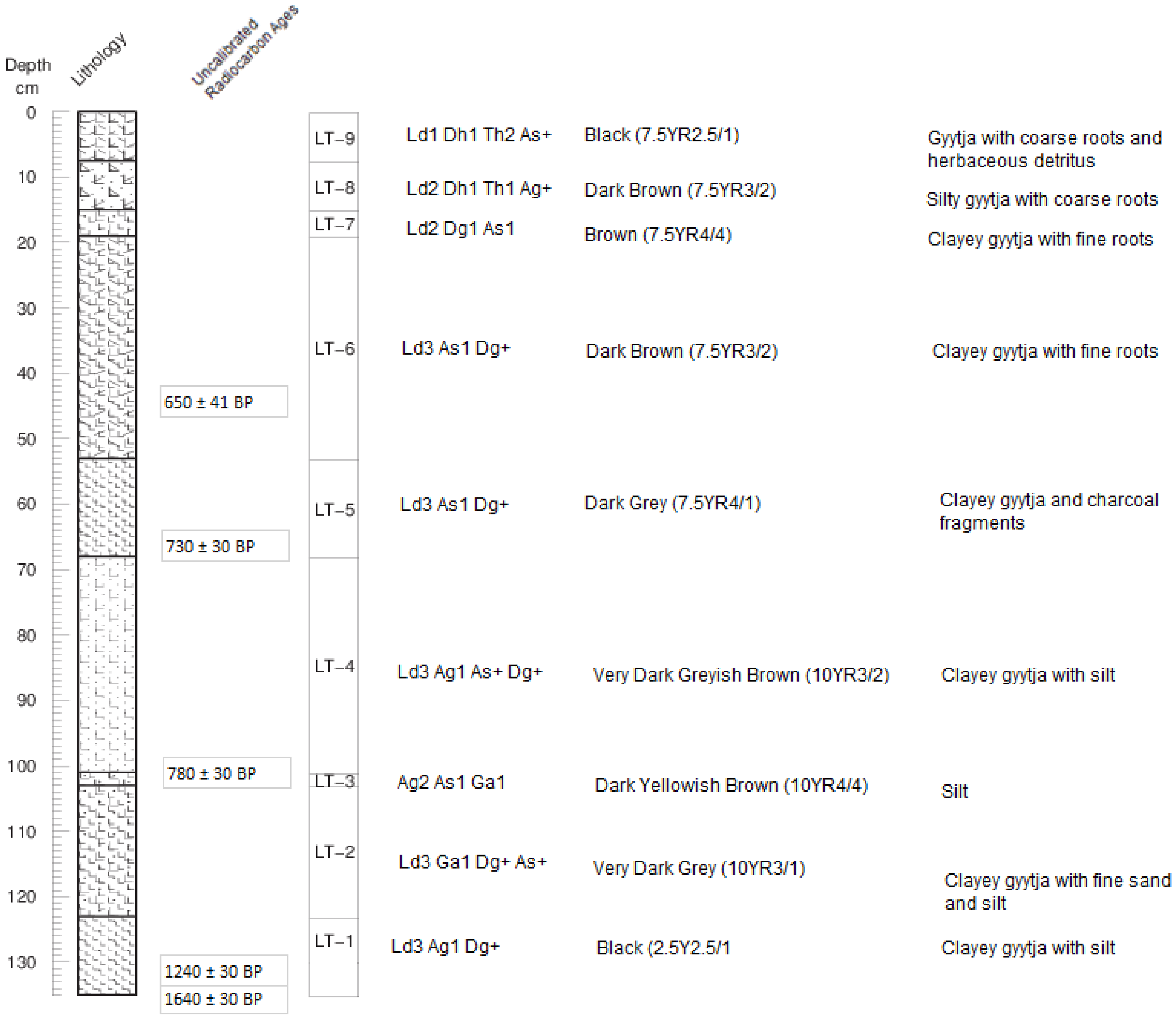

Figure 4.4. Troels-Smith sediment description of the Blood River Vlei core.

4.3.3 Summary of phytolith and non-phytolith indicators of environmental change

Phytoliths were counted in 21 levels, with grass types averaging 94 ± 5.8% of the 329 ± 35 microfossils per sample (Appendix One). Grass silica short cells were the most abundant microfossil morphotypes at 43.9 ± 14.5% (range 57.7%) and were dominated by trapeziform saddles at 13.3 ± 6.2% (range 6.2%), bilobates with 12.1 ± 4.5% (range 17.5%), and rondels averaging 7.5 ± 5.4% (range 20.3%). Trapezoid short cells were rarer at 0.8 ± 0.6% (range 1.8%) for trapezoid polylobates. Non-distinctive parallelipedal bulliforms were grouped together and were the most abundant morphological form at 7.5 ± 5.3% (range 21%) and among long cells, elongate psilates had a mean of 5.3 ± 2.1% (range 8.4%). The acicular hair cells averaged 4.5 ± 2.4% (range 8.2%), while scutiform hairs had a mean of 2 ± 1.4% (range 6.3%).

Woody plant indicators included sclereid and globular phytoliths (Chapter Three, Figure 3.2), but were scarce in this record. Counts of sclereid forms were 1.9 ± 1.6% (range 5.2%) and globular forms were 0.4 ± 0.6 % (range 5.2%). Other microfossils in the count were coprophilous spores 1.9 ± 2.2% (range 6.9%), intact diatoms at 3.6 ± 4.5% (range 17%), and Pseudoschizaceae at 0.3 ± 0.6% (range 2.4%).

The record was dominated by changes in GSSCs, particularly bilobates, rondels and trapeziform saddles that showed similar patterns of increases and declines from ca. 1 220 cal BP to present. Rondels gradually increased from 1 220-750 cal BP, then sharply increased from 720-510 cal BP, and 450-310 cal BP. The most notable changes were declines at ca. 800-700 cal BP and ca. 520-460 cal BP, corresponding with falling abundances of bilobates and saddle trapeziforms but increases in bulliforms, and hair cells, globular, and sclereid phytoliths.

4.3.3.1 Reconstructing grass mosaic states with short cell phytoliths

A locally stable wetland grassland dominated by tallgrasses has been present at Blood River Vlei. GSSC phytoliths representing Arundinoideae and Panicoideae grass subfamilies associated with tallgrass swards/patches had frequencies exceeding 30% (Figure 4.5b). Chloridoideae phytoliths suggesting shortgrass swards/patches in mosaics, were significantly less than the tallgrass representatives in the sequence ($H = 100.57$, $d.f. = 5$, $p\text{-}value < 0.0001$; Figure 4.5b). Three grass zones (i.e., PHY-1 to PHY-3) were identified using the CONISS method (Figure 4.5a; Ter Braak, 1986). The changes of vegetation states of the grass mosaics from the zones are summarised below.

4.3.3.1.1 GSSC zone PHY-1 (1250- 690 cal BP)

A stable C_4 dominated shortgrass state persisted in the basal zone as indicated by the dominance of Panicoideae, made up c. 35-49% of the assemblage. Notable peaks in Panicoideae abundance occur from c. 49% at ca. 960 cal BP and from c. 35% at ca. 1 030 cal BP, then a steady decline to c. 30% at ca. 720 cal BP. The abundance of shortgrasses indicated by Chloridoideae remained stable through the sequence ranging between c. 10-16% but declined sharply from c. 16% at ca. 760 cal BP to c. 5% at ca. 720 cal BP. Arundinoideae declined from c. 37% at ca. 1 250 cal BP to c. 17% at ca. 960 cal BP but then steadily increased to c. 29% at ca. 750 cal BP and fell to c. 9% at ca. 720 cal BP. Pooideae abundance, representing C_3 wetland grasses, increased from c. 4% at the base of the core to c. 23% at ca. 720 cal BP, though with some decline at ca. 1 030-960 cal BP. Stipa types changed little.

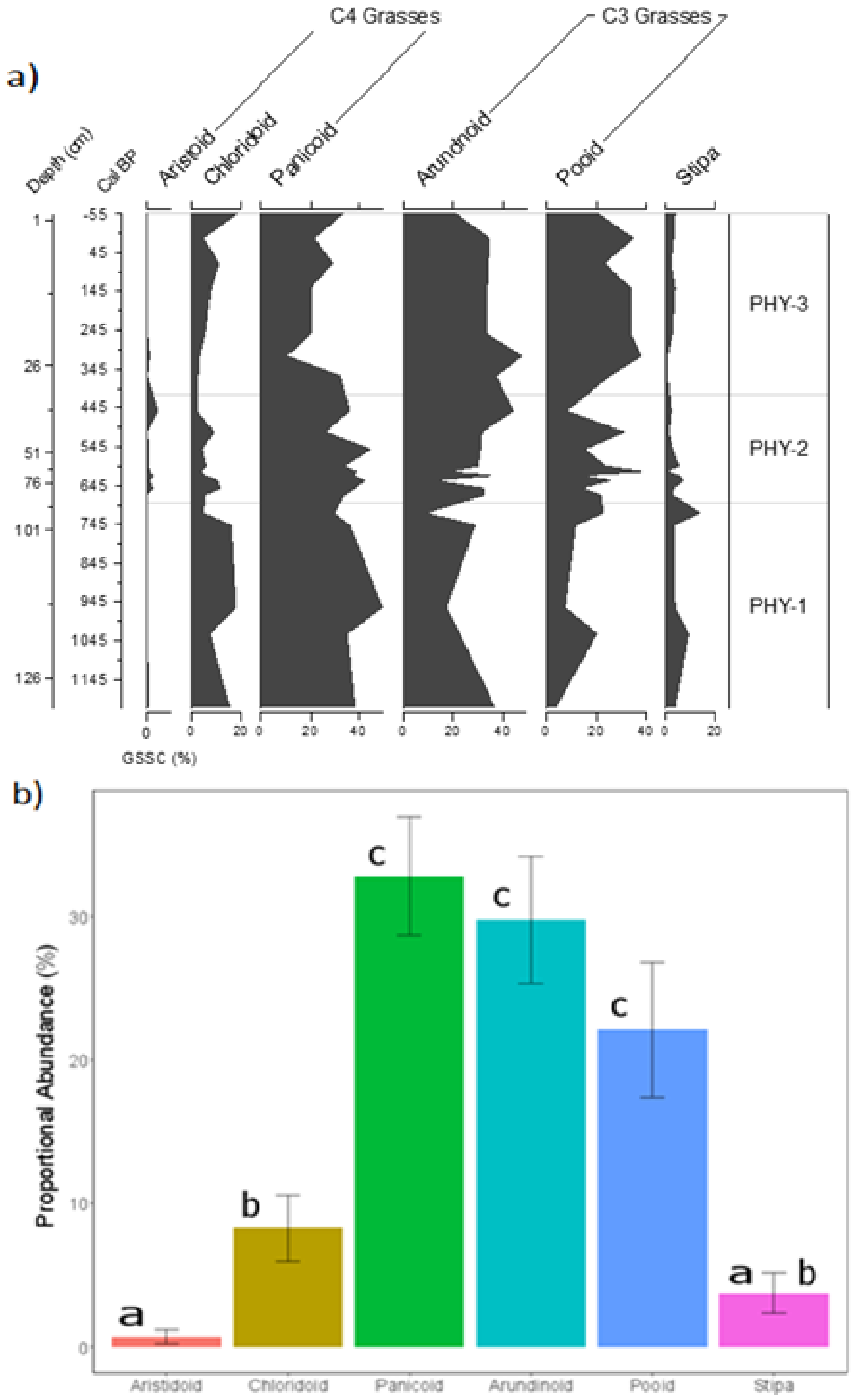

Figure 4.5. a) Changing in abundance of grass subfamilies from short cell phytoliths showing the CONISS zonation of vegetation zones; b) The abundance of grass subfamilies deduced from grass short cells phytolith samples for the whole sequence.

4.3.3.1.2 GSSC zone PHY-2 (690 - 410 cal BP)

An unstable mixed tallgrass state with C_3 and C_4 members was characterised by the coexistence of dryland Aristidoideae with wetland Arundinoideae and Pooideae grasses. Arundinoids dominated the counts accounting for c. 33-44% of the assemblage, notably increasing from c. 13% at ca. 630 cal BP to c. 44% at ca. 450 cal BP. Tallgrasses represented by Panicoideae experienced irregular decreases from c. 42% at ca. 630 cal BP to c. 33% at ca. 509 cal BP. Fluctuations in local wetland grasses like Pooideae was indicated by troughs of c. 14% at ca. 650 cal BP and c. 8% at ca. 510 cal BP, with notable peaks in-between of c. 38% at ca. 610 cal BP and c. 31% at ca. 510 cal BP. Similarly, shortgrass represented by Chloridoideae types fluctuated with peaks of c. 12%, 6%, and 9% at ca. 650, 600 and 500 cal BP, respectively. Although there was a presence of Aristidoideae, abundance was low at c. 1-4%, with the largest peak of c. 4% occurring at ca. 450 cal BP.

4.3.3.1.3 GSSC zone PHY-3 (410 to -55 cal BP)

A stable wetland tallgrass state dominated by Arundinoideae, Panicoideae and Pooideae grass subfamilies had dryland Aristidoideae and few shortgrasses. Arundinoideae and Pooideae abundance increased to c. 34% and c. 19% at ca. 310 and to -50 cal BP, respectively. Arundinoid abundance remained unchanged at c. 34% after falling from c. 48% at ca. 310 cal BP to c. 34% at ca. 260 cal BP. Pooideae types declined from c. 38% at ca. 310 cal BP to c. 23% at ca. 70 cal BP. Stipa types stabilised at c. 2-3% from ca. 300 cal BP after increasing from c. 1% from ca. 340 cal BP. Finally, Chloridoideae and Panicoideae abundance increased from 310 cal BP to the present.

4.3.3.2 Local environmental gradients from short cell phytoliths

The NMDS and CA ordinations showed that grass subfamilies had similar patterns (Figure 4.6). At the C_3 extreme was Pooideae while Stipa was at the opposite C_4 end. The NMDS ordination of the two-dimensional solution had reasonable stress value (Figure 4.6a). There was no separation among vegetation units along the primary axis (NMDS1). However, C_4 grasses were on the negative end of the NMDS1 axis while the positive end was occupied by C_3 grasses. There was separation among subfamilies along the secondary NMDS2 axis with Aristidoideae being the most distant from the other subfamilies compared to Arundinoideae found at the positive end of the gradient.

The first two axes of the CA ordination accounted for 73.8% of the variance (Figure 4.6b). The primary axis (CA1) accounting for 45.5% was dominated by the heavy grazing indicator grass subfamily Aristidoideae. In contrast, other subfamilies clustered. Along the secondary axis (CA2), grass subfamilies were hierarchically structured by a gradient of increasing aridity from purely wetland C_3 grasses to dryland C_4 grasses.

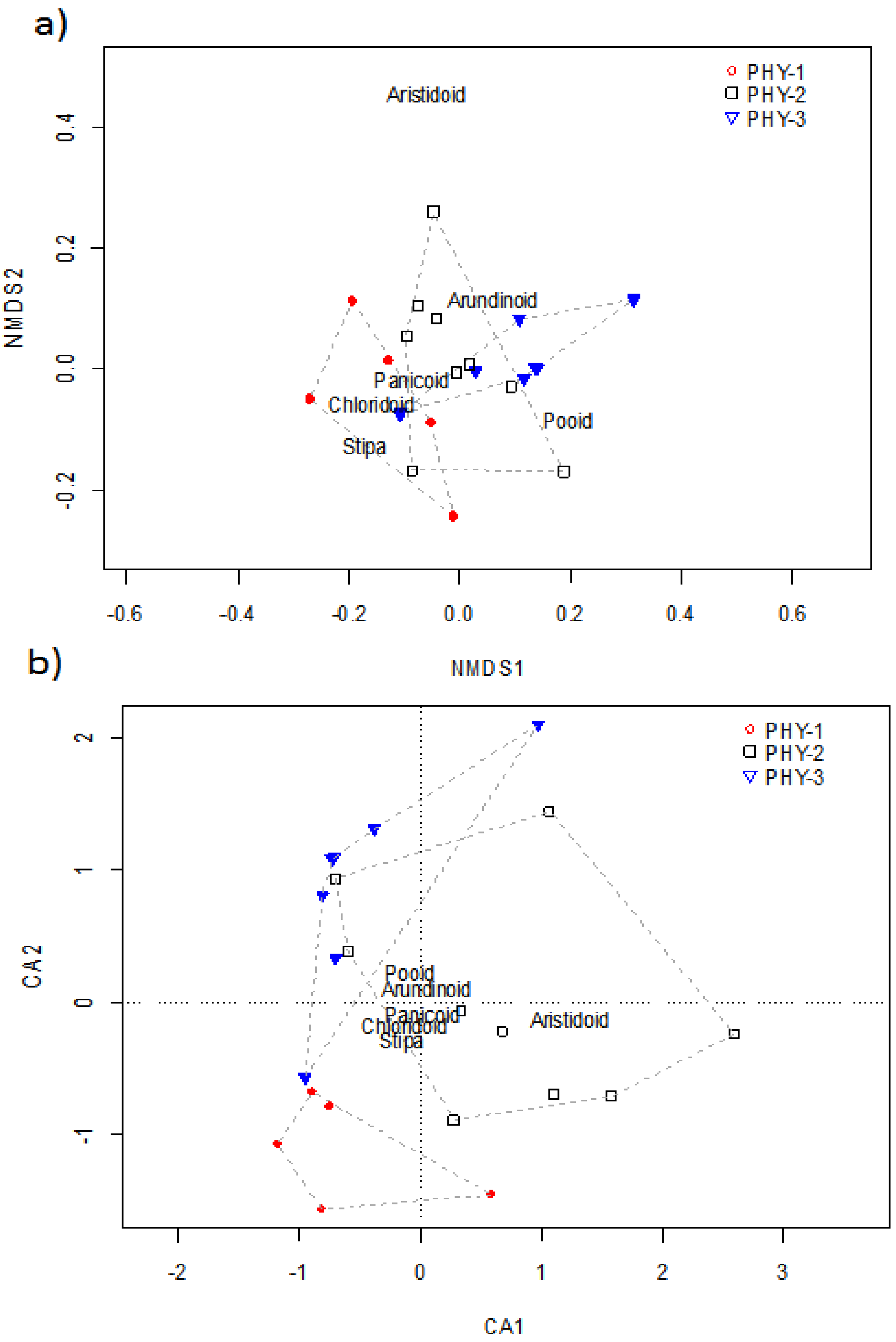

Figure 4.6. Ordination with NMDS and CA of grass subfamilies at different levels within the Blood River Vlei sedimentary sequence with convex hulls denoting the phytolith zones.

Ordination axes CA2 and NMDS1 reflected the C_3-C_4 aridity and grass biomass (sward height) gradients. The axes were significantly correlated (*r* = 0.957, *d.f.* = 19, *p-value* < 0.00001), therefore CA was selected for further analyses. However, compared to the NMDS ordination, there was less overlap in convex hulls that represented vegetation zones (or states) in the CA ordination. Importantly, there were indications of clustering of states around certain points with time for the shortgrass and wetland tallgrass states but was less so with the wide-ranging mixed tallgrass states mosaic (Figure 4.7).

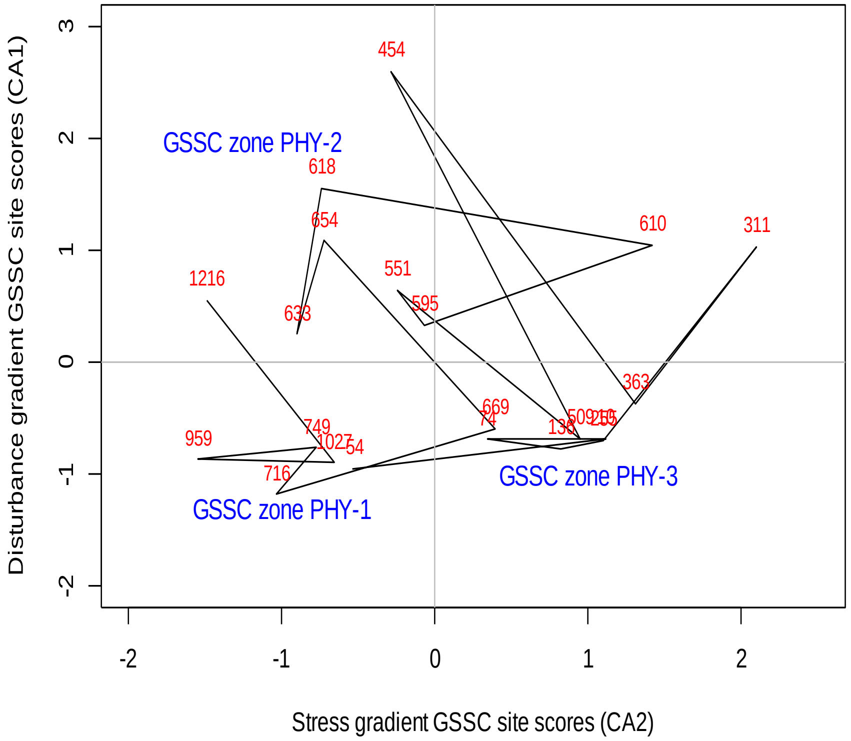

Figure 4.7. Change in wetland grass states with time from the relationship between the primary and secondary axes of the grass subfamilies from phytolith CA ordination.

4.3.3.3 Multiple proxy phytolith indices for vegetation, grazing and local moisture

Overall, three striking changes in grass ratios were noted (Figure 4.8.). The first was an increase in C_3 grasses (Ib%), grass water stress (Fs%), and *Coniochaeta lignaria* spores to GSSC phytolith ratio (Clg%) with time. The second showed corresponding peaks in herbivore biomass indicated by Clg%, grass water stress; and tree abundance at ca. 720, 450 and 260 cal BP. Lastly, local moisture variations were signalled by fluctuations in the aridity indicator Iph%.

4.3.3.3.1 Local C_3-C_4 grass ratio (Ib%)

An irregular pattern of local increases in C_3 grasses (Ib%) was seen from the base of the core to the present (Figure 4.8). The increase occurred from c. 43% at ca. 1 220 cal BP to c. 50% at ca. 1 030 cal BP, followed by a sharp decline to c. 27% at ca. 960 cal BP. A rise followed this to the peak of c. 86% at ca. 310 cal BP then a fall to c. 60% at ca. 70 cal BP.

4.3.3.3.2 Grass aridity index (Iph%)

There were infrequent changes in the local grass aridity index (Iph%) in shortgrass and wetland tallgrass mosaics compared with the mixed tallgrass mosaic (Figure 4.8). The shortgrass mosaic had arid local conditions with Iph% ranging c. 17-29% from ca. 1 220-750 cal BP but this sharply declined to c. 10% at ca. 720 cal BP. Fluctuations in aridity were suggested by notable peaks at c. 24% at ca. 650 cal BP and c. 33% at ca. 510 cal BP and troughs at c. 9.2% at ca. 610 cal BP and c. 6% at ca. 450 cal BP. This period was followed by abrupt increases in aridity with peaks of c. 27% at ca. 310 cal BP and c. 33% at ca. 140 cal BP, followed by a sharp decline to c. 20% at ca. 10 cal BP.

4.3.3.3.3 Tree to grass ratio (Dp°)

Globular phytoliths typical of trees and/or woody plants were present in all the zones in low abundances but had an extended period of absence from ca. 600-310 cal BP (Figure 4.8). From the base of the core (ca. 1 220 cal BP), Dp° did not vary until its steep rise from c. 0.02 at ca. 750 cal BP to c. 0.21 at ca. 720 cal BP. This was followed by an irregular decline to zero at ca. 600 cal BP. There was a reappearance of trees from ca. 310 cal BP followed by their absence at ca. 70 cal BP.

4.3.3.3.4 Grass water stress (Fs%)

Grass water stress (Fs%) was varied in the sequence. However, there was a distinctive pulsed pattern in Fs% from the base to the top of the age-depth model (Figure 4.8). Peaks in water stress were close to the vegetation transitions. The main peaks were c. 41% at ca. 750-650 cal BP, followed by c. 18% at ca. 510-360 cal BP and lastly c. 15% at ca. 310-140 cal BP.

4.3.3.3.5 Local moisture from diatom to grass ratio (Di%)

The increase in the diatom to grass ratio, Di%, indicated a rise in soil moisture from the shortgrass to the tallgrass state (Figure 4.8). The shortgrass state had fewer intact diatoms compare with tallgrass states. Fluctuating moisture was indicated by irregular increases in diatoms with peaks of c. 15% at ca. 630 cal BP and c. 26% at ca. 510 cal BP and troughs of 0% at ca. 595 cal BP and 0% at ca. 450 cal BP, respectively. Also, irregular increases in diatoms occurred across the boundary between the mixed tallgrass and wetland tallgrass states.

4.3.3.3.6 Herbivore biomass from the Sporormiella to grass ratio (Sp%)

Sporormiella indicating herbivore biomass had a patchy abundance in the shortgrass and mixed tallgrass compared with the wetland tallgrass state where it reached its highest abundance

(Figure 4.8). However, peaks occurred at ca. 750 cal BP and at ca. 650 cal BP. The steepest increase was from 0% at ca. 310 cal BP to c. 4% at ca. 255 cal BP, and was followed by a decline to c. 0.5% at ca. 70 cal BP.

4.3.3.3.7 Local herbivore density and/or moisture signal to grass ratio (Clg%)

Coniochaeta lignaria indicating herbivore biomass and soil moisture was present throughout the core with the highest index to grasses (*Clg*%) of c. 35%. The peak at ca. 720 cal BP happened before the transition between shortgrass and mixed tallgrass states. There was also another increase in Clg% to c. 6% at ca. 450 cal BP before the transition between mixed tallgrass and wetland tallgrass states.

4.3.3.4 Assessing grazing mosaics and local environmental conditions with grass phytolith ratios

Only the C_3-C_4 (Ib%) grass ratio had a statistically significantly positive correlation with the CA ordination (Figure 4.9; Table 4.2), while no relationships were found with the other ratios. However, Clg% increased along the disturbance GSSC CA1 axis while Sp% rose along the stress/productivity GSSC CA2 axis. At the xeric end of the productivity/biomass gradient shown by GSSC CA2, there were increases in grass water stress shown by Fs%, trees shown by Dp°, and aridity represented by Iph%.

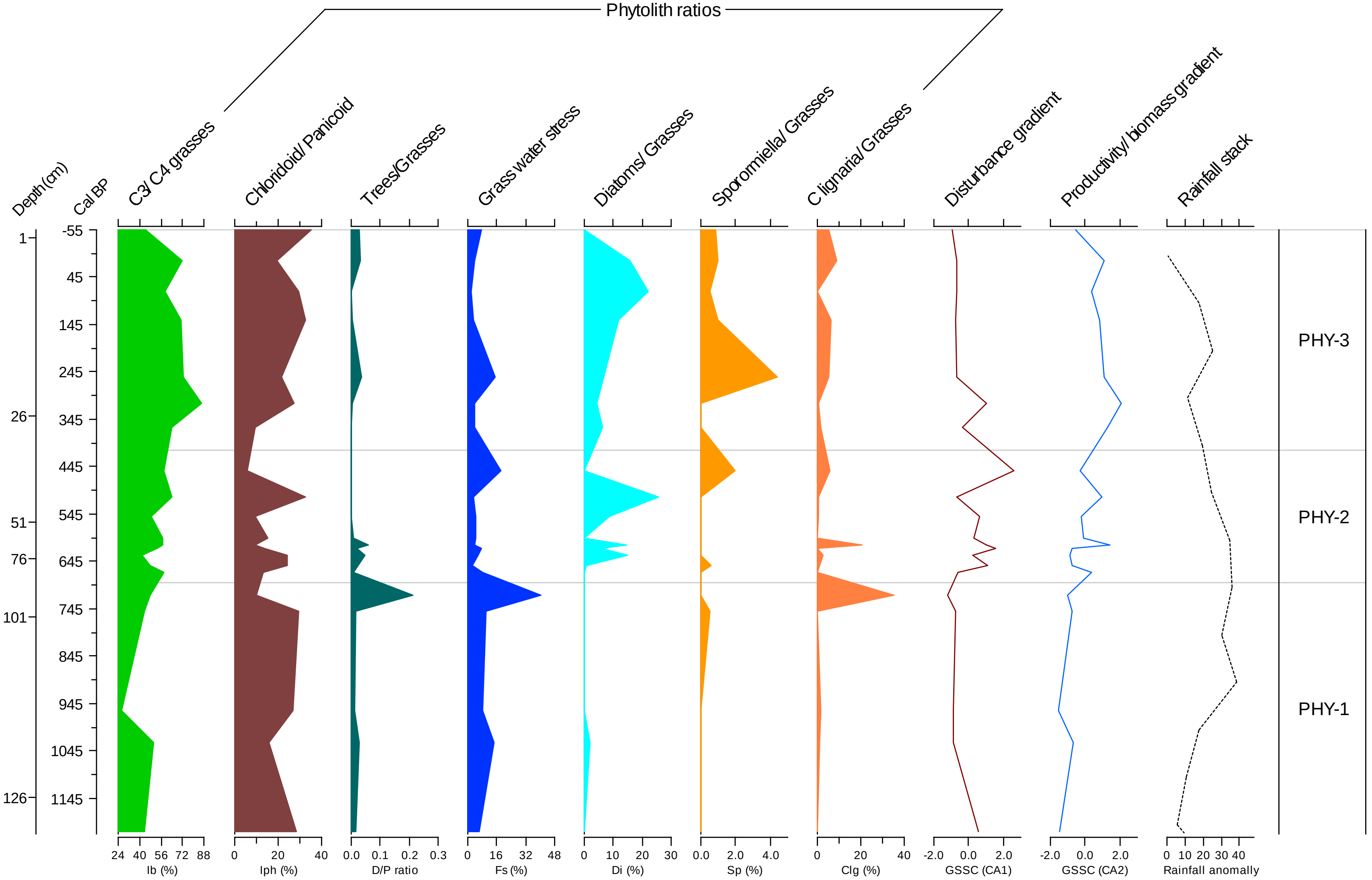

Figure 4.8. Summary of phytolith ratios and CA axes for the Blood River Vlei dataset plotted alongside Chevalier and Chase's (2015) regional rainfall reconstruction.

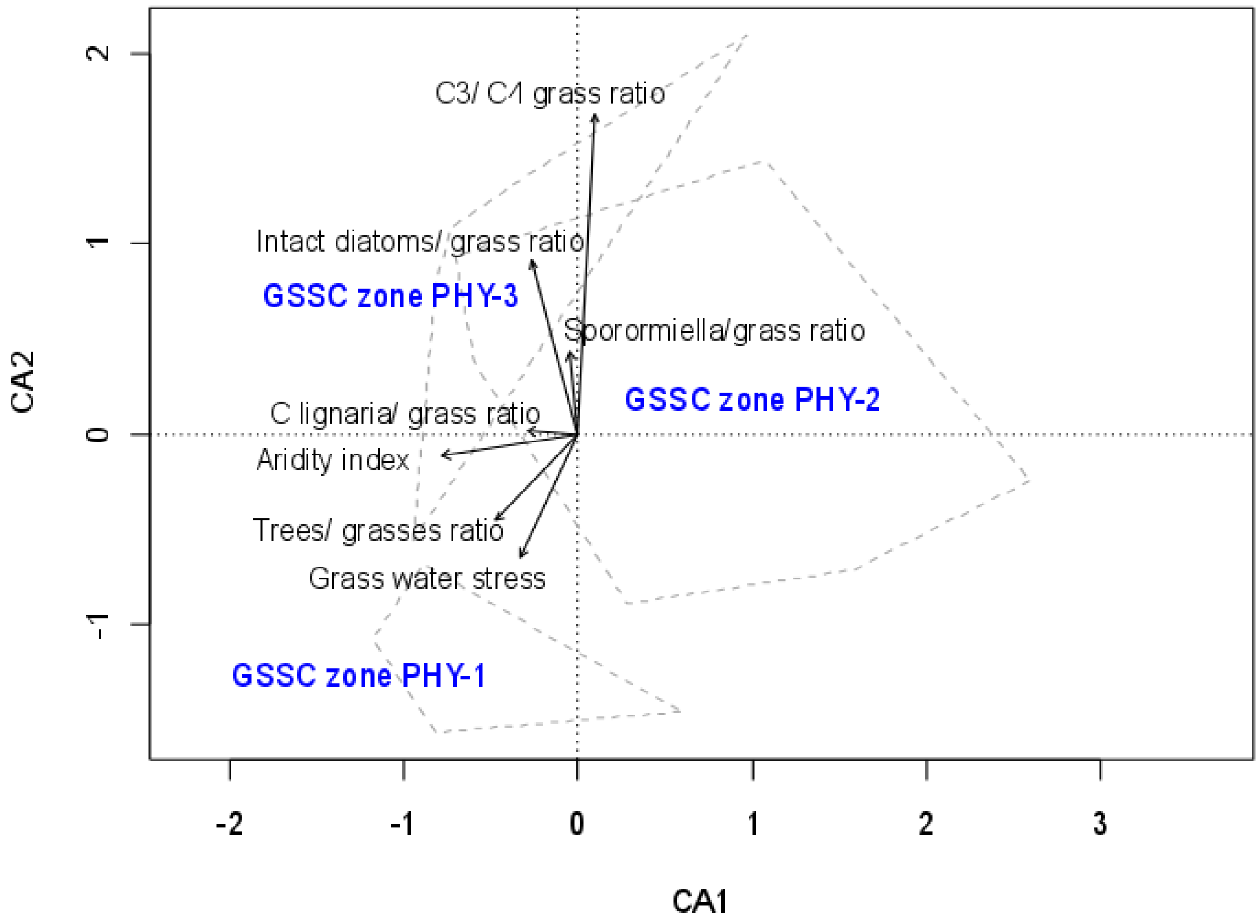

Figure 4.9. Vector-fitted gradients of phytolith ratios on the CA ordination of the GSSC grass subfamily data of Blood River Vlei (permutations = 10 000).

Table 4.2. Relationships between the phytolith-derived environmental proxies along the GSSC CA primary and secondary axes of the Blood River Vlei dataset (permutations = 10 000)

	cosine CA1	*cosine* CA2	r^2	*p-value*
C. lignaria / GSSC (Clg%)	-0.998	0.061	0.024	0.837
Diatom/ GSSC (Di%)	-0.283	0.959	0.258	0.064
Grass water stress (Fs%)	-0.461	-0.887	0.150	0.221
Ib/ C_3-C_4 (Ib%)	0.058	0.998	0.809	**0.0001**
Aridity index (Iph%)	-0.989	-0.146	0.177	0.172
Sporormiella / GSSC (Sp%)	-0.104	0.995	0.054	0.642
Tree/Grass index (Dp°)	-0.720	-0.694	0.122	0.294

4.3.4 Changes in photosynthetic signal and nutrient dynamics from stable isotopes

The stable isotope record showed dynamic changes within the core (Figure 4.10). Patterns of TN and TC were positively correlated ($r = 0.5$, $d.f. = 46$, $p\text{-}value = 0.0003$), as were local nitrogen abundance ($\delta^{15}N$) and local grass signal ($\delta^{13}C$) ($r = 0.501$, $d.f. = 46$, $p\text{-}value = 0.0003$). Total nitrogen had a mean of c. 2.2 ± 0.1%, and a range of 0.5% while TC had a mean of c. 3 ± 1.4% with a range of 6.95%. The $\delta^{15}N$ values had a mean of c. 5.4 ± 0.8‰ ranging c. 3.5‰ and $\delta^{13}C$ had a mean c. 18.0 ± 2.4‰. Lastly, the C:N ratios had a mean of c. 13.6 ± 1.6 and range c. 8.3. It was interesting to see that although there was stasis in TN and TC at two transitions between phytolith zones, the other variables ($\delta^{15}N$, $\delta^{13}C$ and C:N ratio) increased.

Significant differences in $\delta^{13}C$ were found using rank sums among phytolith zones ($H = 29.08$, $d.f. = 2$, $p\text{-}value < 0.0000$; Table 4.3), with significant differences found in comparison between the C_4 dominated shortgrass mosaic and the C_3 dominated tallgrass states (Table 4.4). Overall, a significant negative relationship was found between $\delta^{13}C$ and the GSSC CA2 productivity/biomass gradient (*r* = -0.686, *d.f.* = 17, *p-value* = 0.0012), while no relationship was found between $\delta^{13}C$ and the GSSC CA2 disturbance gradient (*r* = 0.048, *d.f.* = 17, *p-value* = 0.846).

4.3.4.1 GSSC zone PHY-1 (1250-690 cal BP)

Fluctuation declines in nitrogen abundance indicated by $\delta^{15}N$ were matched by the C:N ratio from ca. 840-690 cal BP. Interestingly, TN and TC generally increased with time despite fluctuations between ca. 780-490 cal BP. Declines in nitrogen availability ($\delta^{15}N$) from c. 7.1-3.7‰ occurred from ca. 1 220-820 cal BP, but were followed by an abrupt increase to c. 6% at ca. 750 cal BP. Lastly, a gradual decline in $\delta^{13}C$ values of c. 2‰, associated with a local increase in C_3 grasses, happened from ca. 1 220-720 cal BP.

4.3.4.2 GSSC zone PHY-2 (690-410 cal BP)

There were inverse relationships between TN and $\delta^{15}N$ and between TC and $\delta^{13}C$ in this zone from ca. 580-410 cal BP. Rapid increases in TN of c. 0.1-0.3% and TC of c. 1.9-4.4% were seen from ca. 690-510 cal BP, followed by sharp declines of c. 41% and c. 33% respectively of peak values from ca. 510-490 cal BP. This was followed by stable values from ca. 490-390 cal BP. There were increases in nitrogen availability ($\delta^{15}N$) from c. 5‰ at ca. 690 cal BP to c. 6.5‰ at ca. 640 cal BP, falling to c. 3.9‰ at ca. 550 cal BP. This was followed by a steady increase in $\delta^{15}N$ to c. 5.2‰ and little variation thereon. The $\delta^{13}C$ fell sharply from c. -15.6‰ at ca. 690 cal BP to c. -21‰ at ca. 590 cal BP, as C_3 grass phytoliths increased. C:N ratio values ranged between c. 12-13 from ca. 670-510 cal BP, falling from a peak value of c. 17.2 at ca. 690 cal BP. There was an increase in C:N ratio from c. 12.8 at 510 cal BP to 14.7 at ca. 490 cal BP.

4.3.4.3 GSSC zone PHY-3 (410 to -55 cal BP)

There were inverse relationships between TC and δ^{13}C representing the composition of grass biomass. Irregular declines in δ^{13}C from ca. 390-140 cal BP, corresponded with the increase of C_3 grass phytoliths, and coincided with a rise in the C:N ratio. Nitrogen availability (δ^{15}N) was low during this period from c. 5.9‰ at ca. 310 cal BP to c. 4.6‰ at ca. 230 cal BP, but recovered to c. 5.9‰ at ca. 10 cal BP.

Table 4.3. Kruskall-Wallis rank sum comparison of δ^{13}C values among grass phytolith vegetation zones from Blood River Vlei

Zone	*N*	*δ^{13}C mean*	*s.d.*	*d.f.*	*H*	*p-value*
PHY-1	11	-14.776	0.751	2	29.079	> **0.00001**
PHY-2	21	-18.288	1.648			
PHY-3	16	-19.963	1.484			

Table 4.4. Blood River Vlei pairwise comparisons of δ^{13}C between grass phytolith vegetation zones using the Tukey and Kramer *post-hoc* test

	PHY-1	PHY-2
PHY-2	**0.00067**	
PHY-3	**2.30E-07**	0.06925

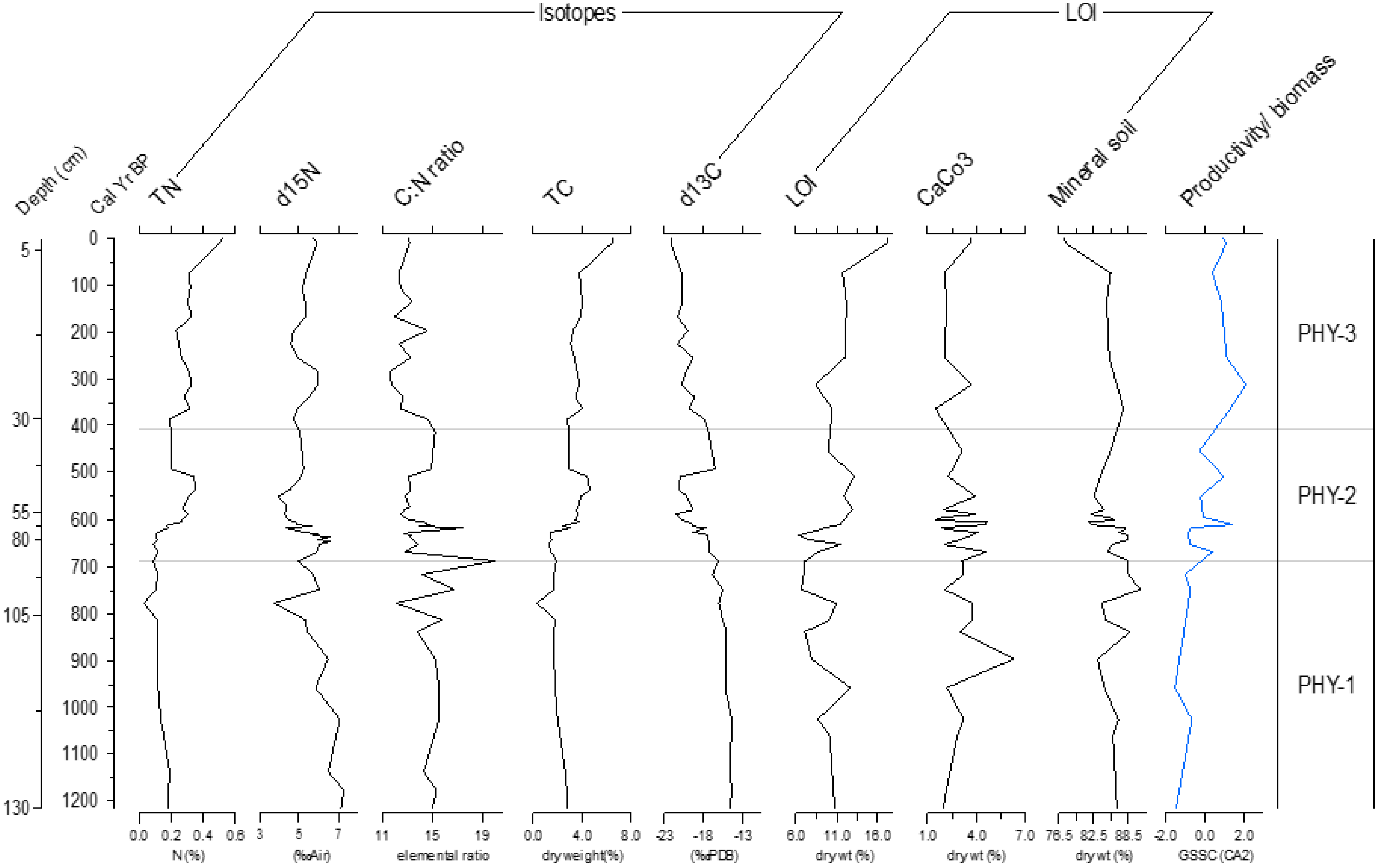

Figure 4.10. Changes in stable isotopes and LOI from bulk sediment samples within phytolith vegetation zones.

4.3.5 Changes in local grass biomass and salinity of the wetland grass mosaic from loss on ignition

Local grass productivity/ biomass and salinity of the wetland grass mosaic edge, represented by LOI and carbonates respectively, varied throughout the sequence (Figure 4.11). No significant correlation was found between LOI and $CaCO_3$ (*r* = -0.139, *d.f.* = 32, *p-value* = 0.433). LOI had a mean of 10.5 ± 2.7% with a range of 11.4%. Carbonates had a mean 3.0 ± 1.1% and a range of 4.8%. There was also no significant correlation between LOI and the local grass productivity/ biomass (GSSC CA2) gradient (*r* = 0.210, *d.f.* = 19, *p-value* = 0.361) and between the disturbance (GSSC CA1) gradient and LOI (*r* = -0.178, *d.f.* = 19 *p-value* = 0.441). Also, no differences were found between LOI rank sums among the GSSC zones (*H* = 5.673, *d.f.* = 2, *p-value* = 0.059; Table 4.5).

4.3.5.1 Shortgrass state GSSC zone PHY-1 (1 250-690 cal BP)

The general decrease in local grass productivity was related to an increase in salinity indicated by the relationship between LOI and $CaCO_3$ from ca. 1 220 cal BP to ca. 690 cal BP. Carbonates peaked at c. 6.3% at ca. 890 cal BP declining thereafter. LOI decreased from ca. 1220-740 cal BP from c. 12.6-6.6%, albeit with peaks of c. 12.6% at ca. 960 cal BP and c. 10.9% at ca. 780 cal BP. Carbonates increased from c. 2% at ca. 1 220 cal BP to peak at c. 6.3% at ca. 890 cal BP before falling to c. 2% at ca. 750 cal BP but increased thereafter.

4.3.5.2 Mixed tallgrass state GSSC zone PHY-2 (690-410 cal BP)

There was variability in LOI and carbonates within this zone, with fluctuations occurring from ca. 670-550 cal BP. A sharp increase in LOI happened at the transition between the shortgrass mosaic and the mixed tallgrass mosaic to peak at c. 11.6% at ca. 650 cal BP, followed by an abrupt decline to c. 6.2% at ca. 630 cal BP. Sharp increases in local grass biomass/productivity led to an LOI peak of c. 13% at ca. 580 cal BP, followed by a decline to c. 9% at ca. 410 cal BP. Curiously, carbonates oscillated widely between ca. 690-550 cal BP ranging between c. 1.5-4.6%, and an irregular decrease to c. 12% at ca. 410 cal BP followed.

4.3.5.3 Wetland Tallgrass state GSSC zone PHY-3 (410 to -55 cal BP)

Although there was relative stability in local grass biomass suggested by the narrow range of LOI values (c. 11-12%) and carbonates (c. 2%) from ca. 250-70 cal BP, the preceding decline in LOI from ca. 360-310 cal BP was associated with increased carbonates. Both LOI and carbonates increased from ca. 70 to (-55) cal BP with carbon reaching a peak abundance of 17.7%; carbonates peaked at 3.9%.

Table 4.5. Comparisons of LOI among grass phytolith vegetation zones

GSSC Zones	*levels*	*mean LOI*	*s.d.*	*d.f.*	*H*	*p-value*
PHY-1	10	9.170	2.010	2	5.673	0.059
PHY-2	17	10.286	2.222			
PHY-3	7	12.804	3.452			

4.3.6 Reconstruction of herbivore biomass with spores

Herbivore biomass indicated by dung spore concentrations was variable within the grass states/phytolith zones (Figure 4.11) and other spores (Appendix Two). The spore signal was dominated by Coniochaetaceae and Sordariaceae represented by *C. lignaria* and *Sordaria*. Though *Glomus, Podospora, Delitschia,* and *Coniochaeta*-type had patchy appearances in the sequence, they occurred in significant numbers during peaks of *Sordaria* and *C. lignaria* in the mixed tallgrass and wetland tallgrass states (zones PHY-2 and PHY-3). *Glomus*'s only appearances were near the boundaries of the vegetation zones. While there was a positive non-significant correlation found between *Sporormiella* and grass productivity/biomass gradient (r =

0.364, *d.f.* = 15, *p-value* = 0.151), a significant positive relationship along the gradient was found for *C. lignaria* (r = 0.664, *d.f.* = 15, *p-value* = 0.0037).

4.3.6.1 Shortgrass state/PHY-1 (1 250-690 cal BP)

This zone with fewer spores was characterised by the gradual increase in the spore concentration dominated by *C. lignaria*, *Sordaria* and a notable presence of *C. gamsii*. Although *C. gamsii* increased in abundance from c. 150 spores cm^{-3} at ca. 1 220 cal BP to peak at 2 230 spores cm^{-3} at ca. 1 060 cal BP, it declined thereafter. Many spore types including *Podospora*, *Sporormiella*, *C. lignaria*, *Sordaria*, *Cercophora* and *Chaetomium* increased in abundance from ca. 1 060-690 cal BP. The large *Glomus* spores briefly appeared at ca. 720 cal BP before the transition between the shortgrass and tallgrass state.

4.3.6.2 Mixed tallgrass state/PHY-2 (690-410 cal BP)

There was a sharp increase in numbers of most spores, particularly from ca. 630-450 cal BP, with peak *Sporormiella* concentration of 1.81x10^{4} spores cm^{-3} occurring in this zone. *Coniochaeta lignaria*, *Coniochaeta*-type, *Sordaria*, *Sporormiella* and *Cercophora* were also abundant. There were two matching peaks in local herbivore biomass suggested by increased abundance of *Sporormiella*, *C. lignaria*, *Cercophora* and *Sordaria* Type 55b at ca. 600 cal BP and at 490 cal BP. *Delitschia* was first within this zone at a low concentration of 194 spores cm^{-3} at ca. 570 cal BP, while *Glomus* peaked at 220 spores cm^{-3} at the transition between the mixed tallgrass and wetland tallgrass states.

4.3.6.3 Wetland tallgrass state/PHY-3 (410 to -55 cal BP)

Coniochaeta lignaria was dominant compared to reduced *Sporormiella*, *Gelasinospora* and *Sordaria* Type 55b abundance from ca. 360 to (-55) cal BP. There were two peaks in *C.*

lignaria concentration from ca. 360-200 cal BP of 4.89 x10^4 spores cm^{-3} and at ca. 310 cal BP of 4.81 x10^4 spores cm^{-3}, followed by a decline to c. 1.82 x10^4 spores cm^{-3} at ca. 260 cal BP. It is interesting that herbivore density increased in the lead up to the modern as suggested by rises in *C. lignaria, C. gamsii*, *Coniochaeta*-type, *Cercophora,* and *Sordaria*, this despite tall grass dominance.

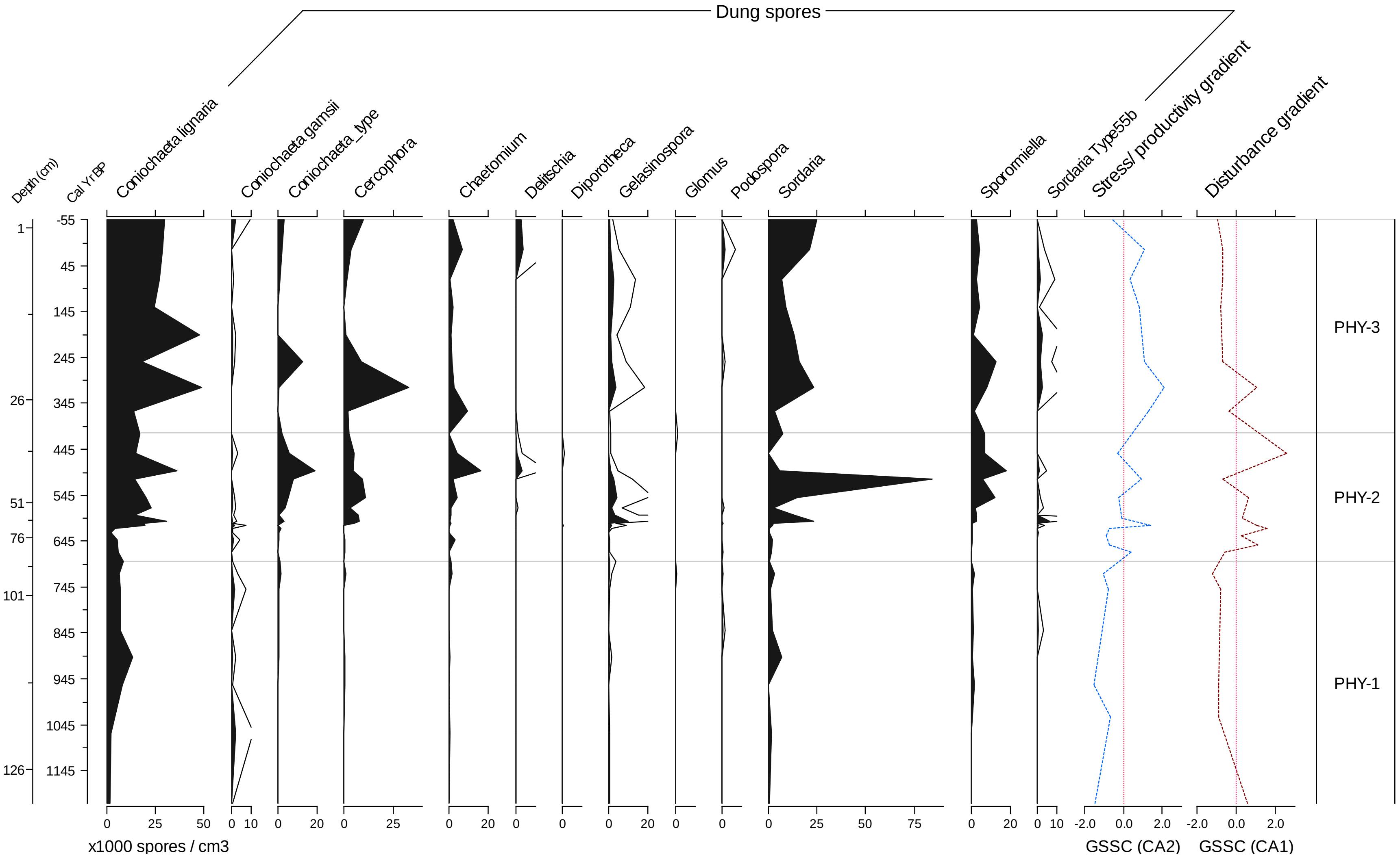

Figure 4.11. Changes in herbivore biomass shown by dung fungal spores within the vegetation zones (grass states). Plotted alongside are the phytolith CA scores for the primary and secondary axes.

4.3.7 Reconstructing fire activity using charcoal

Charcoal abundance indicating fire intensity and burned area was considered fire activity. Charcoal abundance increased with time in all charcoal size classes (Figure 4.12). Macrocharcoal and microcharcoal abundance were positively correlated ($r = 0.795$, $p\text{-value} < 0.00001$, $d.f. = 28$). Macrocharcoal abundance was lower and with few peaks in the shortgrass state. There were irregular increases in charcoal abundance in the mixed tallgrass state, with peak activity occurring between ca. 610-450 cal BP. An increase in charcoal abundance from ca. 450-390 cal BP coincided with the transition between the mixed tallgrass and wetland tallgrass. However, charcoal abundance declined from ca. 200 cal BP.

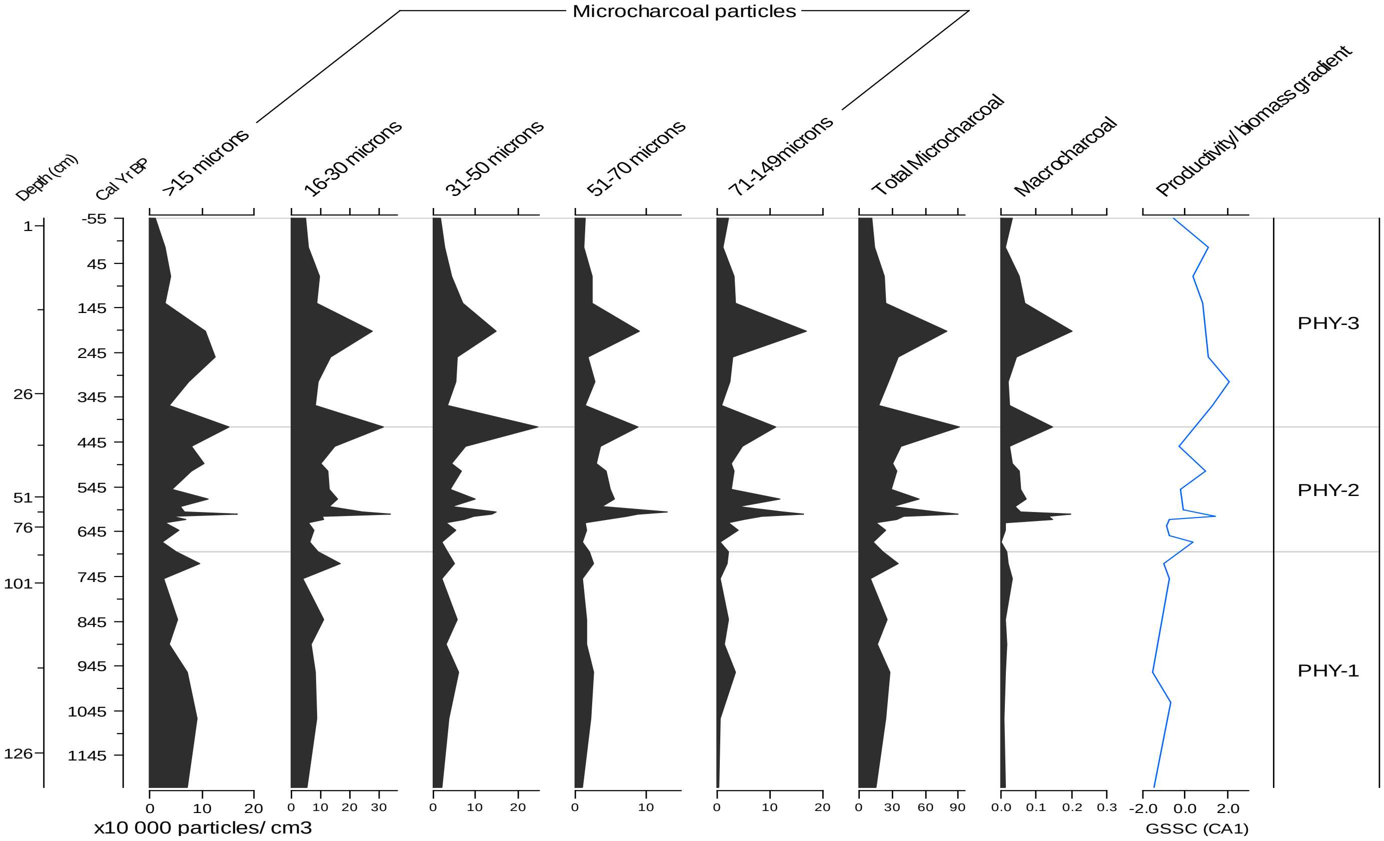

Figure 4.12. Changes in charcoal abundance in vegetation zones at Blood River Vlei plotted alongside the phytolith CA scores for the primary axis.

4.3.8 Reconstructing grazing intensity and grass mosaic states with spores

Grazing intensity or pressure, which increases from tallgrass to shortgrass mosaics, was reconstructed with an ordination of spores. *Sporormiella*, *Cercophora* and *Chaetomium* spores were negatively associated with the primary axis (NMDS1) of the ordination (Figure 4.13). An acceptable ordination stress value of 0.21 was found for the two-dimensional solution. *Coniochaeta lignaria*, *Gelasinospora*, *Podospora*, and *Sordaria* types were positively related to the primary axis. *Coniochaeta lignaria*, shared by all samples, was the least useful for separating samples. *Delitschia* were more negatively associated with the primary axis while *C. gamsii* was positively related to local positive values along the primary axis. The abundance of *Sporormiella*, *Glomus*, *Sordaria*-type 55b increased along the secondary axis while *Cercophora*, *Sordaria*, and *Chaetomium* decreased. There was no clear separation of spores with phytolith vegetation zones, but the vector-fitted line of spore sums was negatively correlated with the primary axis ($r^2 = 0.422$, *p-value* < 0.0008).

Sporormiella and *C. lignaria* were inversely related to the primary ordination axis (Figure 4.14). The regressions were significant for *Sporormiella* (*null deviance* = 137 950, *residual deviance* = 52 460, *d.f. residual* = 28, *p-value* = 0) and *C. lignaria* (*null deviance* = 266 630, *residual deviance* = 236 100, *d.f. residual* = 28, *p-value* = 0.089), with variances of 2 110 and 9 290 respectively (Table 4.6). Thus, the primary axis (Dung spores NMDS1) was considered a grazing intensity or grass productivity/biomass gradient, indicative of state transitions from tallgrass to shortgrasses.

Significant differences in grazing intensity represented by spores NMDS1 were found among vegetation states ($H = 7.92$, $d.f. = 2$, *p-value* = 0.019; Table 4.7). No differences in productivity were found between the tallgrass states but they differed from the shortgrass state

(Table 4.7). However, no significant correlations were found between GSSC CA1 (disturbance gradient) and grazing intensity from dung spores NMDS1 (*r* = 0.039, *d.f.* = 15, *p-value* = 0.883), and between grazing intensity and the GSSC CA2 biomass gradient (*r* = -0.294, *d.f.* = 15, *p-value* = 0.252).

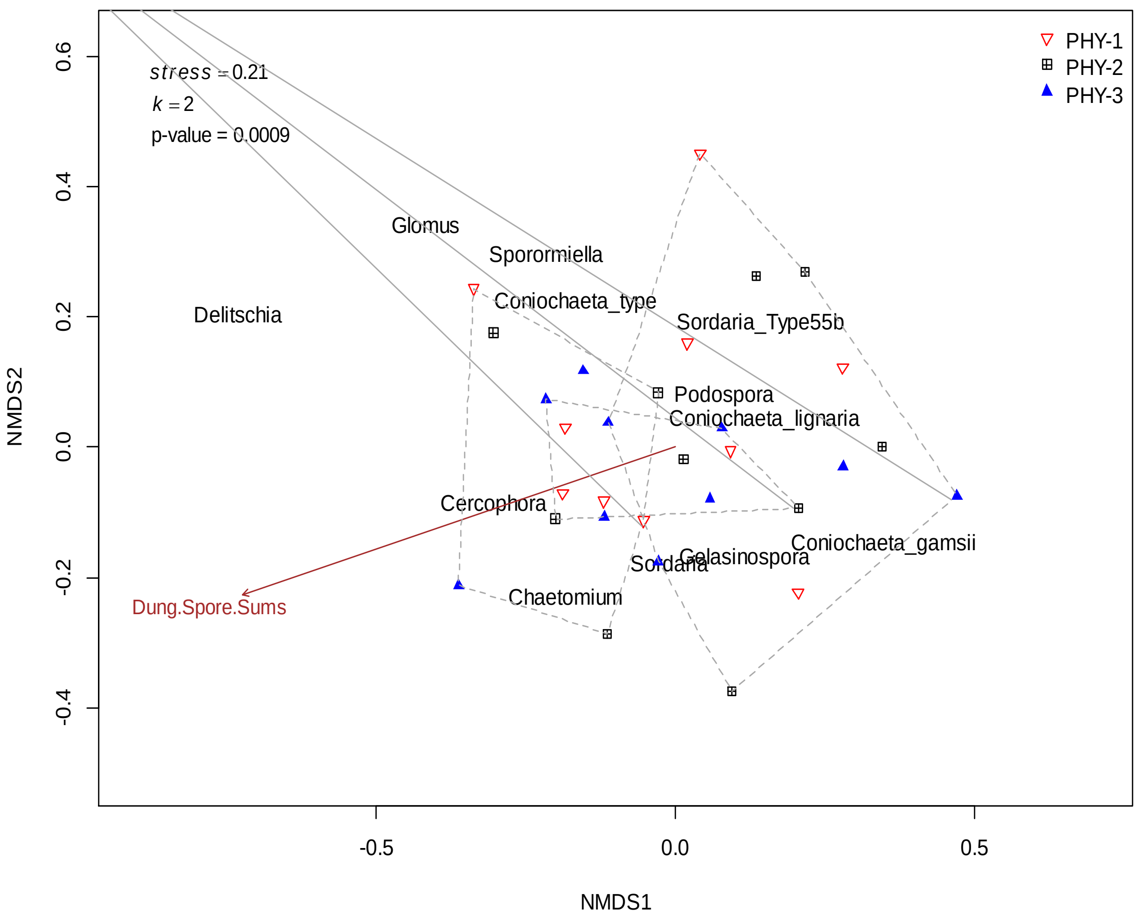

Figure 4.13. NMDS ordination of the dung spore assemblage showing grass phytolith vegetation zones and with convex hulls around dung spore zones.

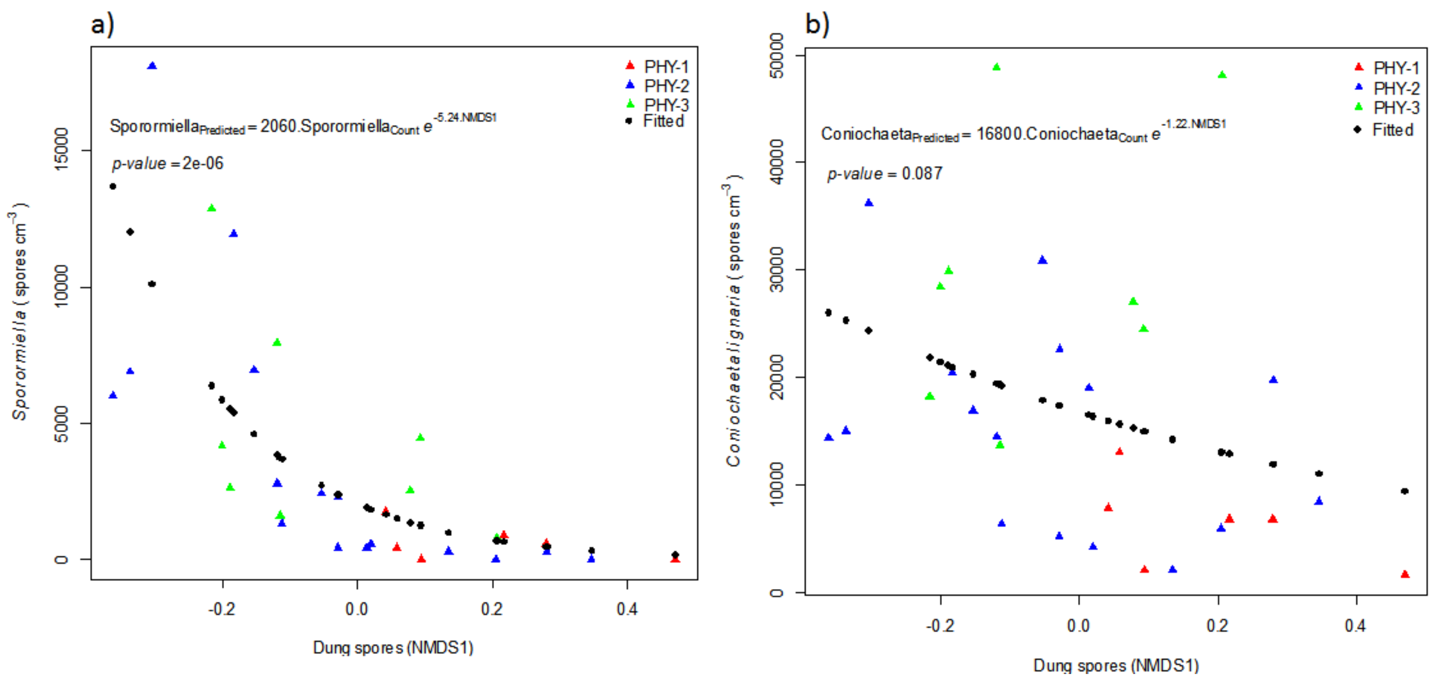

Figure 4.14. Relationships between *Sporormiella* (a) and *Coniochaeta lignaria* (b) spores with the primary axis (NMDS1) of the dung spore ordination.

Table 4.6. Relationships between *C. lignaria* and *Sporormiella* abundance with the dung spore's primary axis (dung spores NMDS1) (Figure 4.15)

Dependent variable	Parameters	Coefficients	Std. Error	t-value	*p-value*
Sporormiella	Intercept	2 060	0.139	37.8	< 2e-16
	Dung spores (NMDS1)	-5.24	0.882	-5.94	2.15e-06
Coniochaeta lignaria	Intercept	16 710	0.139	70.1	<2e-16
	Dung spores (NMDS1)	-1.22	0.686	-1.774	0.087

Table 4.7. Comparisons of local grass productivity deduced dung spore abundance primary gradient (dung spores NMDS1) among vegetation states using the Tukey and Kramer (Nemenyi) *post-hoc* test of dung spores NMDS1 rank sums and Tukey distribution of posterior probabilities

	Shortgrass	Mixed tallgrass
Mixed tallgrass	**0.025**	
Wetland tallgrass	**0.048**	1

4.3.9 Reconstructing fire activity from the charcoal assemblage

Fire activity dependent on grass biomass was reconstructed from the ordination of charcoal fragments. Charcoal particle size and abundance increased along the primary NMDS1 ordination axis (Figure 4.15; $r^2 = 0.82$, $p\text{-value} < 0.00001$). A low stress value of 0.053 suggested the ordination represented similarities in charcoal particle sizes from the sedimentary sequence. Most particles were in the 51-70µm class at the centre of the ordination.

Charcoal abundance increased significantly with the primary ordination axis (*null deviance* = 3 668 240, *residual deviance* = 232 640, *d.f. residual* = 28, *p-value* < 0.00001), with a variance of 8 430 (Figure 4.16; Table 4.8). Statistically significant differences in fire activity represented by charcoal NMDS1 were found among grass states/phytolith zones (*H* = 9.09, *d.f.* = 2, *p-value* = 0.011). Significant differences were found between the shortgrass (*mean* = 0.044, *s.d.* = 0.035) and the mixed tallgrass (*mean* = -0.028, *s.d.* = 0.07) from the Tukey and Kramer test (*p-value* = 0.008).

Table 4.8. The relationship between combined charcoal and the primary ordination axis (charcoal NMDS1) representing fire activity at Blood River Vlei (Figure 4.16)

Parameters	Coefficients	Std. Error	t-value	*p-value*
Intercept	12.5430	0.03386	370.47	**<2e-16**
Charcoal (NMDS1)	9.22590	0.46468	19.85	**<2e-16**

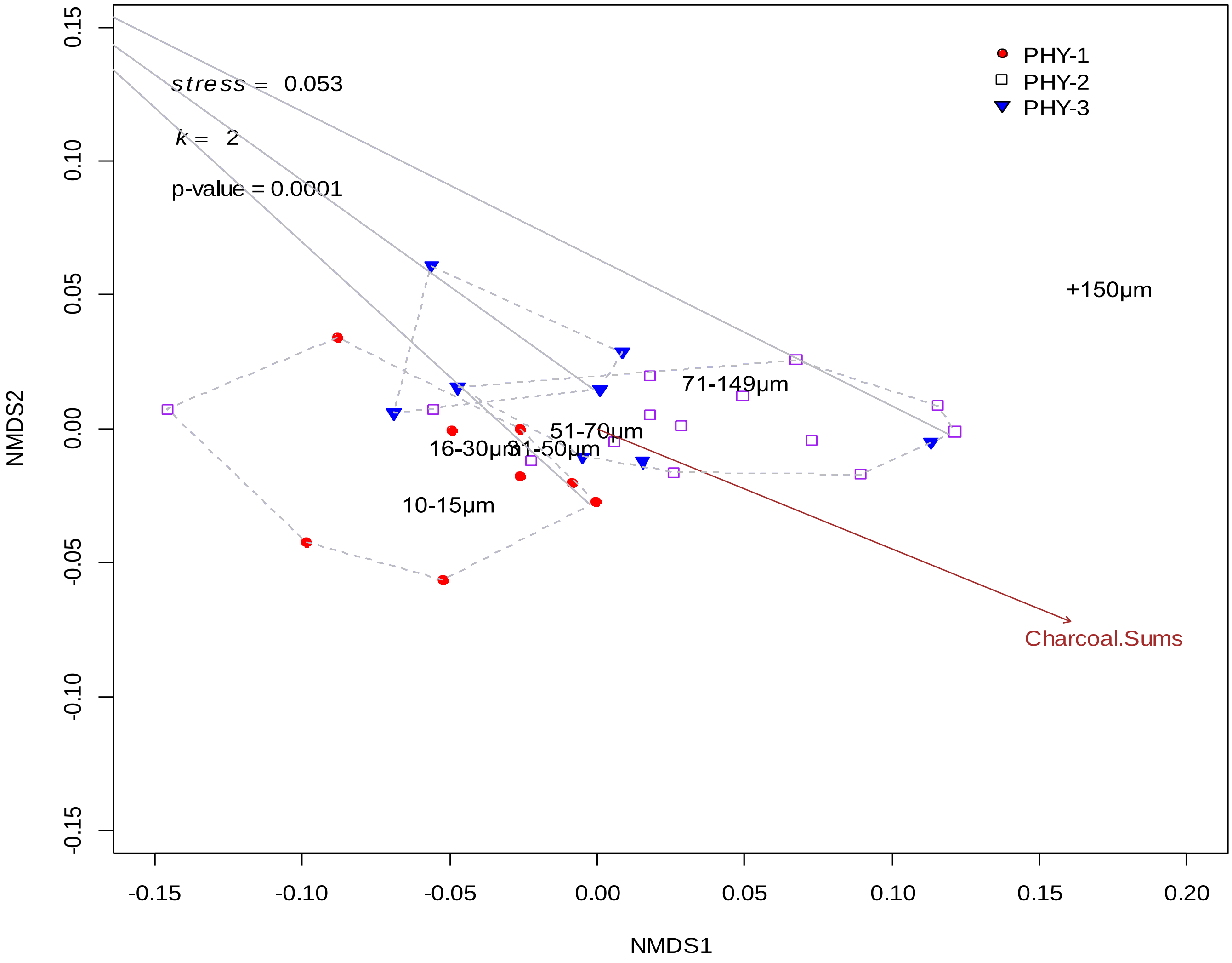

Figure 4.15. The NMDS ordination of charcoal size and abundance with convex hulls showing charcoal zones.

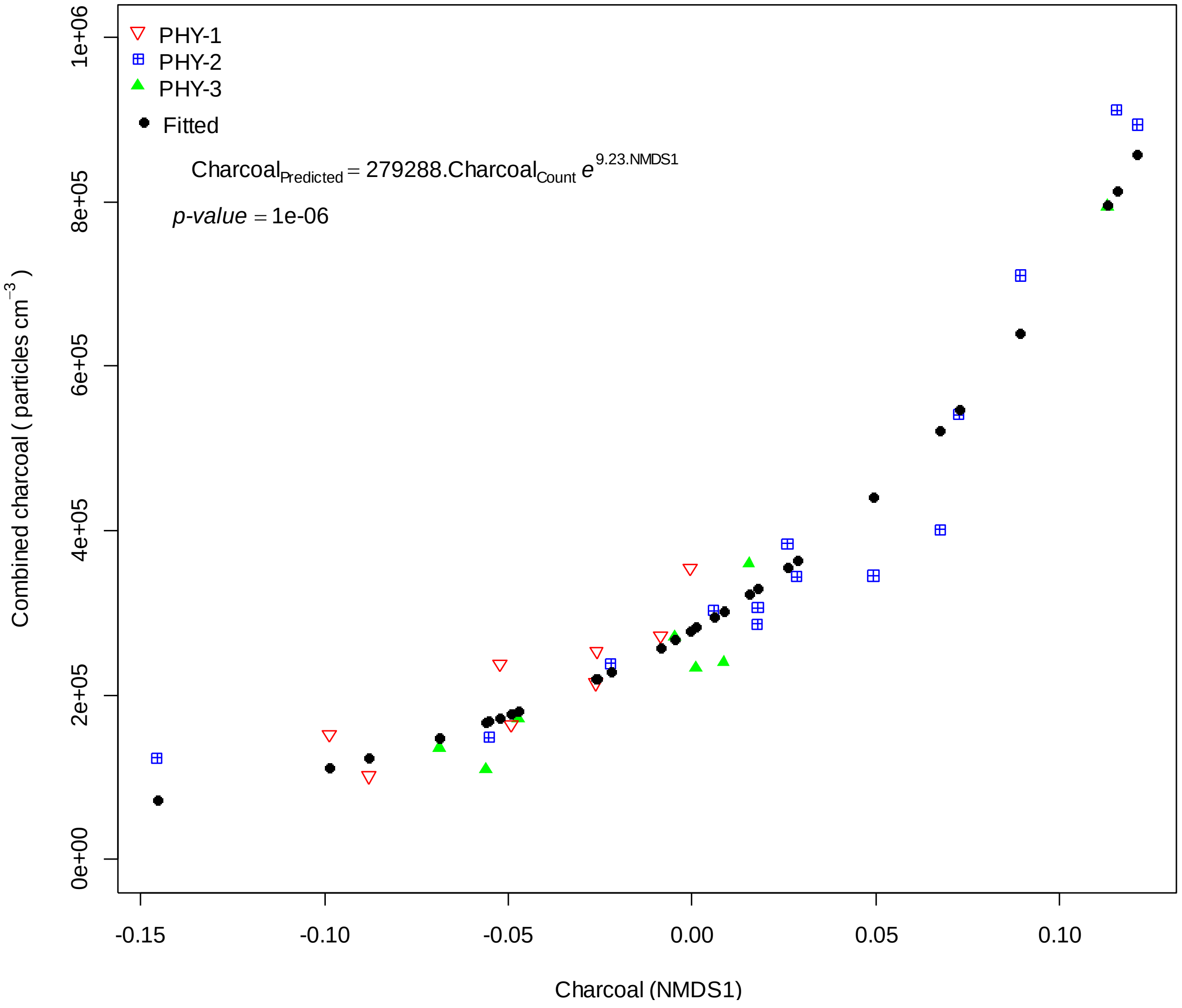

Figure 4.16. Relationship between combined charcoal and primary charcoal ordination axis (NMDS1) at Blood River Vlei. The regression is represented by black dots.

4.3.10 Vegetation dynamics related to fire activity and grazing intensity

Changes in grass states with time were deduced by relating fire activity (macrocharcoal, charcoal NMDS1) to grazing intensity (*Sporormiella*, dung spores NMDS1) (Figure 4.17). Although dung spores NMDS1 and charcoal abundance NMDS1 increased together, there was no significant correlation found (*r* = -0.278, *d.f.* = 28, *p-value* = 0.137; Figure 4.18). However, shortgrass and wetland tallgrass states separated along the main diagonal of the fire activity and grazing intensity gradients; the mixed tallgrass state overlapped with both.

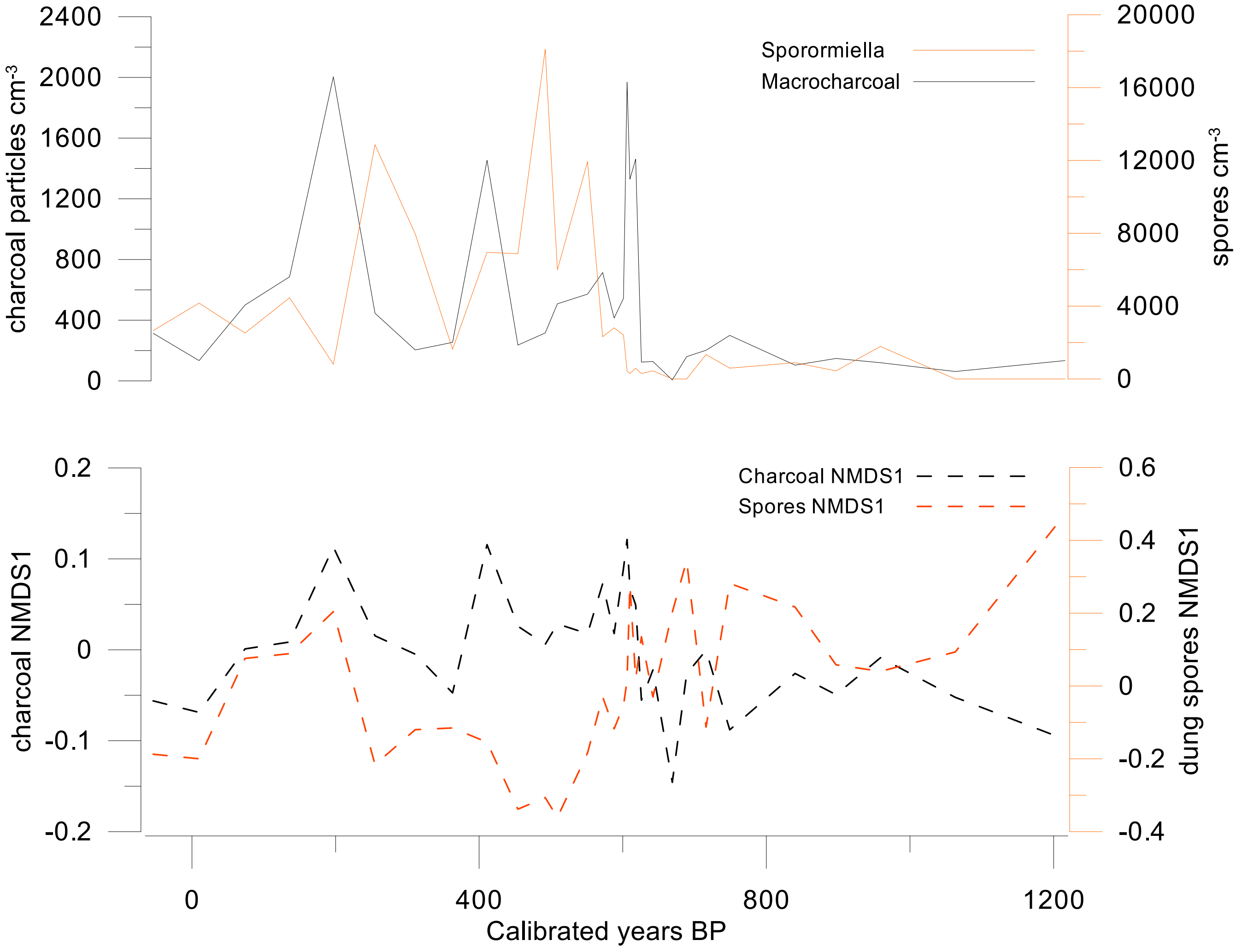

Figure 4.17. Changes in importance of fire activity and grazing intensity with time at Blood River Vlei deduced from a) *Sporormiella* concentration and macrocharcoal concentration; b) charcoal abundance (charcoal NMDS1) and dung spore abundance (dung spores NMDS1) as measured by position on the ordination axes.

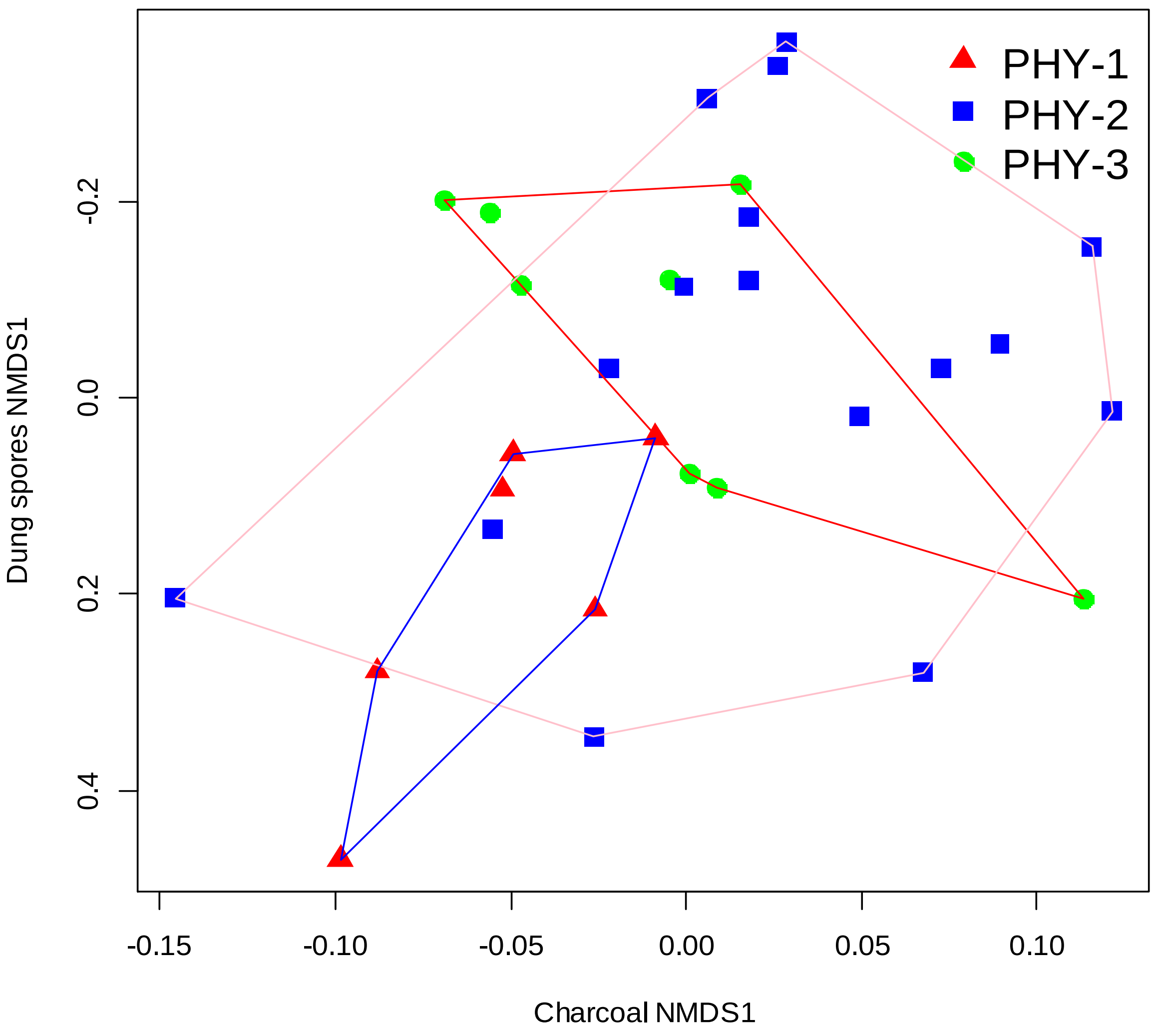

Figure 4.18. Relating vegetation states from phytolith to fire activity (charcoal NMDS1) and grazing intensity (dung spores NMDS1). The dung spore gradient has been reversed to show the direction of the *Sporormiella* increase that reflects grazing intensity.

4.3.11 Soil salinity and erosion from with XRF elemental analysis

The soil elemental concentrations within phytolith vegetation zones were variable (Figure 4.19). Elemental concentrations mostly tracked the patterns in phytolith zones except the middle zone, with correlations indicated in Appendix Three. Overall, there were minor changes in elemental concentrations between ca. 1 220-900 cal BP, but this changed after ca. 900 cal BP, characterised by corresponding and contrasting changes of elemental concentrations. A positive relationship was found between Zr:Rb ratio from the direct core scan and dry powder scans (*r* = 0.725, *d.f.* = 20, *p-value* = 0.0001) but a negative one between Zr:Rb and Mg:Ca ratios (*r* = -0.700, *d.f.* = 14, *p-value* = 0.0027).

Within the shortgrass state, elemental concentrations were stable and high. There were notable peaks of Fe at ca. 1 030 cal BP, and a sharp fall in Fe and Ti from ca. 820-790 cal BP. Increases in Rb, K and Ti from ca. 770-690 cal BP coincided with declines in Zr and Sr.

In the second zone, mixed tallgrass state, concurrent falls in K and Rb from ca. 660-470 cal BP corresponded to increasing Fe. Declines in Ti, Sr, Zr and Zr:Rb ratio concentrations occurred from ca. 690-590 cal BP. The Mg:Ca ratio increased at the transition between zones. Zr:Rb and Mg:Ca ratios were inversely related in this zone.

At the terminal wetland tallgrass state, changes in elemental concentrations mirrored the grass productivity. Despite high concentrations from ca. 410-340 cal BP of most elements, they declined from ca. 360 to -55 cal BP. Declines in K, Rb, Sr, Ti, and Mg:Ca ratio from ca. 340 cal BP happened when Fe concentrations rose with peaks at ca. 260 and 140 cal BP.

4.3.12 Relationships between fire activity and grazing intensity with soil nitrogen in grass mosaics

Nitrogen availability increased from the shortgrass to the mixed tallgrass states based on the relationships between $\delta^{15}N$ and charcoal NMDS1, and between $\delta^{15}N$ and dung spores NMDS1. The wetland tallgrass state was intermediate in nitrogen availability. No correlation was found between dung spores (NMDS1) and $\delta^{15}N$ (*r* = 0.321, *d.f.* = 26, *p-value* = 0.105; Figure 4.20). However, a negative correlation was found between charcoal NMDS1 and $\delta^{15}N$ (*r* = -0.669, *d.f.*= 26, *p-value* < 0.00001; Figure 4.21). There were quadratic linear relationships found between herbivore biomass/grazing intensity represented by *Sporormiella* and TN, and between local fire indicated by macrocharcoal and TN (Figure 4.20). The relationship between *Sporormiella* and TN was significant (r^2 = 0.32, *d.f.* = 25, *p-value* = 0.003; Table 4.8) but it was not significant between macrocharcoal concentration and TN (r^2 = 0.01, *d.f.* = 25, *p-value* = 0.319; Table 4.8).

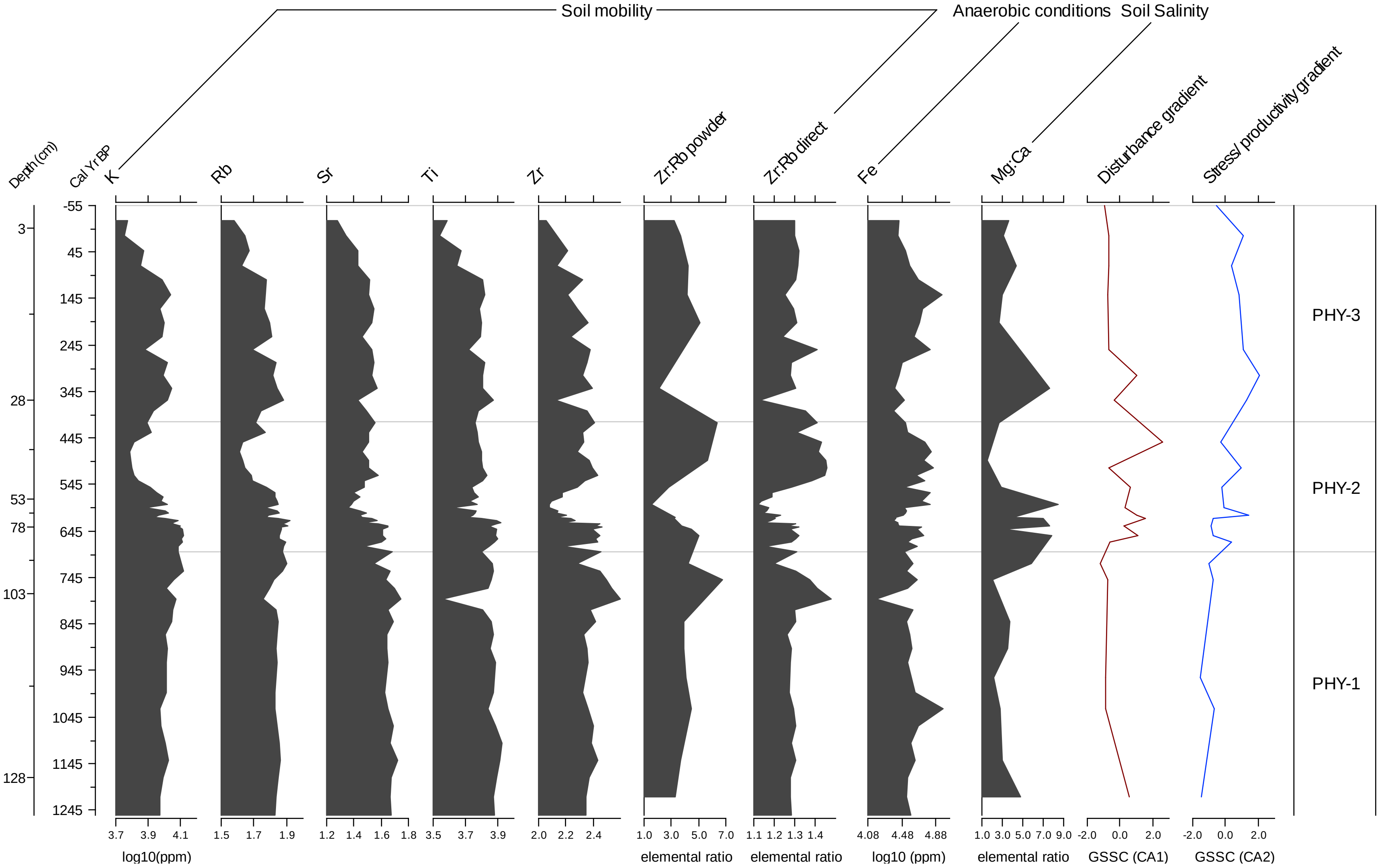

Figure 4.19: Changes in soil elemental concentrations within the grass zones (states) from phytoliths at Blood River Vlei.

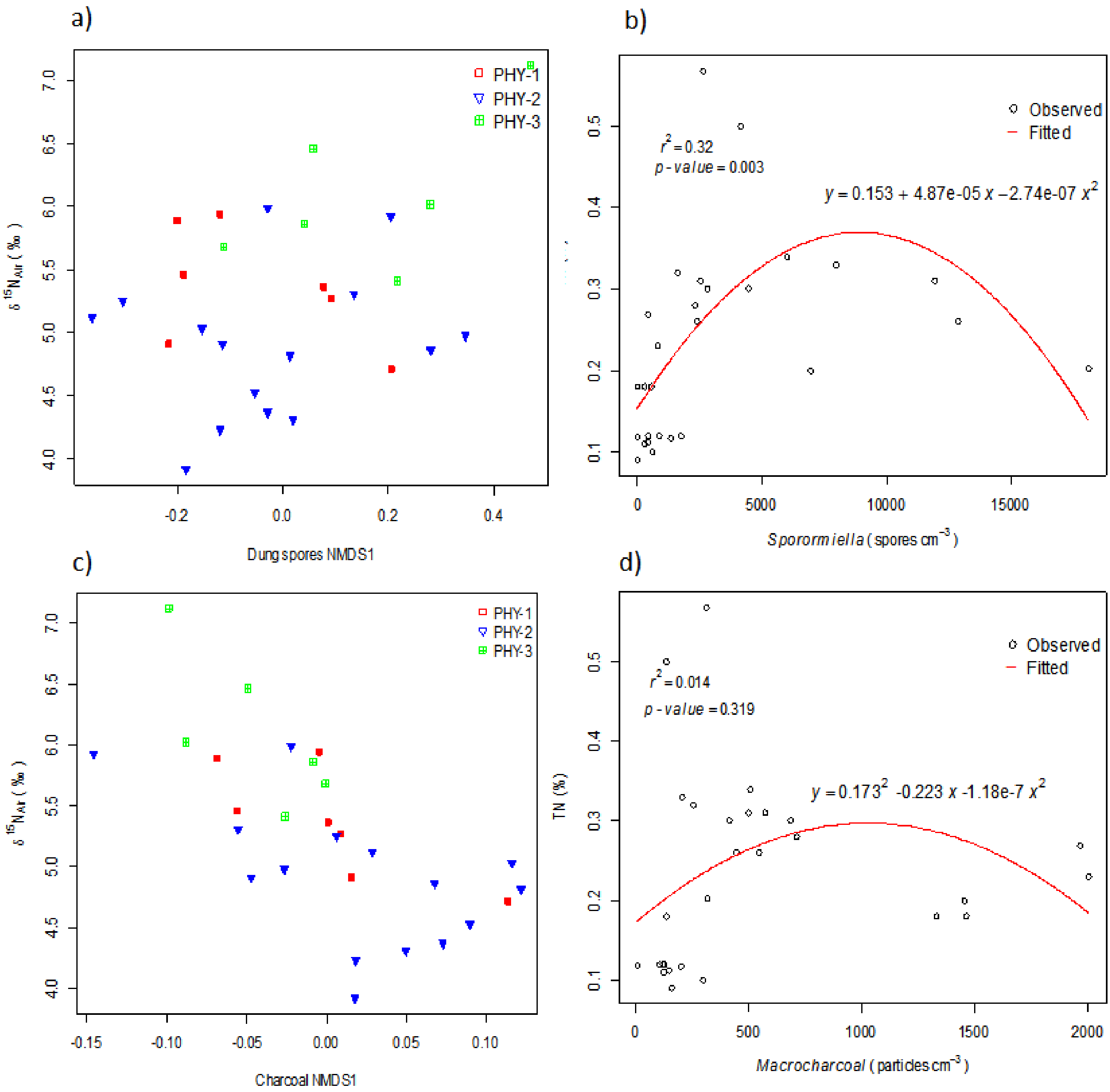

Figure 4.20. Relationships between disturbances and nitrogen. Diagrams a and c) relate nitrogen availability (δ^{15}N) to dung spores NMDS1 and charcoal NMDS1; b and d) relate TN to *Sporormiella* and macrocharcoal.

Table 4.9. The relationships of herbivore biomass (*Sporormiella*) and fire activity (macrocharcoal) to TN at Blood River Vlei

Process	Proxy	Coefficients	Std. error	t-value	Pr(>|t|)	$F_{2, 25}$	*adj.* r^2	*p-value*
Grazing	Intercept	0.153	0.028	5.38	1.45E-05	7.35	0.319	0.003
	Sporormiella	4.87E-05	1.29E-05	3.78	0.001			
	Sporormiella^2	-2.74E-09	8.13E-10	-3.38	0.002			
Fire	Intercept	1.73E-01	4.66E-02	3.70	0.001	1.197	0.014	0.318
	Macrocharcoal	2.43E-04	1.57E-04	1.55	0.134			
	Macrocharcoal^2	-1.18E-07	7.93E-08	-1.49	0.149			

4.3.13 Grazing intensity and fire activity effects on soil stability

Fire and grazer driven effects on wetland grass biomass represented by charcoal NMDS1 and dung spores NMDS1 were either above or below a soil stability (Zr:Rb ratio) value of c. 1.3 corresponding with the shortgrass states (Figure 4.21). However, no significant correlations were found between Zr:Rb ratio with dung spores NMDS1 (r = -0.269, *p-value* = 0.167), and between Zr:Rb ratio with charcoal NMDS1 (r = -0.065, *p-value* = 0.741).

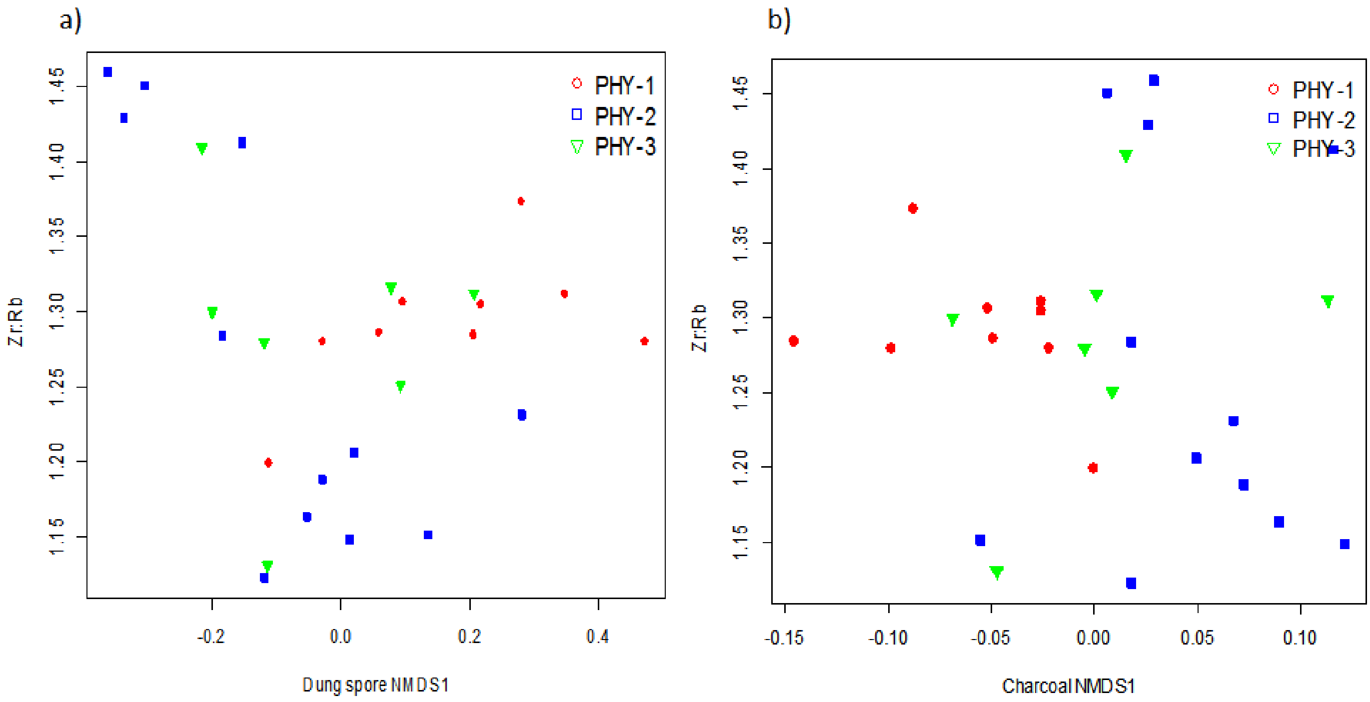

Figure 4.21. The relationships of grazing intensity and fire activity to soil disturbance (Zr:Rb ratio) from dung spore NMDS1 and charcoal NMDS1.

4.4 Discussion

4.4.1 Vegetation dynamics

Grass phytoliths from the montane key resource area suggested a wetland grassland mosaic with multiple stable states in the last 1 250 years (Figure 4.5a, 4.6 and 4.7). Changes in the composition of grass clades in the states are interpreted in terms of soil moisture, grazing pressure, and fire activity. The sequence of states was from shortgrass, mixed tallgrass, to wetland tallgrass.

The shortgrass state that persisted from ca. 1 250-690 cal BP was suggested by the dominance of C_4 Chloridoideae and Panicoideae phytoliths (Figure 4.5a). Low LOI suggested that grass biomass was low. However, high $\delta^{13}C$ values (Figure 4.10) were consistent with C_4 grass dominance (Kotze and O'Connor, 2000; Mucina and Rutherford, 2006). The presence of trees around the wetland was marked by globular phytoliths (Figure 4.9), which suggests that grass fuel was too low to promote fires that kill trees (Bond et al., 2001; O'Connor et al., 2014). Also, heavy grazing and drought may have reduced soil moisture, thus promoting tree establishment around wetlands (Tinley, 1977).

Low grass biomass and high carbonate ($CaCO_3$) values from ca. 960-780 cal BP relative to other zones (Figure 4.10; Table 4.4), plus a high aridity index (Iph%) (Figure 4.9), suggested dry and saline soil conditions typical of grazing lawns (Di Bella et al., 2014; Fox et al., 2015; Jarman, 1972; Veldhuis et al., 2014). However, there was transition to a mixed tallgrass state from ca. 690 cal BP marked by an increase in grass biomass in the landscape.

Shifts in dominance between Panicoideae and Arundinoideae suggested unstable coexistence in the dynamic mixed tallgrass state from ca. 690-410 cal BP (Figure 4.5a). In this dynamic tallgrass mosaic, there was an increase in low biomass C_4 Aristidoideae associated with heavy grazing. *Aristida* grasses usually increase in productive grasslands when fires promote heavy grazing of Panicoideae/ Andropogoneae tallgrasses (e.g., Acocks, 1953; Hempson et al., 2015; Kepe and Scoones, 1999). Independently, peak local grazing highlighted by the sharp transition in the $\delta^{13}C$ vegetation signal (Figure 4.10) to more positive at ca. 510 cal BP coincided with more Aristidoideae. During this period, swings in local grass biomass pointed out by the aridity index (Figure 4.9) matched peaks in soil salinity signalled by the Mg:Ca ratio and carbonates (Figure 4.19, 20). These conclusions suggest that grass subfamilies represent changes in grazing pressure and local moisture.

The dynamic tall grassland also suggested that high fire activity displaced trees as reflected by the sharp fall in the tree to grass ratio (Figure 4.8). Abundant grass fuel linked with intense fires kill trees and/or seedlings around wetlands and areas in wider landscapes (Bond, 2008a; Evangelista et al., 2016; Just et al., 2015; Vesey-Fitzgerald, 1970; Wakeling et al., 2011).

Phragmites dominated the last grass state from ca. 410 cal BP that included trees. The former was indicated by more Arundinoideae phytoliths and the latter by an increase in the tree to grass ratio (Figure 4.5a and 4.8). While wetland margin C_3 Arundinoideae and Pooideae grasses were stable, C_4 Aristidoideae disappeared from this part of the landscape from ca. 260 cal BP. The increase in tree cover from ca. 260-140 cal BP may have been related to dry climate conditions or reduced fire because it coincided with low regional rainfall and low charcoal abundance (Figure 4.23). Also, since fire return intervals are longer around wetlands (Just et al., 2015; O'Connor et al., 2011), trees have time to establish (e.g., Wakeling et al., 2011).

Interestingly, tree encroachment of wetlands by *V. sieberiana* in the region is considered recent (e.g., Acocks, 1953; O'Connor et al., 2014). However, the montane grassland site suggests there have been periods of high tree abundance in last 1 250 years.

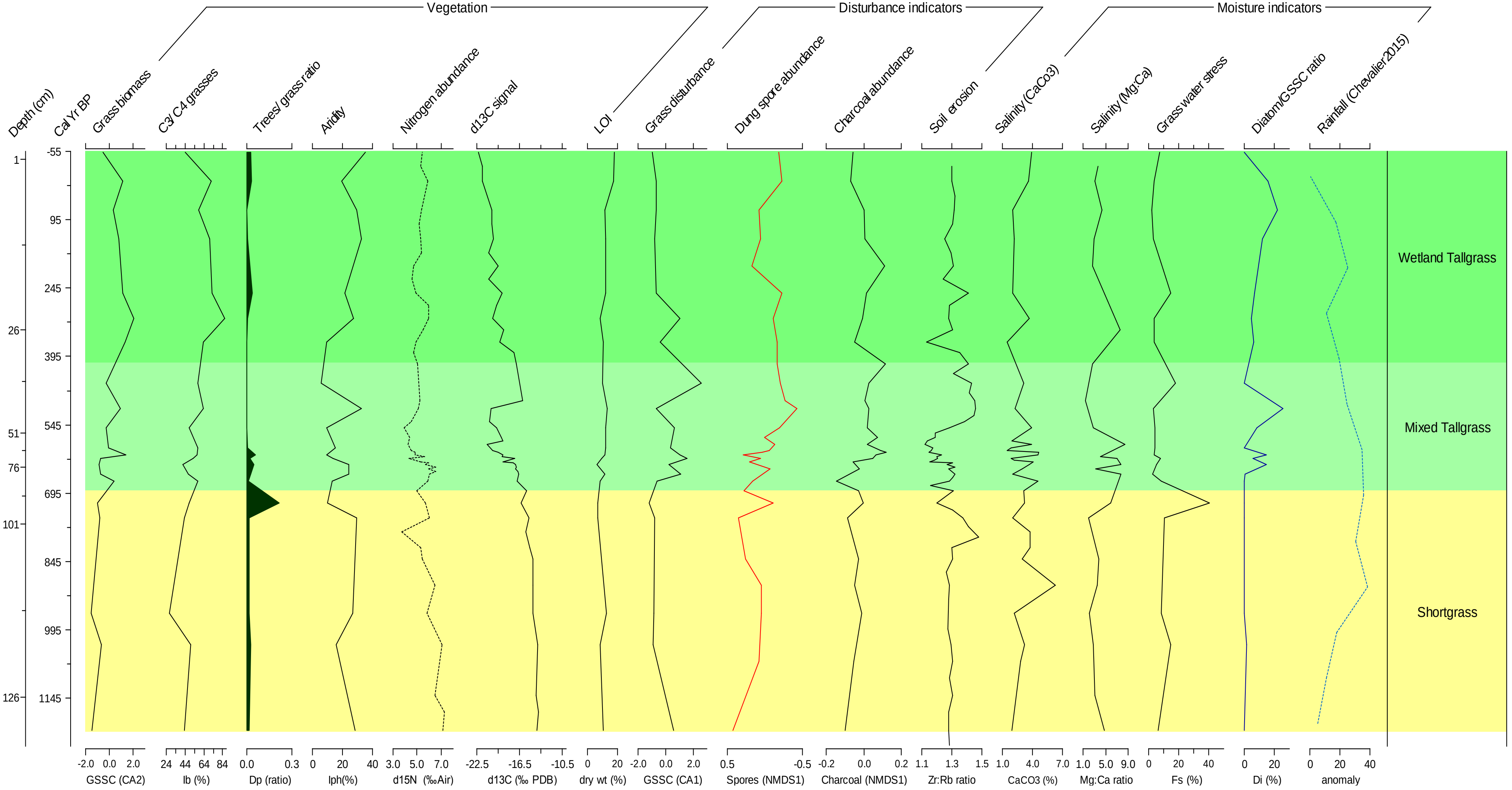

Figure 4.22 Multiple proxy summary of vegetation, disturbance, soil, and climate from the Blood River Vlei sedimentary sequence.

4.4.2 Drivers of vegetation transitions and multiple states at the key resource area

The multiple proxy data suggest that transitions among stable states of grass biomass were driven by the interplay among regional rainfall, landscape fire activity, local grazing pressure, and local soil moisture (Figure 4.24). At the regional scale, heavy grazing delayed the recovery of tallgrasses when rainfall increased from ca. 1 200 cal BP. This was suggested by the presence of *Sporormiella* and dry soil conditions signalled by few diatoms. (Figure 4.23).

However, low rainfall in a tallgrass mosaic from ca. 600-300 cal BP increased local grazing pressure following increased fire activity marked by the rise in charcoal. Conditions of high fire and grazing promoted local increases of Aristidoideae and wetland reed grasses. The importance of grazing suggested a key resource area actively controlled with fire suggested its importance to pastoralists. Lastly, since fires increased local grazing pressure, this suggests that flammability of tallgrasses was related to the palatability of grasses (Figure 4.23). The following sections describe the drivers of the two transitions among stable states of grass biomass (Figure 4.23).

4.4.2.1 Transition (T1) from shortgrass to mixed tallgrass state [ca. 720-700 cal BP]

The gradual transition from the shortgrass to mixed tallgrass stable state from ca. 720-670 cal BP was driven by positive feedback responses between rainfall and local soil moisture (Figure 4.22). Increased rainfall in the region caused a rise in grass productivity or biomass at the key resource area. This was suggested by the rise in Panicoideae and Arundinoideae phytoliths (Figure 4.5a) and LOI (Figure 4.22). However, moisture varied but remained high as suggested by changes in salinity ($CaCO_3$) and more diatoms (Figure 4.22). High C:N ratios are associated with poor-quality litter from mature tallgrasses with low protein content in tissue compared with carbon (Anderson et al., 2007; Ojima et al., 1994). Thus, the high soil C:N ratios independently supported wet local conditions (Figure 4.10).

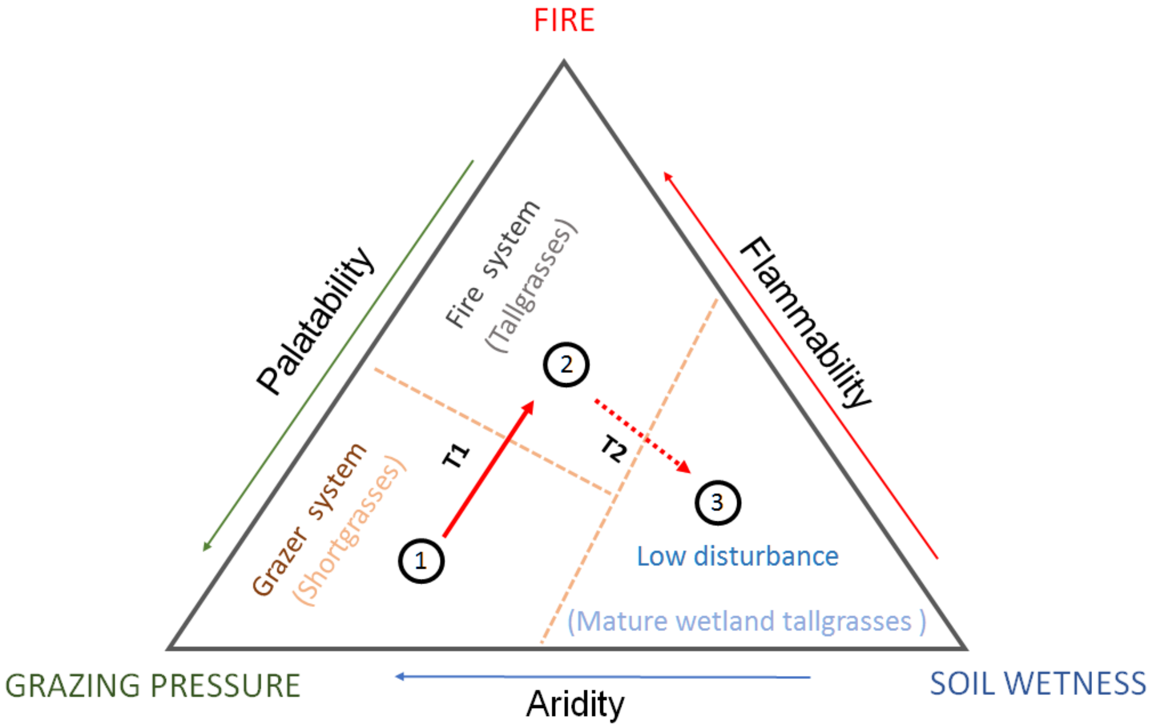

Figure 4.23. Phase space summary diagram of vegetation state-transitions, their drivers, and stability domains at Blood River. Grazing pressure increases shortgrasses by controlling palatability and aridity of soils. In contrast, soil wetness drives fire activity and flammability of tallgrasses. State-phase transitions (T_i) without a threshold are shown by a solid arrow and the threshold by a dashed one.

4.4.2.2 Transition (T2) from the mixed tallgrass to wetland tallgrass state [ca. 450-310 cal BP]

Drought, fire, and grazing caused a gradual vegetation state phase transition from the mixed tallgrass to wetland tallgrass mosaic from ca. 410 cal BP (Figure 4.22). The regional palaeoclimate rainfall record pointed to dry conditions lasting from ca. 600-300 cal BP (Chevalier and Chase, 2015; Ekblom and Stabell, 2008; Holmgren et al., 1999; Sundqvist et al., 2013). Low regional rainfall led to arid local conditions at the key resource area as suggested by falling elemental iron concentrations (Figure 4.19). In this period, fire and grazing were high as indicated by more charcoal and spores that led to increased soil disturbance marked by a rise in the Zr:Rb ratio (Figure 4.22). The spread of *Phragmites* highlighted by more Arundinoideae leading to the wetland tallgrass state is suggested that depends on disturbance.

However, the rise in diatom counts from ca. 450-70 cal BP, suggesting a rise in local soil moisture, paints a different picture from regional climate (Figure 4.8). First, the data suggest the decoupling of local moisture conditions from regional rainfall. Second, they suggest the role of tallgrass cover in modulating soil water retention at local-scales (Knapp, 1984; McNaughton, 1984). Third, because soil erosion was related to the increase in *Phragmites* reed grasses, moisture must be considered within the context of catchment-level changes. Many wetlands in the region were formed from discontinuities along the *Blood River* in the last 800-150 years when siltation was high in the region (Tooth et al., 2014). Thus, the cut-off basins along the rivers experienced different hydrological conditions from the main river. Therefore, local wetland hydrology does not necessarily reflect changes in regional rainfall.

4.4.3 Evidence of multiple grass states and stability domains

The vegetation states suggest multiple stability domains of grass biomass along gradients of local soil moisture, fire, and grazing. Unlike previous sediment proxy studies focusing on relationships between herbivore densities and vegetation (Ekblom and Gillson, 2010b; Gill et al., 2009; Lejju et al., 2005), changes in grass biomass within vegetation states were evaluated in terms of consumer control. Heavy grazing in dry periods and continuous grazing in general, were expected to suppress grass biomass and alter soil functioning (e.g., Bell, 1971; Fynn et al., 2015; Illius and O’Connor, 2000). This section discusses grass states at the key resource area with stability domains.

Grass states discussed in section 4.1 are here considered multiple stable states driven by interactions among soil moisture, fire, and grazers. Two distinct vegetation states and one overlapping with both were suggested by the ordination of grass phytoliths (Figure 4.6b).

They were also independently supported by the relationship between fire activity and grazing intensity from gradients of spores and charcoal (Figure 4.18).

The shortgrass and wetlands tallgrass states were distinct in terms of relative grass biomass indicated by the gradient of grass subfamilies. Still, tallgrass states had common taxa (Figure 4.6b; Figure 4.24). Sharp soil moisture gradients around wetlands (e.g., Keddy, 1984; Kotze and O'Connor, 2000; Lock, 1972; Vesey-Fitzgerald, 1970), are important for structuring grass communities. As expected, plant size and biomass increased from Chloridoideae to Panicoideae to Arundinoideae phytoliths, matching the sequence of changes in biomass of grass states. The overlap between the mixed tallgrass and wetland tallgrass states suggests continuous and comparable biomass despite its variability in mosaics of the former (Figure 4.10; *p-value* = 0.06). This suggests on the one hand that climate is considered a key driver of biomass around wetlands (Barboni and Bremond, 2009; Bremond et al., 2005). However, heavy grazing can override it when controlling grass communities (van Coller and Siebert, 2015; Waldram et al., 2008).

Heavy grazing and aridity (soil moisture) controlled increases of Chloridoideae shortgrasses (Figure 4.7), suggesting they promoted grazing lawn patches (Cromsigt and Olff, 2008; McNaughton, 1984; Veldhuis et al., 2014). Loss of grass cover in heavily grazed soils increases aridity because of sharp temperature gradients that favour shortgrasses (e.g., McNaughton, 1984; Pietola et al., 2005; Veldhuis et al., 2014). Therefore, spores alone are not enough for examining grazing pressure because they do not preserve well in dry soils (Moore et al., 1994). Also, the relationship between grazing and fire on grass biomass suggested by charcoal and spore gradients gave insight into stability.

Fire activity was limited in the shortgrass state and wetland tallgrass states as pointed out by negative values along the charcoal gradient (Figure 4.18). There was not enough fine fuel in the former state left by heavy grazing (Archibald et al., 2005b; Waldram et al., 2008), and less flammable grass fuel in the latter extinguished fires spreading from landscapes (O'Connor et al., 2011; Simpson et al., 2016; Vesey-Fitzgerald, 1970). Increases in soil wetness in the wetland tallgrass states were supported by the abundance of diatoms (Figure 4.22).

Charcoal poorly represented the importance of fires in the mesic grassland. For example, charcoal was highest in the dynamic mixed tallgrass state dominated by C_4 tallgrasses and reeds that experienced frequent fire and grazing (Figure 4.12). This was surprising since fire dominates control of grass production in mesic grasslands (Archibald and Hempson, 2016; Balfour and Howison, 2001; O'Connor et al., 2011). Fires increased following rainfall increases from ca. 1 200-600 cal BP in the region that caused a rise in local grass biomass (Chevalier and Chase, 2015; Figure 4.22). In the following dry period from ca. 600-300 cal BP, pastoralists present in the region may have used fire to make grasses edible for livestock (e.g., Hall, 1981; Huffman, 2004). The presence of *Aristida* grasses in the dynamic and unstable vegetation state also suggests fires promoted continuous grazing at the key resource area (Kepe and Scoones, 1999). Interestingly, the global decoupling of fire and climate seen in proxy records in the last 200 years is linked to increased human local activities at wetlands (e.g., Marlon et al., 2008).

Grass phytoliths gave a better signal of local grazing pressure compared with spores. More Chloridoideae phytoliths, especially in the shortgrass states, suggested herbivore control of grass production (Lock, 1972; Waldram et al., 2008). However, spores were few (Figure 4.12) suggesting the arid soil conditions from ca. 1 250-690 cal BP marked by low diatom counts affected their preservation (Figure 4.8; Wood and Wilmshurst, 2012).

Although rainfall gradually recovered from the arid phase from ca. 1 400-1 200 cal BP (Chevalier and Chase, 2015), heavy grazing promoted shortgrasses (e.g., Muthoni et al., 2014; Waldram et al., 2008). Since soil moisture affected spore preservation, wet local soils and fires caused later increases in spores (Figure 4.18). Therefore, we must assume that grazing pressure was much higher in the shortgrass state compared to the mixed tallgrass state.

The above explanations suggest three stability states of grass biomass in separate domains controlled by interactions among moisture, fire activity, and grazing pressure. First, a grazer domain is represented by the shortgrass state from ca. 1 250-690 cal BP. Heavy grazing promotes palatable lawns that reduces grass biomass, fuels, and soil moisture. Second, there was a dynamic fire domain represented by the mixed tallgrass state. Mesic climate conditions increase soil moisture which promote grass productivity and high fire activity. Fires attracted grazers, causing intermittent increases in grazing pressure and unstable grass biomass. Last, a low disturbance domain includes the productive wetland tallgrass. Wet conditions at the wetland margin limited grazing effects because of unpalatable reeds that did not carry fires. The persistence of five of the six grass subfamilies in the grass mosaic in the sediment sequence suggests key resource areas are resilient.

4.4.4 Disturbance effects on soil processes

Modification of vegetation by climate and disturbances at the key resource area caused changes in soil nitrogen availability, erosion, and salinity. Nitrogen availability indicated by δ^{15}N was higher in shortgrass compared with tallgrass states suggesting more available nitrogen and herbivore inputs (Figure 4.20a and c). These results supported contemporary studies from grasslands classifying tallgrass fire systems as nutrient-poor and herbivore-driven shortgrass systems as nutrient-rich (Allred et al., 2011; Blair, 1997; Hobbs et al., 1991; Tilman, 1985).

More fire activity and increasing grass biomass lowered soil nitrogen availability (Figure 4.22). Nitrogen availability declined with fire represented by charcoal NMDS1 following the establishment of tallgrasses (Anderson et al., 2007; Figure 4.20c). Surprisingly, plant litter quality represented by low C:N ratios was high in tallgrass mosaics from ca. 600-510 cal BP and at ca. 360-280 cal BP (Figure 4.10). Although low C:N ratios are also associated with aquatic plants in sediments (Leng et al., 2005), here they are linked with wetland grasses because the basin was susceptible to drying, and because the values are similar to those from grazing lawns (e.g., Craine et al., 2009).

Plant litter quality changed with fire and heavy grazing from ca. 590-510 cal BP and 670-640 cal BP in the mixed tallgrass mosaic (Figure 5.10). This suggests that fire increased nitrogen mineralisation (Hobbs et al., 1991). Or herbivores supplemented soil nitrogen with dung and urine (Cromsigt and Olff, 2008; McNaughton et al., 1988; Wal et al., 2004). Alternatively, it could mean that herbivores promote palatable shortgrass patches with low stem to leaf ratios (Hobbs, 1996; McNaughton et al., 1988). Fire and herbivore controls of grass biomass and cover extended to soil stability.

Increases in local gazing pressure and fire removed grasses and increased soil erosion (Figure 4.21b). Most soil disturbance represented by the Zr:Rb ratio happened in the dynamic mixed tallgrass with high fire and grazing. Although tallgrass patches experienced less soil disturbance from 790-690 cal BP compared with shortgrasses, this pattern was not consistent. Interestingly, increases in nitrogen availability coincided with erosion (Figure 4.22). Therefore, nitrogen enrichment at wetlands depends on deposits from herbivores (i.e., dung, urine, grazing) and surrounding soil.

4.4.5 Long-term management of key resource areas in mesic grasslands

Key resource areas are important parts of rangelands where they contribute to herbivore survival while also affecting vegetation and soil processes (Grant and Scholes, 2006; Illius and O'Connor, 1999). In mesic grasslands, duplex soils are particularly vulnerable to erosion when grass cover is lost (Acocks, 1953; Tinley, 1982; Titshall et al., 2000), suggesting that key resource areas are vulnerable (Illius and O'Connor, 1999). Data from the montane grassland indicates that herbivores used the wetland for at least 1 250 years, a period marked by changes in vegetation and soil. Dry conditions from ca. 600-300 cal BP appear to have been associated with most soil disturbance happening when pastoralists increased fires and grazing.

Local herbivore effects spread over lengths of rivers with effects on wetland hydrology like siltation, and encroachment by reeds and trees. Modern analogues of the stable states are useful for monitoring benchmarks to the benefit of bird, insect and mammal species (e.g., Station, 1998; van Coller and Siebert, 2015; Walker et al., 2000). However, herbivores affected grass productivity and soils, challenging disequilibrium.

4.4.6 Conclusion

The key resource area idea has implications on the structure, function, and stability of grasslands over long timescales. At the montane grassland, multiple vegetation states were driven by fire, grazing pressure, and soil moisture along grass stability domains affected nitrogen cycling and soil erosion. Heavy grazing reduced grass biomass by supporting a shortgrass state from ca. 1 250-690 cal BP associated with more available nitrogen and saline soils. The unstable mixed tallgrass state from ca. 690-410 cal BP replaced shortgrasses driven by variable rainfall, disturbance, and soil moisture. There were increases in grass productivity, grazing pressure, fire activity, and soil erosion. The wetland tallgrass state from ca. 410 cal BP to present had reduced fire and grazing because of reeds. The data provide support for the idea that herbivores control some levels of grass productivity and soil, especially in dry periods.

Key resource areas are important for keeping livestock and wildlife in dryland ecosystems, as fragmented modern landscapes limit dispersal by animals. Still, grazer driven soil erosion in fragile grassland soils remains a challenge. As a management strategy, burning is unsuitable because it may increase negative effects of herbivores on vegetation and soils. Management of grazer densities and types offer a better approach for controlling grass productivity. However, changes in rainfall and land use are primary drivers of density-dependent local herbivore effects on vegetation. Importantly, fires became necessary for suppressing grass productivity at later stages.

Chapter Five. **Fire and grazing as alternate consumers of grass biomass in a savanna park**

5.1 Introduction

In savannas, rainfall and disturbances by fire and grazing are important drivers of vegetation dynamics and ecosystem functioning (Anderson et al., 2007; Huntley, 1982; McNaughton, 1983; Scholes and Archer, 1997). These drivers regulate grass production (Allred et al., 2011; Archibald et al., 2005b; Waldram et al., 2008), tree *versus* grass dominance (Ekblom and Gillson, 2010b; Scholes and Archer, 1997; Walker et al., 1981), and nutrient cycling (Allred et al., 2011; Blair, 1997; Hobbs, 1996). Indigenous herbivores in African savanna parks cause shifts in vegetation states from woodland to open grassland (Dublin et al., 1990; Walker et al., 1981; Wiegand et al., 2006), and from tallgrasses to grazing lawns (Hempson, Archibald, Bond, et al., 2015; McNaughton, 1984; Waldram et al., 2008). However, our understating of ecological drivers of shifts among persistent vegetation states and their effects on soils is limited at long timescales.

Alternate stable vegetation states driven by many spatial and temporal drivers occur as discrete units in mosaic landscapes (Bormann and Likens, 1979; Connell and Sousa, 1983; Gillson, 2015; Staver et al., 2011). In rangelands, herbivores at high densities support patches with short-statured, palatable, and arid-adapted shortgrasses (Lock, 1972; Veldhuis et al., 2014; Vesey-Fitzgerald, 1970; Waldram et al., 2008). These grazing lawns are remarkably persistent (McNaughton, 1984; Veblen, 2012). In comparison, rainfall and wet soils support tallgrass patches (Bell, 1971; Rietkerk et al., 2000; Vesey-Fitzgerald, 1970; Waldram et al., 2008). However, unreliable rainfall, fire, and grazing cause unstable grass biomass and vegetation states (Vetter, 2005; Westoby et al., 1989).

Stability domains of grass biomass are useful for identifying dynamic vegetation phases and resilience based on reactions of grass communities to rainfall, fire, and disturbances (Perrings and Walker, 1997). Tallgrass and shortgrass mosaics represent fire/rainfall and grazer domains, from high to low grass biomass, respectively (Allred et al., 2011; Archibald, 2008; Waldram et al., 2008). Resilience of grass states in phase domains, i.e., a measure of their ability to withstand disturbance without transitioning to another level of biomass, depends on collective traits of the grass community (Belsky, 1992; Hempson, Archibald, Bond, et al., 2015; McNaughton, 1977; Walker et al., 1999).

Tallgrass phases resist grazing by growing fast and tall (Belsky, 1992; Forrestel et al., 2015; Grime, 1977). Many tallgrasses are flammable and depend on fire to regenerate. However, re-grazing promoted by fire leads to the loss of reproductive flowering parts and decline in tallgrasses (Augustine and McNaughton, 1998; O’Connor, 1991). In comparison, short-statured, clonal and palatable lawn grasses with intercalary meristems located at the base benefit from continuous heavy grazing (Lock, 1972; van der Plas et al., 2013; Veldhuis et al., 2014; Waldram et al., 2008). Functional grazing assemblages where herbivores help each other in turn to suppress grass biomass are important for maintaining grazing lawns (Arsenault and Owen-Smith, 2002; Cornelissen and Vulink, 2015; Cromsigt and Olff, 2008; Vesey-Fitzgerald, 1960). Mega-grazers like white rhino (*Ceratotherium simum*) are particularly skilled in supporting the development of lawns (Owen-Smith, 1988; Waldram et al., 2008).

However, reorganisation of grass species and herbivores after increased disturbances may result in a vegetation state phase transition or threshold along a biomass gradient (May, 1977; Noy-Meir, 1975; Rietkerk and van de Koppel, 1997). Overuse of grazing resources by indigenous and domestic herbivores cause catastrophic shifts in vegetation toward persistent phases with very low grass biomass and/or cover, degraded soils and reduced nutrient cycling

(Abel and Blaikie, 1989; Sinclair and Fryxell, 1985; van de Koppel et al., 1997). Prevention of undesirable ecosystem states is a rangeland management goal based on understanding drivers of vegetation transitions. The natures of phase transitions (gradual *versus* abrupt) representing regime shifts between fire and herbivore phases are poorly understood at long timescales.

Key resource areas are centres of ecological regime shifts because grazer populations in surrounding landscapes depend on wetland grass production (Illius and O'Connor, 1999; Scoones, 1991; Vetter, 2009a). Thus, the locales support herbivores during critical dry climatic periods when grass quality and quantity decline in wider landscapes. However, resilience of key resource areas is subject to debate because of their potential for overuse, transitioning to low grass cover, soil aridity and erosion that signal degradation (Gillson and Hoffman, 2007; Illius and O'Connor, 1999; Muthoni et al., 2014; Owen-Smith, 1996; Rietkerk et al., 1997; Scoones, 1991; Sullivan and Rohde, 2002; Vetter, 2009a).

In this chapter, I present a c. 1 050 years multiple proxy sedimentary record from a savanna key resource area in Hluhluwe-iMfolozi Park (HiP), South Africa. Diverse and plentiful indigenous herbivores live in the park proclaimed in 1895 (McCracken, 2008; Owen-Smith, 1988). However, Iron Age farmers and pastoralists from ca. 1 650- 80 cal BP also occupied it (Hall, 1981; Huffman, 2004). I use stability domains of grass biomass to assess persistent grass states (tallgrass *versus* shortgrass) and soil processes, shifts among states, and resilience to changing rainfall, fire, grazing pressure, and people. The multiple proxies used include stable isotopes, sediment organic carbon, fossil spores, charcoal, and soil elemental analyses. I used charcoal and spores to deduce grass states and check them with isotope and elemental signals for soil nitrogen cycling, aridity, and erosion. I did not use pollen and grass phytolith proxies for vegetation. A regional multiple proxy record (Chevalier and Chase, 2015) gives the context of rainfall for separating local from regional hydrological drivers of wetland grass biomass. The following questions guided the study:

1. Are long-term changes of grass biomass states suggestive of stability domains at key resource areas?
2. How do grass traits related to fire activity and grazing pressure, separate vegetation states and consumer domains?
3. How does disturbance and fire affect nitrogen availability and soil erosion at the key resource area?
4. Are vegetation states at the key resource area resilient to local disturbance and regional rainfall variability?
5. What are the implications of ecological resilience of multiple grass states on the long-term management of savanna landscapes?

5.2 Methods

5.2.1 Study area

The study area is found in HiP, a mesic to semi-arid savanna in KwaZulu-Natal, South Africa (Figure 5.1). The ~90 000 ha park has a north-south topographic relief and rainfall gradient. Rainfall is higher (700-1 000mm) in the rugged northern Hluhluwe section compared with the drier lowland iMfolozi (Brooks and Macdonald, 1983). The tree-ring climate record for Zululand suggests varying rainfall for the region in the last 1 000 years (Hall, 1976; Tyson, 1971). In addition, multiple proxy regional rainfall records from the beginning of the Holocene c. 10 000 years ago also indicate variable rainfall, with alternating wet and dry cycles (Chevalier and Chase, 2015).

The core was collected near the confluence of the Black and White iMfolozi rivers, in the iMfolozi section of HiP. The key resource area is found in an area with rainfall of c. 635

mm p.a. and mean monthly temperatures ranging from 13-35°C (Balfour and Howison, 2001). African buffalo (*Syncerus caffer*), impala (*Aepyceros melampus melampus*), white rhino, and waterbuck (*Kobus ellipsiprymnus*) are among the many grazers using the wetland grassland (Olsen, 2015).

Grass mosaics in the park are dominated by tall bunchgrasses, but lawn grasses are common in the heavily grazed south (Archibald et al., 2005a; Hall, 1981). Tall bunchgrasses (tallgrasses) are mostly represented by *Themeda triandra*, *Sporobolus pyramidalis*, *Hyparrhenia filipendula* and *Eragrostis curvula*. They occupy the 'sourveld grassland' signified by low palatability in winter (Figure 5.1; Mucina and Rutherford, 2006). *Phragmites australis* at the wetland margin was the only C_3 grass in the landscapes with C_4 grasses. In comparison, lawn grasses (shortgrasses) are disproportionately higher at heavily grazed fertile floodplains (Archibald et al., 2005a; Cromsigt et al., 2017). These hardy grasses include *U. mossambicensis*, *Panicum. coloratum*, *P. deustum*, *Cynodon. dactylon*, *E. superba* and *S. nitens* (Downing, 1974; Hall, 1981). The fertile soils are usually associated with fine-leaf savanna species including *Vachellia karroo*, *V. nilotica*, *V. robusta*, *V. tortilis*, and *Senegalia burkei*, and broad-leaf *Euclea* and *Maytenus* species (Bond et al., 2001; Whateley and Porter, 1983).

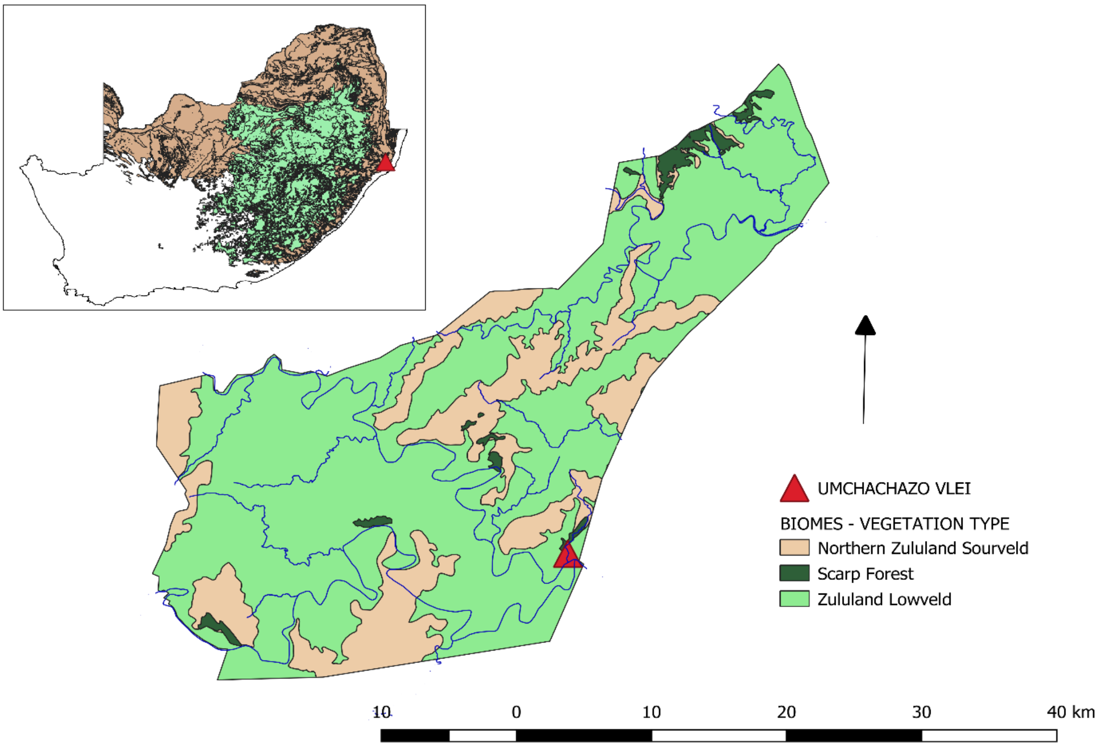

Figure 5.1. The location of the study site (Umchachazo Vlei) in HiP. The biome map for the region is from Mucina and Rutherford (2006).

Figure 5.2. Umchachazo Vlei floodplain grassland at HiP where we collected a sediment core (*picture taken by Lindsey Gillson*).

Although tree cover increased along the riparian zone in the park, it was much lower prior to the 1950s (Brooks and Macdonald, 1983; Hall, 1981; West et al., 2000). Continuous heavy grazing in mesic Hluhluwe is considered one of the drivers of tree invasion leading to the migration of grazers into iMfolozi (Brooks and Macdonald, 1983; Le Roux et al., 2017). White rhino at c. 12 500 kg/km^2 dominate herbivore biomass in the park (Waldram et al., 2008). More herbivore biomass is concentrated in the Umfolozi section with c. 85% of the Serengeti per unit area (Owen-Smith, 2005). Iron Age societies from ca. 1 500-60 cal BP used the area (Hall, 1981), but indiscriminate hunting of indigenous animals happened in the last 200 years (McCracken, 2008). Remnants of some past human settlements have been mapped in the park, especially along the White Umfolozi River valley (Hall, 1981; Penner, 1970).

Herbivore populations are regulated within the park through removals/translocations to safeguard vegetation and ecosystem functioning (Archibald et al., 2005a; Brooks and Macdonald, 1983; McCracken, 2008; Waldram et al., 2008). Herbivore densities in the park before farmers arrived at ca. 1 700 BP are unknown (Hall, 1981). They may have been high and later mingled with that of domestic herbivores. However, trophy hunting and wildlife trade that peaked from 1820-1860 caused heavy losses of indigenous herbivores in the region (Baldwin, 1863; McCracken, 2008). The rinderpest epidemic in the early 20th century also decimated wild and domestic herbivores (Le Roux et al., 2017; McCracken, 2008). However, disease control (i.e., of African trypanosomiasis) from 1929-30 led to killing of many wild herbivores (Le Roux et al., 2017; McCracken, 2008). In this period, control of herbivore populations was given to the Division of Veterinary services from 1930-1950. Fortunately, herbivore densities recovered from the1950s and are now managed using carrying capacity. i.e., the upper limit of herbivores that are supported by the estimated environmental resources (Le Roux et al., 2017; Owen-Smith, 1988).

Fire management policies in the park has changed many times (Balfour and Howison, 2001). Pastoralists living in the park before its establishment in 1895 may also have used fires to promote grazing (Berry and Macdonald, 1979; Hall, 1981). Prescribed burning, i.e., fire control to meet management objectives, was used from the 1950s to increase grass productivity and for clearing woody plants (Archibald et al., 2017; Balfour and Howison, 2001; Downing, 1974). At present, fires are patchy and less frequent at herbivore-dominated Umfolozi where grass fuel loads are low compared with Hluhluwe (Archibald et al., 2005a, 2017; Waldram et al., 2008).

A 203cm sedimentary core was obtained for multiple proxy sediment analyses at Umchachazo Vlei 28°20’38.63” S, 31°58’29.41” E, 50 m.a.s.l, using a vibracorer (Baxter and Meadows, 1999). The sedimentary basin is more than 200m in diameter. Three samples along the core were sent to laboratories for AMS ^{14}C radiocarbon dating. The Troels-Smith method was used to describe the sediment core (Kershaw, 1997). Below are descriptions of methods used for assessing vegetation stability domains and soil dynamics.

5.2.2 Multi-proxy palaeoecological reconstructions

5.2.2.1 Stable isotope analyses

Vegetation dynamics, stability, and soil nutrients were investigated from sediment stable isotope analysis (δ^{13}C, δ^{15}N, C, N, and C:N ratio). An indication of past C_3 and C_4 grass dominance around the wetland margin was based on differences in isotopic discrimination of δ^{13}C during photosynthesis (Fredlund and Tieszen, 1997). δ^{13}C enrichment was related to C_4 tallgrasses and shortgrasses. In contrast, δ^{13}C depletion is generally linked to the dominance of *P. australis* reed grasses, although algae and trees may contribute to the signal (Michener and Lajtha, 2007). Isotopic discrimination of δ^{15}N depends on many factors including: productivity of algae at wetlands (Michener and Lajtha, 2007), nitrogen availability in soils (Craine et al., 2009), dependence on illuviation (inputs to wetland from upland soil), dung and urine deposits (Cromsigt and Olff, 2008; McNaughton et al., 1989), and differences in the decomposition rates of vegetation (Michener and Lajtha, 2007; Wynn and Bird, 2007).

Persistent grass states, tallgrass *versus* shortgrass, were deduced from CONISS cluster analysis of stable isotope data (Bennett, 1996; Ter Braak, 1986). High TC and LOI values indicated tallgrasses that produce much litter (Ingram et al., 2008), but low values suggested either drought (Wang et al., 2015) or heavy grazing (Ingram et al., 2008). The C:N ratio is related to stemminess or lignin content of residual plant tissue (Engloner, 2009; Meyers, 1994; Ojima et al., 1994; Potthast et al., 2010), was used to make guesses about sward height in stands. Mature wetland tallgrasses, particularly *P. australis*, are expected to produce litter with more structural carbon compared to shortgrasses (Engloner, 2009). However, inputs from aquatic and woody plants also influence the C:N ratio (Michener and Lajtha, 2007). Nevertheless, herbaceous biomass should dwarf that of algae or trees at wetland margins dominated by grasses, suggests that C:N signals represent grass dynamics.

5.2.2.2 Charcoal and spore analyses

The influence of fire and grazing pressure on grass states was independently assessed from relationships between spores and charcoal (see Chapter Two section 3.2.5 and 3.2.6). Stability domains of grass biomass suggesting the importance of fire or grazing (Perrings and Walker, 1997), were guessed from ordination gradients of spores and charcoal. Fire is expected to increase with grass biomass, and soil moisture, and peaks in tallgrass states (or mosaics) in landscapes linked with more charcoal (Leys et al., 2015). However, less charcoal may mark rarely burned reed grasses (Just et al., 2015; O'Connor et al., 2011) or its limited spread to wetland grazing lawns (Archibald et al., 2005b; Waldram et al., 2008).

Heavy grazing promotes C_4 shortgrass mosaics that may reduce local soil moisture because of poor cover (Veldhuis et al., 2014). This results in increases of *Sporormiella* (Ghosh et al., 2017; Graf and Chmura, 2006; Hillbrand et al., 2012), and possibly a decline in *Coniochaeta lignaria* linked to soil moisture. Therefore, grazing pressure and fire activity at opposite ends of grass biomass stability domains, also reflect a soil moisture gradient.

5.2.2.3 XRF soil elemental analyses

Herbivore effects on soil stability and macronutrients were investigated with stable isotopes and XRF elemental analyses. Heavy grazing, trampling and soil compaction around the wetland margin was expected to reduce grass biomass, soil porosity and water infiltration (Pietola et al., 2005; Rietkerk et al., 1997; Schrama et al., 2013). Therefore, soil disturbance pointed out by a rise in the Zr:Rb ratio (Schillereff et al., 2014), would increase because the erosive force of water is higher over bare surfaces. Erosion and compacted soils on the other hand reduce nitrogen availability in soils (Rietkerk and van de Koppel, 1997; Schrama et al., 2013). However, soil salinity is evidenced by calcium, magnesium, and potassium salts associated with compacted soils (Craine et al., 2009; Seagle and McNaughton, 1992; Stock et al., 2010), and dry conditions (Gill et al., 2012). In contrast, moist clayey sediments/soils contain more iron (Tinley, 1982).

5.3 Results

5.3.1 Sediment dating and age-depth model

Radiocarbon dates from three subsamples taken along the core were analysed for AMS^{14}C at Beta Analytic (Table 5.1). Dates were calibrated using the Southern Hemisphere Calibration Curve SHCal13, then used to develop an age-depth model for the core (Hogg et al., 2013). The top 30cm of sediment of the 233cm depth with dense roots was excluded. However, a false depth of 0cm was included in dates for the year 2011. Piece-wise linear regression was used to create an age-depth model with sampling at 0.5cm intervals in Clam2.2. (Blaauw, 2010; Figure 5.3). Interpolated age estimates for the 95% confidence interval age-depth model ranged from 4-243 years, with a mean 140 years based on the maximum posterior probabilities of the calibrated ages (Blaauw, 2010; Figure 5.3). Interpolated ages (cal BP) increased with depth along the core.

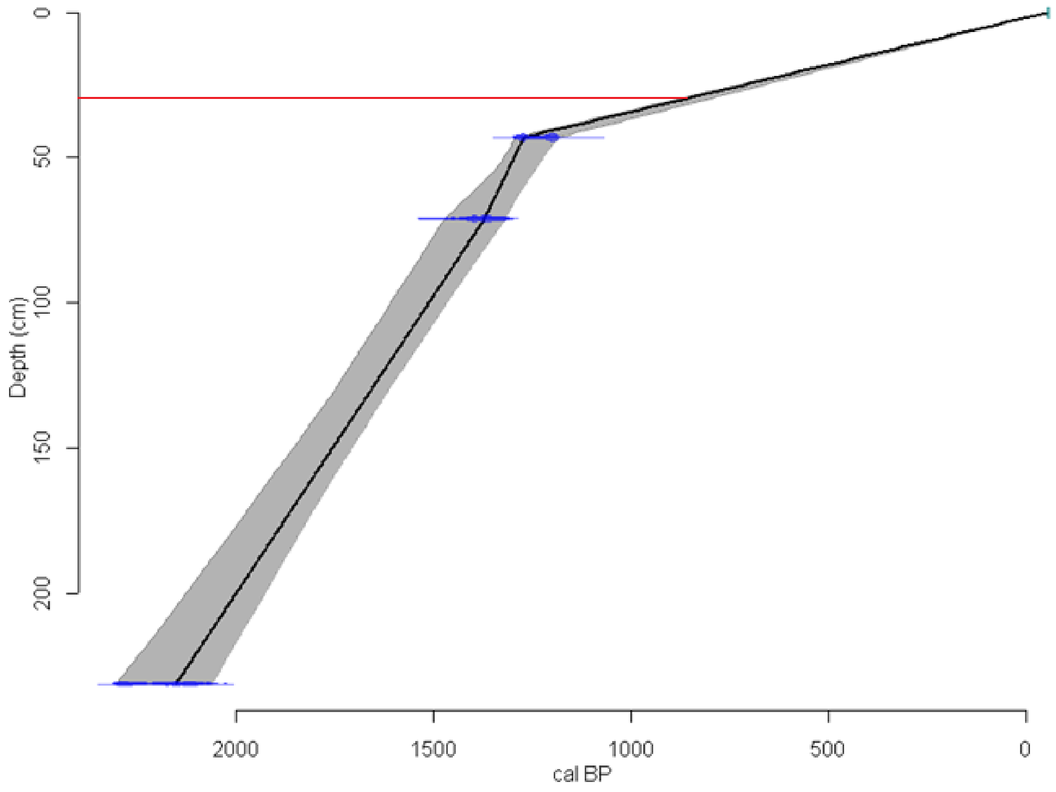

Figure 5.3. Piece-wise linear age-depth model for Umchachazo Vlei. Age estimates are shown by the solid black line and 95% confidence limits in grey. Dates below the red line match with the analysed bottom section.

Table 5.1. Calibrated radiocarbon ages and calendar dates for the Umchachazo Vlei core from the Southern hemisphere calibration curves (Hogg et al. 2003)

Lab	**Collection ID**	**Lab ID**	**Depth (cm)**	**Humin $\delta^{13}C$ (‰)**	**Radiocarbon age**	**95% CI calibrated radiocarbon ages**	**Probability (%)**	**95% CI calendar dates**	**Probability (%)**
BETA	UM13	Beta-410179	43	-17.7	1 360 ± 30 BP	1 184-1 295 cal BP	95	666-766 AD	95
QUB	UM41	UBA-26949	71	-17.5	1 538 ± 32 BP	1 307-1 433 cal BP	93	517-643 AD	93
						1 442-1 454 cal BP	1.4	497-508 AD	1.4
						1 462-1 468 cal BP	0.6	482-488 AD	0.6
BETA	UM201	Beta-410176	231	-15.4	2 200 ± 30 BP	2 060-2 074 cal BP	2.3	125-111 BC	2.3
						2 078-2 211 cal BP	58	262-129 BC	58
						2 222-2 307 cal BP	34.6	358-273 BC	34.6

5.3.2 Sediment description

The core from 30-233cm was described using a modified Troels-Smith (Figure 5.4; Kershaw, 1997). The four homogeneous units found consisted mostly of gytjja (HTS1-HTS4). They were composed of Ld (*Limus detrituosus/*organic lake mud), Ag (*Argilla granosa*/silt), As (*Argilla steatodes*/clay), Th (*Turfa herbacea*/coarse roots of herbaceous origin > 5mm), Dh (*Detritus herbosus*/plant or animal fragments > 2mm), Dl (*D. lignosus*/plant or animal fragments > 2mm), Dg (*D. granosus*/plant or animal fragments ca. 0.1mm), and Ga (*Grana arenosa/*fine sand). Unit HTS-3 differed from the rest, with silt affecting colour and texture of sediment. Fine plant and animal fragments were present in minute quantities.

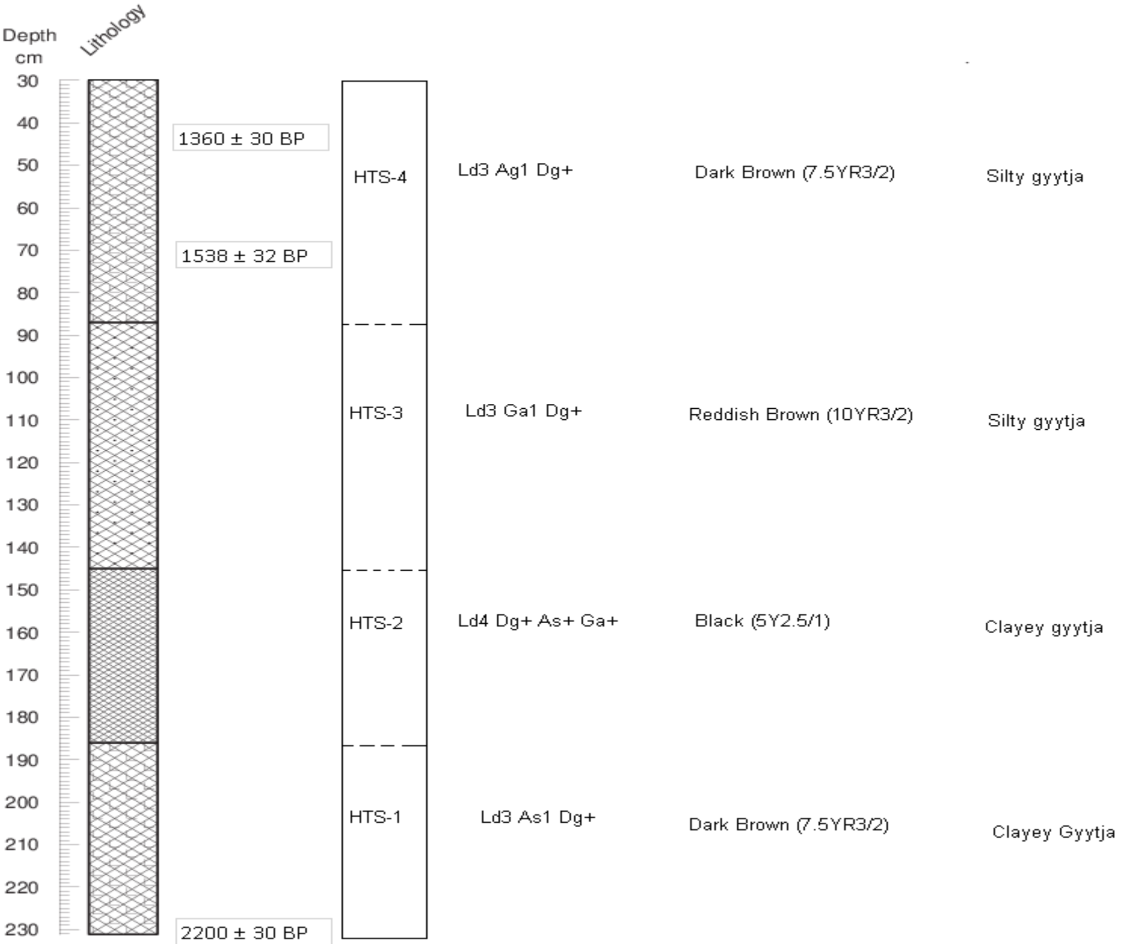

Figure 5.4. Troels-Smith sediment description for the clayey Umchachazo Vlei core.

5.3.3 Reconstructing local grass biomass and soil nitrogen dynamics from stable isotopes

Changes in grass biomass and nitrogen availability were indicated by TC and $\delta^{15}N$, respectively (Figure 5.5). Total nitrogen had a mean of c. 0.14 ± 0.06% with a range of c. 0.3% while TC had a mean of c. 1.57 ± 0.68% and a range of c. 3.1%. The photosynthetic signal of vegetation indicated by $\delta^{13}C$ had a mean of -16.39 ± 1.08‰ and a range of c. 7.1‰. In comparison, $\delta^{15}N$ was c. 5.75 ± 0.69‰ and range of c. 2.65‰. The indicator of grass stemminess, the C:N ratio, had a mean of c. 11 ± 1.04 and a narrow range of 5.21. A significant linear correlation was found between TN and TC ($r = 0.975$, *d.f.* = 65, *p-value* = $2.2e^{-16}$), while none was found between $\delta^{15}N$ and $\delta^{13}C$ ($r = 0.034$, *d.f.* = 65, *p-value* = 0.758).

The CONISS clusters/ zones from stable isotope data pointed to five grass states (Figure 4.5). The zones were HISO-1 (ca. 2 140-2 020 cal BP), the dynamic HISO-2 (ca. 2 020-1 610 cal BP), HISO-3 (ca. 1 610-1 340 cal BP), HISO-4 (ca. 1 340-690 cal BP), and HISO-5 (ca. 690 to -55 cal BP). Transitions between zones were sharp, especially between HISO-1 and HISO-2 and between HISO-2 and HISO-3.

Total nitrogen increased irregularly with time, especially from c. 0.09% at ca. 2 040 cal BP to c. 0.23% at ca. 1 650 cal BP [c. 226-139 cm]. It later declined to c. 0.07% at ca. 1 500 cal BP [c. 108 cm]. The increase in TN from c. 0.07% at ca. 1 380 cal BP to c. 0.16% at ca. 1 280 cal BP [c. 73-45 cm] was followed by stability and more increases from c. 0.14% at ca. 530 cal BP [c. 19 cm] to c. 0.37% at ca. -24 cal BP [c. 0.5 cm), respectively. Patterns of TC resembled those of TN.

Nitrogen availability signalled by $\delta^{15}N$ was plentiful in the dynamic zone (HISO-2) and the terminal zone (HISO-4) had high TC but was lower in zones HISO-1 and HISO-3. Increases of $\delta^{15}N$ from c. 4.4‰ at ca. 2 020 cal BP to c. 6.67‰ at ca. 1 950 cal BP were followed by a decline to c. 5.11‰ at ca. 1 790 cal BP [c. 157 cm]. Later increases from c.

6.71‰ at ca. 1 610 cal BP [c. 121 cm] were reversed by the fall to c. 4.7‰ at ca. 1 600 cal BP [c. 119 cm]. Recovery followed from c. 4.43‰ at ca. 1 450 cal BP [c. 88 cm] to c. 6.7‰ at ca. 690 cal BP [c. 23 cm].

Although the $\delta^{13}C$ photosynthetic signal of local vegetation changed little from the mean of c. -16.39 ± 1.08‰ at three of the isotope zones, it varied in zone HISO-2. The zone experienced irregular increases in $\delta^{13}C$ from c. -17.6‰ at ca. 1 970 cal BP [c. 231cm] to -14‰ at ca. 1 790 cal BP [c. 142cm] before falling to c. -17.4‰ at 1 600 cal BP [c. 119cm].

The indicator of the stem to leaf ratio of grass litter, the C:N ratio, was variable in the dynamic zone HISO-2. The C:N ratio rose from c. 9.7 at 2 090 cal BP [c. 219cm] to 14.3 at 1 790 cal BP [c. 142cm] followed by a decline to c. 9.1 at 1 500 cal BP [c. 97cm]. Later, gradual recovery and settling of the C:N ratio at c. 11.1 happened from ca. 1 330 -960 cal BP [c. 61-30cm].

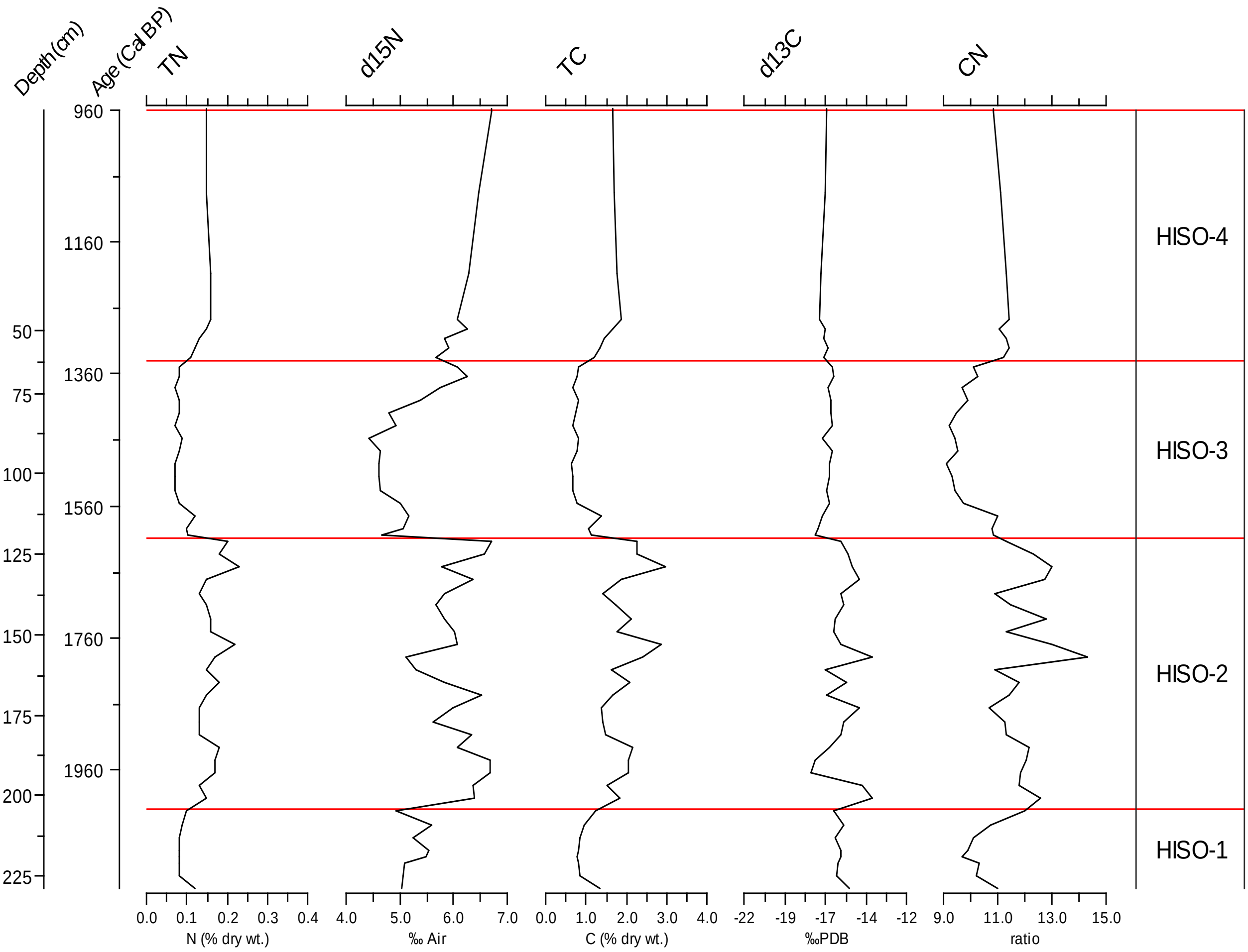

Figure 5.5. Summary of stable isotope values and zones from the Umchachazo Vlei core.

5.3.4 Changes in grass biomass and salinity from LOI

Changes in local grass biomass suggested LOI mirrored TC from the stable isotope zones (Figure 5.6). Loss on ignition for sediment organic carbon had a mean of c. 6.30 ± 1.98% and range of c. 6.28%. The mean of calcium carbonate ($CaCO_3$) related to salinity was c. 2.98 ± 4.91% with a range of c. 4.01%. A positive linear correlation was found between LOI and $CaCO_3$ ($r = 0.624$, *d.f.* = 34, *p-value* = 0.000047), and between LOI and δ^{13}C ($r = 0.35$, *d.f.* = 32, *p-value* = 0.042).

There were significant differences in grass biomass indicated by LOI among stable isotope zones ($H = 22.35$, *d.f.* = 2, *p-value* < 0.000051), and between zones (Table 5.2).

Dynamic grass biomass at the wetland was evidenced by a falling and rising LOI from c. 4.4% at ca. 2 120 cal BP to c. 9.6% at ca. 1 650 cal BP. This was followed by a sharp decline in LOI to c. 3.4% at ca. 1 540 cal BP. A gradual increase in LOI to c. 3.9% at ca. 1380 cal BP was followed by a sharp increase to c. 7.4% at ca. 1 290 cal BP while less change happened till ca. 1 090 cal BP, and then the value increased to c. 8.4% at ca. 960 cal BP. Carbonates were variable between c. 1.6-5.4% from ca. 2 200-1 610 cal BP, peaking at 5.4 at ca. 1 610 cal BP. A sharp fall in salinity followed to c. 1.1% at ca. 1 500 cal BP was followed by an increase to c. 5.2% at ca. 1 310 cal BP.

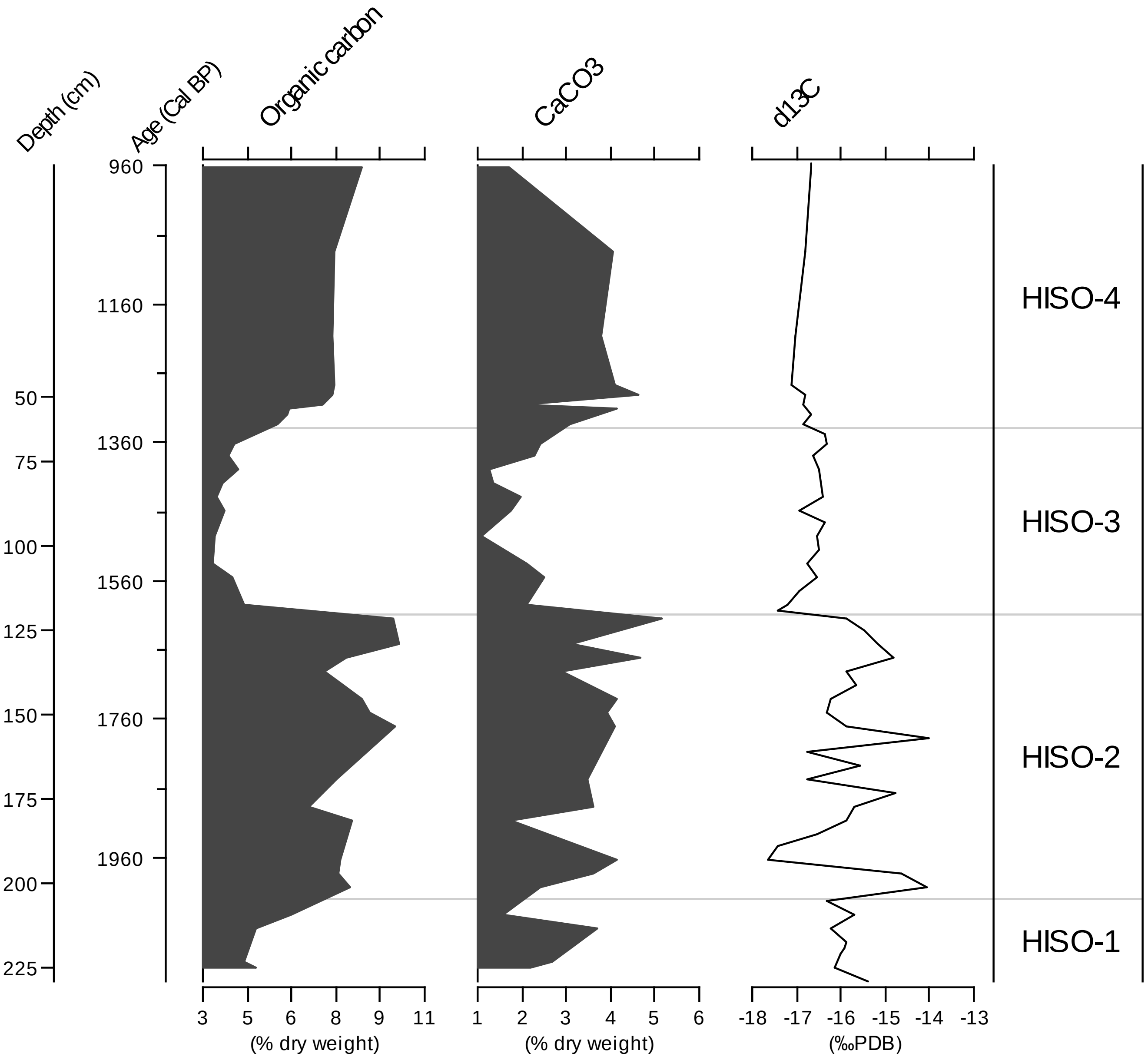

Figure 5.6. Changes in grass biomass and salinity at the wetland margin pointed to by organic carbon LOI and $CaCO_3$ within stable isotope zones used for grass states at Umchachazo Vlei.

Table 5.2. Pairwise comparisons of wetland grass biomass signalled by LOI rank sums among stable isotope zones from the Tukey and Kramer test (unadjusted *p-values*)

	HISO-1	HISO-2	HISO-3
HISO-2	0.065		
HISO-3	0.836	**2.70E-05**	
HISO-4	0.656	0.347	**0.042**

5.3.5 Reconstructing grazing pressure using spores

Local grazing pressure and herbivore biomass in the landscape was dynamic as shown by varying spores (Figure 5.7), and other non-pollen types (Appendix Four). *Coniochaeta lignaria* also linked with local soil moisture was the most common followed by *Sordaria*. *Coniochaeta*-type (T.UG-1173 and T.UG-1144), i.e., similar in morphology to *Xylariaceae*-type, were also common with a mean of 7 616 ± 4 970 spores cm^{-3}. Two spore clusters or zones (HiSP-1 and HISP-2) with a boundary at ca. 1 740 cal BP, were found with the CONISS method (Bennett, 1996; Ter Braak, 1986). The basal zone HiSP-1 (ca. 2 200-1 740 cal BP) was associated with high *C. lignaria*. In comparison, HiSP-2 (ca. 1 740-960 cal BP) was associated with more *Sporormiella* associated with increased herbivore biomass and/or local grazing pressure. The isotope zones were used to give a vegetation context of changes in herbivore biomass.

5.3.5.1 Zone HISO-1 (ca. 2 140-2 020 cal BP)

Increases in grazing pressure biomass and soil moisture were indicated by rises in abundance of *C. lignaria*, *Gelasinospora*, *Sordaria*, *Chaetomium* and *Sporormiella*. *Apiosordaria* was absent in the zone.

5.3.5.2 Zone HISO-2 (ca. 2 020-1 610 cal BP)

Varying grazing pressure was indicated by shifts in spore numbers. Increases happened from ca. 2 020-1 910 cal BP followed by declines. More increases happened from ca. 1 810-1 750 cal BP. Striking changes in *C. lignaria* concentrations were seen from c. 48 840 spores cm^{-3} at ca. 2 040 cal BP to c. 216 800 spores cm^{-3} at ca. 1 910 cal BP, followed by an abrupt decline. *Sordaria* Type 55b in the sequence was plenty from ca. 2 060-1 850 cal BP. There was an increase in *C. lignaria* from c. 34 380 spores cm^{-3} at ca. 1 890 cal BP to the peak of c. 318 570 spores cm^{-3} at ca. 1 770 cal BP that coincided with increases in

Apiosordaria, *Cercophora*, *Chaetomium*, *Gelasinospora*, *Podospora*, *Glomus* and *Sporormiella*.

5.3.5.3 Zone HISO-3 (ca. 1 610-1 340 cal BP)

Compared to zone HISO-2, spore concentrations were lower in zone HISO-3 following declines in *C. lignaria* from ca. 1 560-1 440 cal BP. *Coniochaeta lignaria* indicating local soil moisture were fewer and less variable compared with other spores (i.e., *Sporormiella*, *Chaetomium*, *C. gamsii*, and *Coniochaeta*-type). Interestingly, contemporaneous increases in spores associated with herbivore biomass (e.g., *Apiosordaria*, *Chaetomium*, *Coniochaeta*-type and *Sporormiella*) happened from ca. 1 440-1 340 cal BP. Also, swings in *Apiosordaria*, *Chaetomium*, *Coniochaeta*-type and *Sporormiella* numbers happened before the transition between zones HISO-3 and HISO-4.

5.3.5.4 Zone HISO-4 (ca. 1 340-690 cal BP)

A rise in local grazing pressure indicated by increased spore concentrations from ca. 1 340-1 280 cal BP, tapered off at ca. 1 210 cal BP. Peak concentrations of *Chaetomium*, *Coniochaeta*-type, and *Sporormiella* representing herbivore biomass/grazing pressure occurred at ca. 1 280 cal BP of c. 2 220 spores cm^{-3}, 11 610 spores cm^{-3}, and 10 840 spores cm^{-3}, respectively. Concentrations of *Cercophora*, *C. lignaria*, and *Sporormiella* were unchanged from ca. 1 210-960 cal BP. However, increases were observed for *Chaetomium*, *Coniochaeta*-type, and *C. gamsii* that occurred from ca. 1 090-960 cal BP.

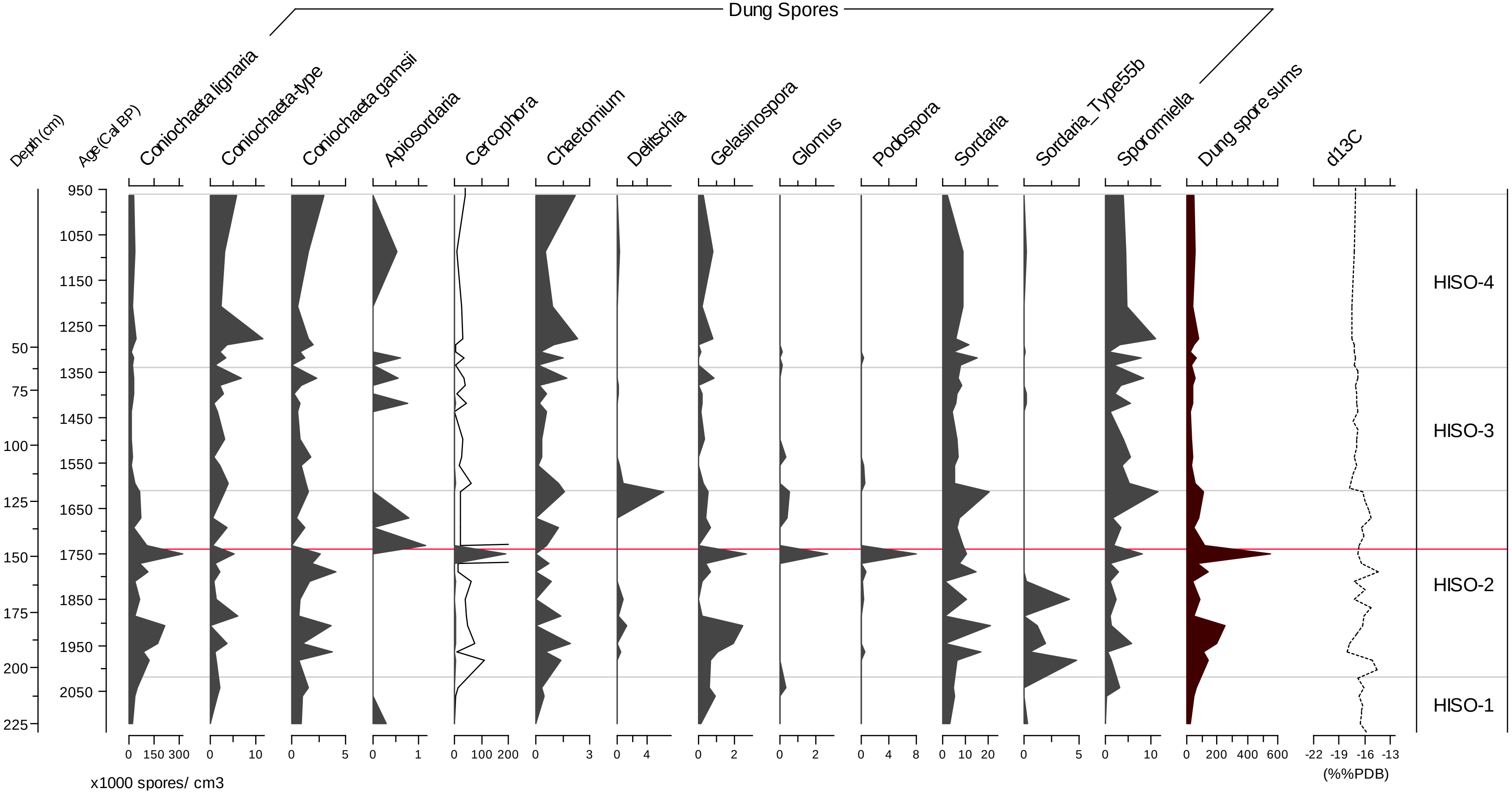

Figure 5.7. Changes in dung spore concentrations indicating local grazing pressure and/or herbivore biomass within isotope zones used for grass states at Umchachazo Vlei. The red line separates dung spore CONISS clusters.

5.3.6 Reconstructing fire activity from charcoal

The presence of charcoal throughout the sediment sequence signalled that fire activity was important at the key resource area (Figure 5.8). Summaries of charcoal concentrations are: mean microcharcoal was 201 500 ± 138 910 particles cm^{-3} (n = 35, *range* = 542 450), mean macrocharcoal was 234 ± 460 particles cm^{-3} (n = 41, *range* = 2906), and combined charcoal was 202 890 ± 139 270 particles cm^{-3} (n = 31, *range* = 545 100). Local and landscape fire activity represented by macrocharcoal and microcharcoal respectively, were positively correlated (r = 0.445, *d.f.* = 29, *p-value* = 0.0122). However, macrocharcoal and microcharcoal did not always change in the same direction.

Charcoal amounts were high for all size ranges in basal zones HISO-1 and HISO-2 (Figure 5.8). Fire activity declined in zone HISO-3 represented by a sharp decline in charcoal concentration but increased again in zone HISO-4. Interestingly, macrocharcoal was stable from ca. 1 590-960 cal BP. In comparison, microcharcoal increased from c. 8.2x10^{5} particles cm^{-3} at ca. 1 310 cal BP to 21.9x10^{5} particles cm^{-3} at ca. 1 090 cal BP, decreasing thereafter.

Four charcoal concentration CONISS clusters or zones were found (Figure 5.8). They were CH-1 from ca. 2 140-2 020 cal BP, CH-2 from ca. 2 020-1 740 cal BP, CH-4 from ca. 1 740-1 710 cal BP, and CH-4 from ca. 1 710-960 cal BP. However, stable isotope zones used for inferring local vegetation were used to assess charcoal amount with time (Figure 5.8).

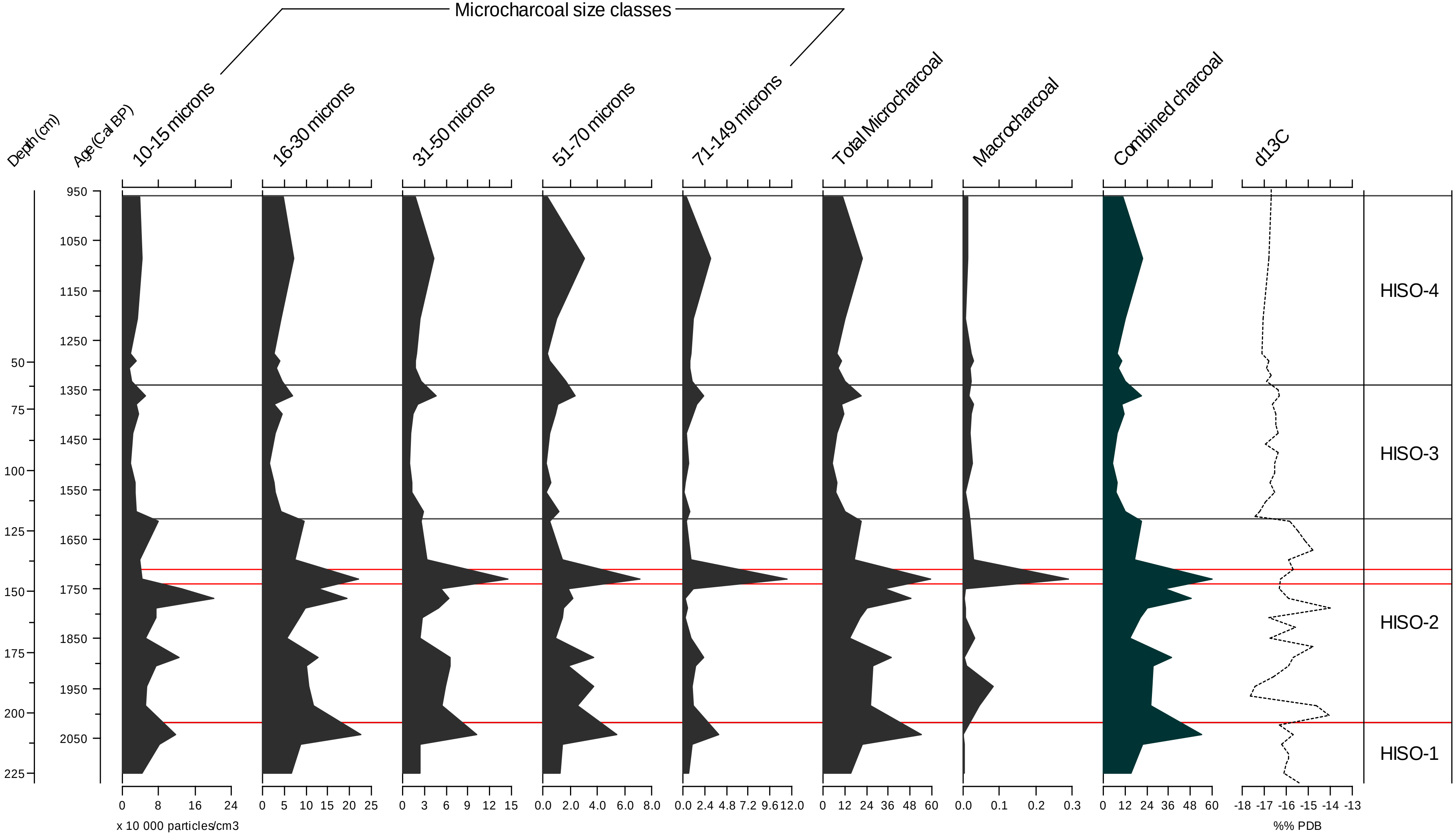

Figure 5.8. Changes in charcoal concentrations within the isotope zones used for grass states at Umchachazo Vlei. Charcoal CONISS clusters shown by red horizontal lines.

5.3.7 Reconstructing local grazing pressure using spores

The effect of grazing pressure on grass biomass (tallgrass to shortgrass) was pointed out by the spore ordination gradients (Figure 5.9). The spores formed two overlapping clusters along the primary ordination axis NMDS1 (Figure 5.9). Spore zone/cluster (HiSP-1) was associated with *Apiosordaria*, *Gelasinospora*, *C. lignaria*, *Podospora* and *Cercophora*. *Apiosordaria*, *Cercophora* and *Podospora* in the Lasiosphaeriaceae family were not distinguishable along the primary axis. Spore zones could not be separated with *C. lignaria* associated with moist local conditions. In comparison, cluster HiSP-2 included spores normally associated with grazing pressure and shortgrasses (i.e., *Sporormiella*, *Chaetomium*, and *Sordaria*), were positioned at the negative end of the primary axis (Baker et al., 2013; Cugny et al., 2010; Johnson et al., 2015). Although total dung spore concentration (Spore.sums) increased along the primary axis, it was negatively correlated with the secondary axis/NMDS2 ($r^2 = 0.48$, *p-value* < 0.004).

Coniochaeta lignaria that dominated the spore signal, had a positive curvilinear relationship with the primary axis of ordination ((Figure 5.10; Table 5.3; *residual deviance* = 855 180, *d.f.* = 33 *p-value* = 0.000025). The regression model had a null deviance of 1 650 970 with quasipoisson variance of 31 860. In contrast, *Sporormiella* whose increase is associated with a rise in grazing pressure, decreased linearly along the primary axis (Figure 5.10; Table 5.3; *residual deviance* = 54 968, *d.f.* = 33 *p-value* = 0.0037). The regression model had a null deviance of 75 870 with quasipoisson variance of 1 880.

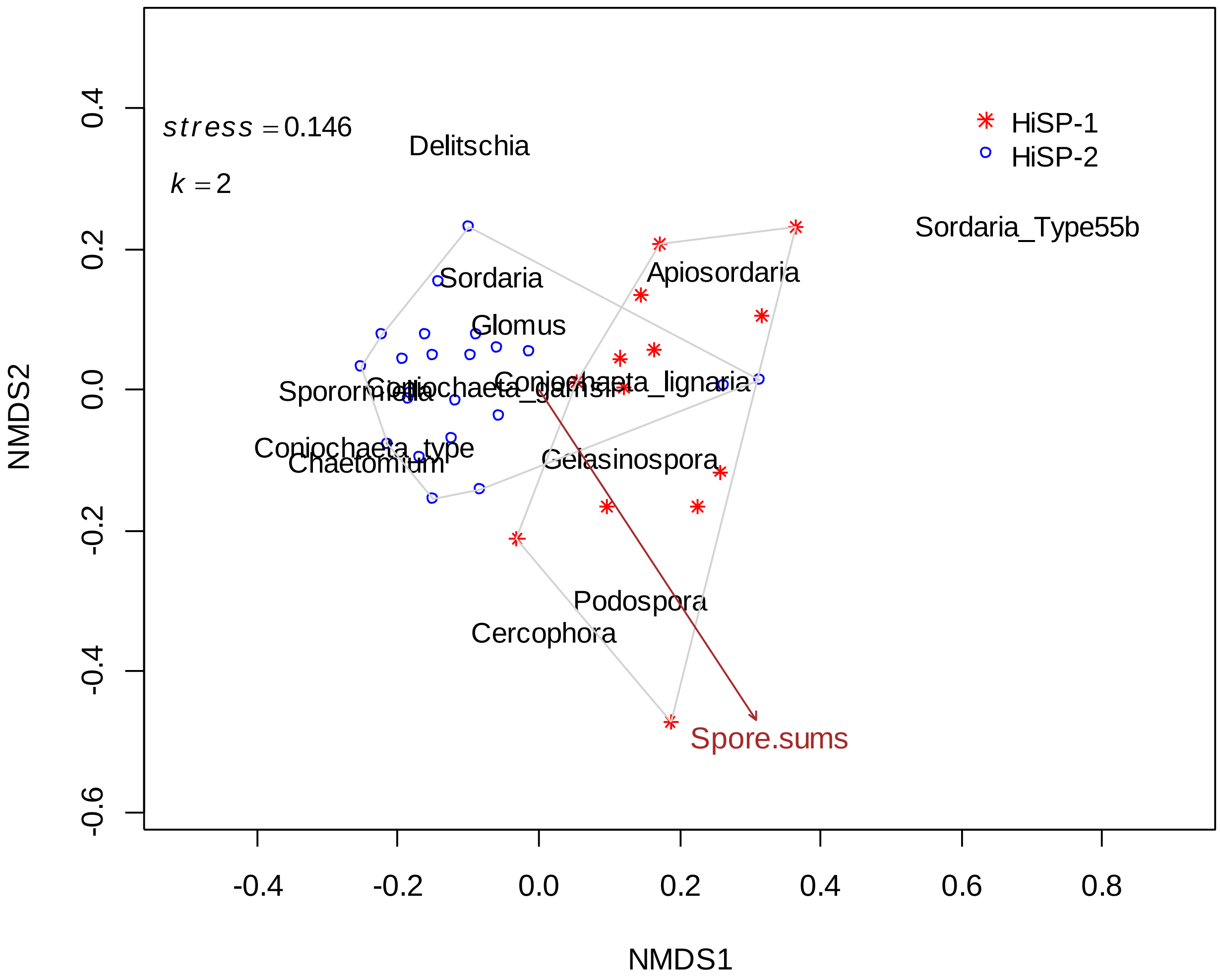

Figure 5.9. NMDS ordination of spores for finding the grazing pressure gradient from spores. Spore clusters or zones are shown by convex hulls.

Table 5.3. Relationship between *Sporormiella* and *Coniochaeta lignaria* with the primary spore ordination gradient at Umchachazo Vlei.

Dependent variable	Parameters	Coefficients	Std. Error	t-value	*p-value*
Sporormiella	Intercept	3 262	0.135	59.948	**< 2e-16**
	Dung spores (NMDS1)	-2.549	0.816	-3.125	**0.0037**
Coniochaeta lignaria	Intercept	48 530	0.148	73.002	**<2e-16**
	Dung spores (NMDS1)	3.430	0.701	4.896	**0.000025**

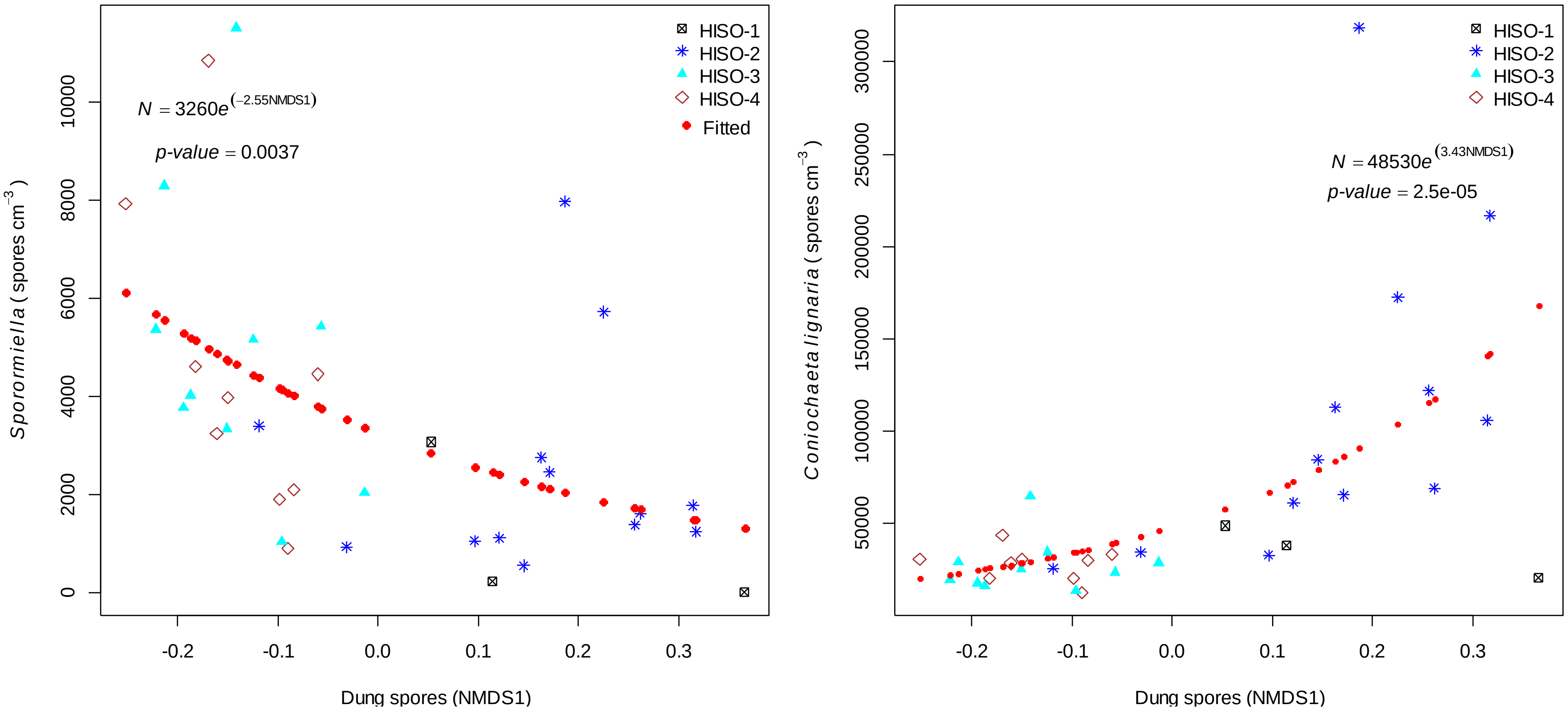

Figure 5.10. Finding the grazing pressure gradient from the relationship between the spore primary ordination axis and a). *Sporormiella*; and b) *Coniochaeta lignaria* at Umchachazo Vlei.

5.3.8 Reconstructing grass biomass and fire activity with charcoal

The relationship between fire activity and grass biomass/sward height with time was got by ordinating charcoal concentrations (Figure 5.11). Total charcoal concentrations (Sums), had a significant but negative relationship with the primary NMDS ordination axis ($r^2 = 0.84$, *p-value* < 0.00001). Large macrocharcoal particles associated with tallgrass biomass around wetland margins were associated with positive values along the primary axis. However, microcharcoal particles linked to distal transport were negatively associated with the primary axis. Surprisingly, there was a temporal signal of particle sizes with older charcoal zones (CH-1 and CH-2) linked with microcharcoal and the younger zone (CH-4) with macrocharcoal.

An overall negative relationship was found between the combined charcoal concentration indicating a decline in grass biomass/grass sward height along the primary axis (*residual deviance* = 233 200, *d.f.* = 29, *p-value* < 0.0000001; Figure 5.12a; Table 5.4). The regression had a null deviance of 2 494 650 and quasipoisson variance of 8 660. Although macrocharcoal increased along the primary axis, this was false for isotope vegetation zone HISO-2.

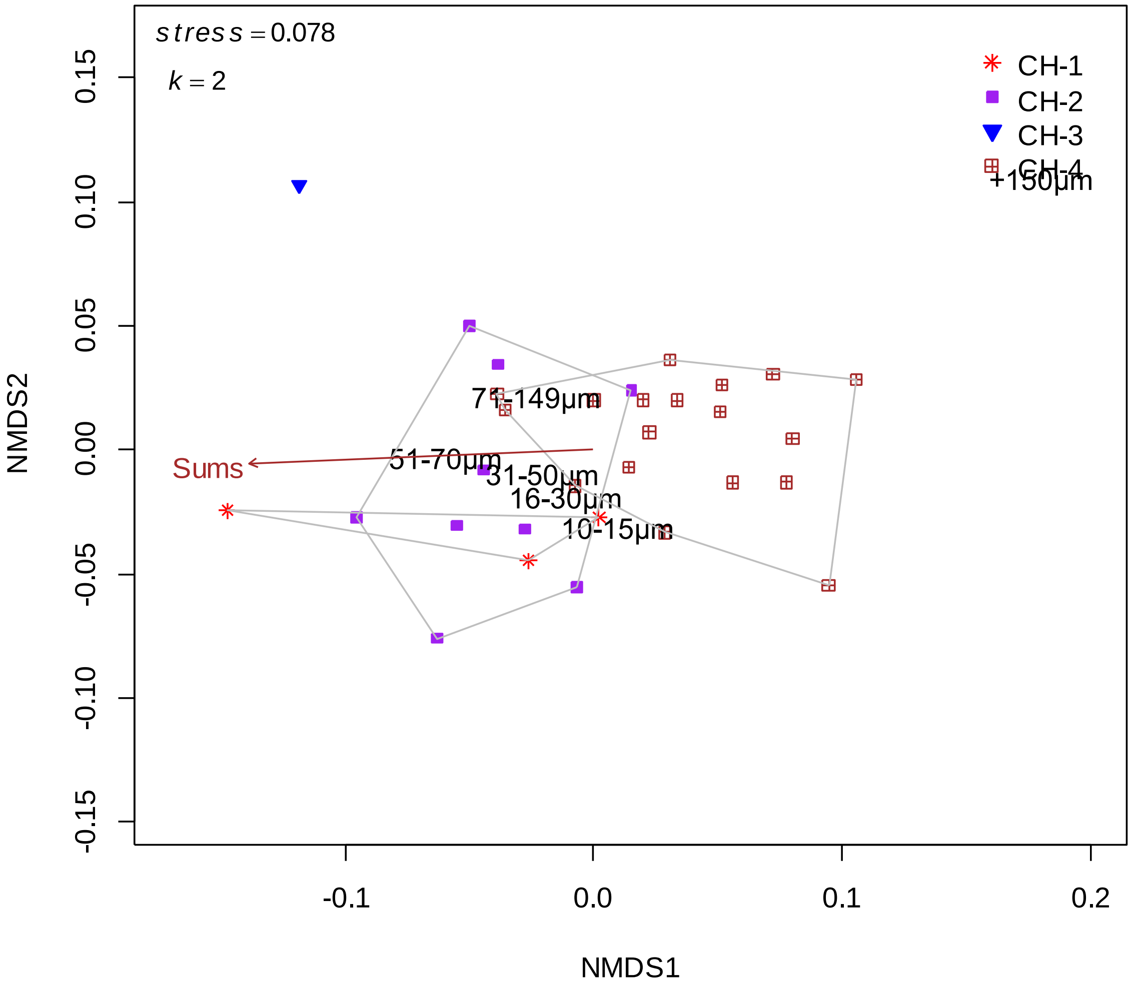

Figure 5.11. NMDS ordination of charcoal sizes and concentration data at Umchachazo Vlei. Convex hulls showing charcoal zones or clusters.

Table 5.4. The relationship combined charcoal concentration and the charcoal ordination NMDS1 grass biomass gradient at Umchachazo Vlei.

Parameters	Coefficients	Std. Error	t-value	*p-value*
Intercept	170 910	0.042	370.47	<2e-16
Charcoal (NMDS1)	$8.08x10^{-5}$	0.573	19.85	<2e-16

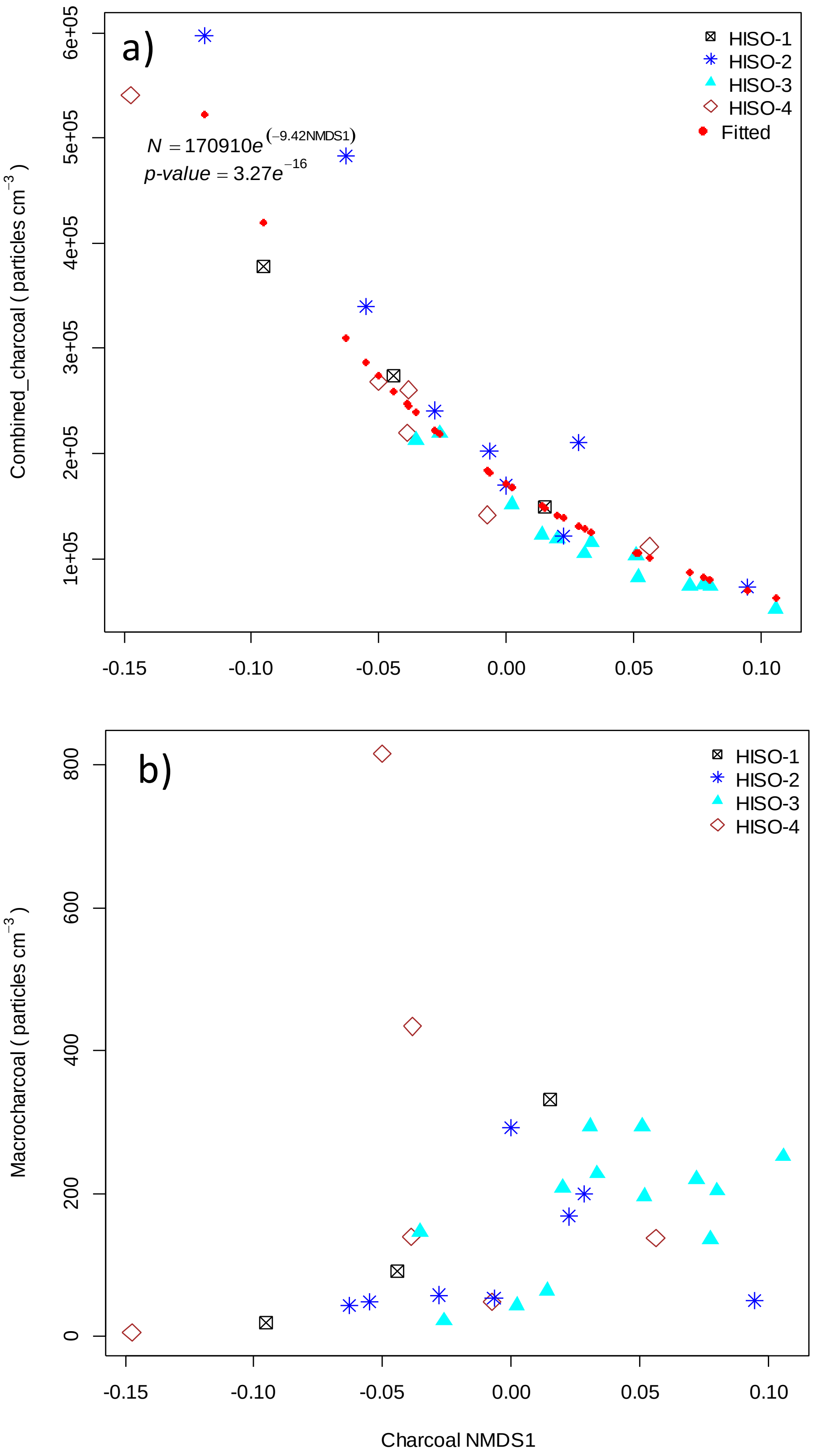

Figure 5.12. The relationship between the charcoal NMDS ordination primary axis at Umchachazo Vlei with a) combined charcoal amounts; b) macrocharcoal.

5.3.9 Local states of grass biomass from fire and grazing

In tandem, fire activity and grazing pressure reflected changing states of grass biomass with time from charcoal and spore concentrations (Figure 5.13). High fire activity linked to tallgrass states, and heavy grazing associated with more spores, were confirmed by the negative correlation between charcoal NMDS1 axis and dung spores NMDS1 (r = -0.603, $d.f.$ = 29, p-$value$ = 0.00033; Figure 5.17). Although an increase in charcoal caused a decline in spores. Positive relationships between fire and grazing happened from ca. 2 000-1 710 cal BP and ca. 1 360-1 290 cal BP shown by patterns in *Sporormiella* and macrocharcoal (Figure 5.13a), and between charcoal NMDS1 and dung spores NMDS1 (Figure 5.13b).

Furthermore, disturbance intensities separated grass states supporting the vegetation units from stable isotope zones (Figure 5.17). High fire activity was related to tallgrass states I and II, and were distinct from shortgrass states. Heavy grazing was associated with shortgrass states I and II, although the latter overlapped with tallgrass state II.

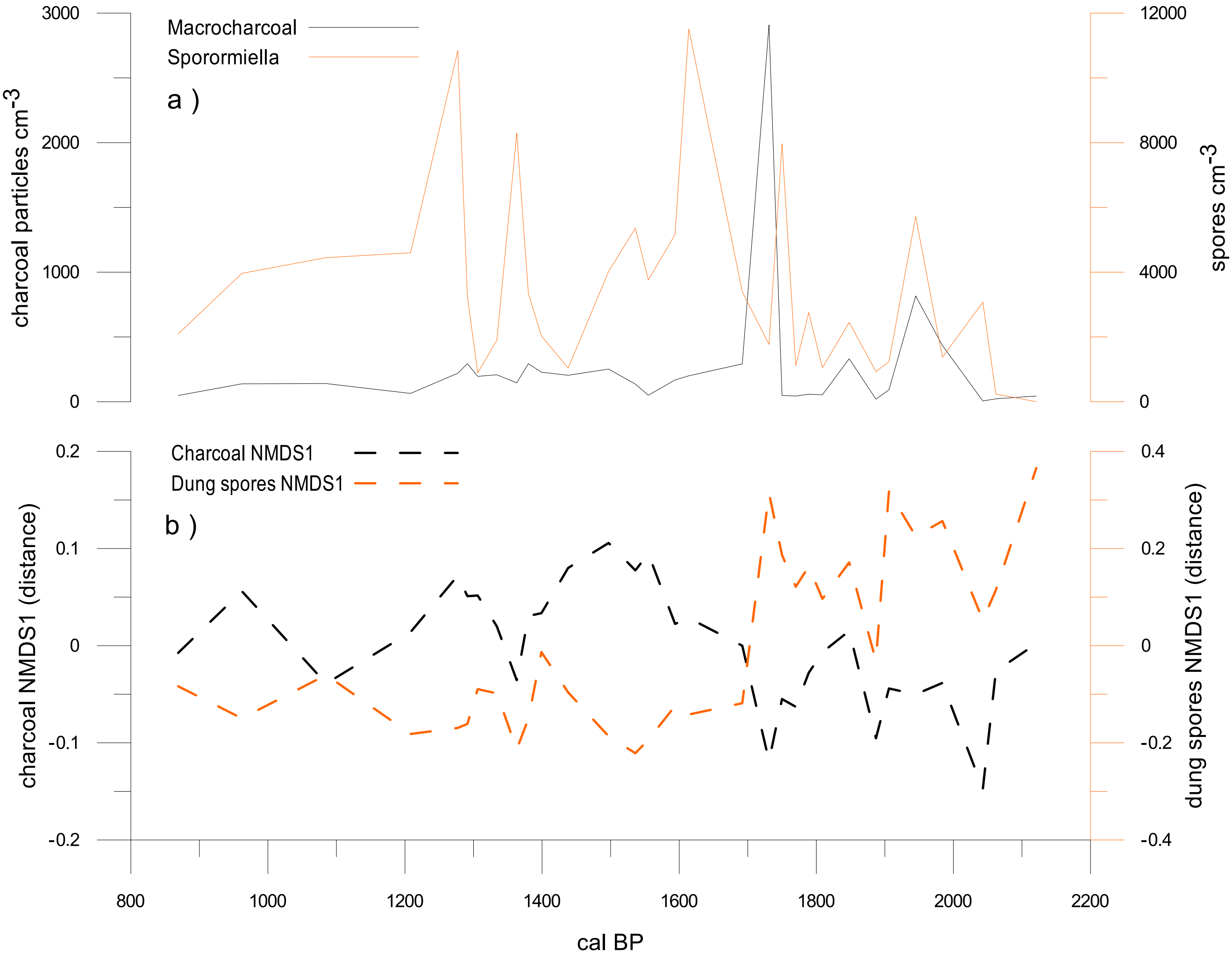

Figure 5.13. Changes in grass biomass at the key resource area deduced from a) interactions between grazing pressure and fire activity indicated by *Sporormiella* concentration and macrocharcoal concentration; b) relationship between disturbance and grass productivity/biomass shown by charcoal NMDS1 and dung spore NMDS1 at Umchachazo Vlei.

5.3.10 Soil salinity and erosion from XRF analysis

Stable isotope zones were used to interpret XRF elemental data (Figure 5.14). Elemental concentrations from ca. 2 200-1 280 cal BP compared to ca. 1 280-950 cal BP. Correlations among elements are listed in Appendix Five.

The bottom isotope zones had variable elemental concentrations compared with the top zone. Transitions between zones coincided with variations in Sr and Zr. Zone HISO-1 had contrasts between Mg:Ca and Zr:Rb ratios indicating salinity and soil disturbance, respectively, since declines in the former coincided with an increase in the latter. A general decline in Zr, Sr and Ti was seen. Changes in Fe, K, Rb, and the Mg:Ca happened in zone HISO-2. Sharp increases in concentrations of heavy elements Rb and Ti and Zr marked zone HISO-3, where Fe reached its lowest concentration at ca. 1 510 cal BP. Apart from varying Fe in zone HISO-4, other elements were unchanged. Positive correlations were found between Zr:Rb ratios ($r = 0.982$, $d.f. = 18$, $p\text{-}value < 0.000001$), and Fe and Fe_2O_3 ($r = 0.49$, $d.f. = 18$; $p\text{-}value = 0.49$) from direct core scans and powdered samples.

5.3.11 Fire and grazing effects on local nitrogen availability and soil properties

Nitrogen availability ($\delta^{15}N$) changed within the stable isotope vegetation zones (Figure 5.15) but was not correlated with grazing pressure indicated by dung spore NMDS1 and $\delta^{15}N$ ($r = 0.180$, $d.f. = 33$, $p\text{-}value = 0.301$). Or with fire activity represented by charcoal NMDS1 with $\delta^{15}N$ ($r = -0.296$, $d.f. = 29$, $p\text{-}value = 0.106$). Neither was nitrogen correlated with grazing pressure indicated by *Sporormiella* ($r = 0.137$, $d.f. = 33$, $p\text{-}value = 0.433$), nor with local fire activity suggested by macrocharcoal ($r = 0.170$, $d.f. = 29$, $p\text{-}value = 0.360$).

However, a significant negative correlation was found between soil disturbance indicated by the Zr:Rb ratio and grazing pressure represented by dung spores NMDS1 ($r^2 = 0.54$, $d.f. = 13$, $p\text{-}value = 0.002$; Table 5.16). A positive relationship was found between soil disturbance (Zr:Rb ratio) and local grass biomass gradient from charcoal marked by charcoal NMDS1 ($r = 0.647$, $p\text{-}value = 0.007$, $d.f. = 14$). Also, a negative relationship was found between grass biomass and soil disturbance from the LOI and Zr:Rb ratio, respectively (Figure 5.16c; Table 5.5).

Table 5.5. Regression relationships at Umchachazo Vlei between a) grazing pressure (dung spores NMDS1), and soil disturbance (Zr:Rb ratio); b) fire activity (charcoal NMDS1), and soil disturbance (Zr:Rb); c) local grass biomass (LOI), and soil disturbance (Zr:Rb).

Parameters	Coefficients	Std. Error	t-value	Pr (t)	$F_{2,13}$	*adj.* r^2	*p-value*
Zr:Rb intercept	2.143	0.466	4.604	>0.00001	9.91	0.54	**0.002**
Spores NMDS1	-8.245	1.872	-4.405	0.001			
Spores NMDS1^2	24.137	15.150	1.593	0.135			
Zr:Rb intercept	2.14	0.341	6.291	0.00002	12.83	0.61	**0.0008**
Charcoal NMDS1	22.650	4.555	4.673	0.0003			
Charcoal NMDS1^2							
LOI intercept	10.5%	0.830	12.642	>0.00001	42.06	0.82	**0.000004**
Zr:Rb	0.542	-1.730	-3.190	0.006			
Zr:Rb^2	0.100	0.072	1.332	0.202			

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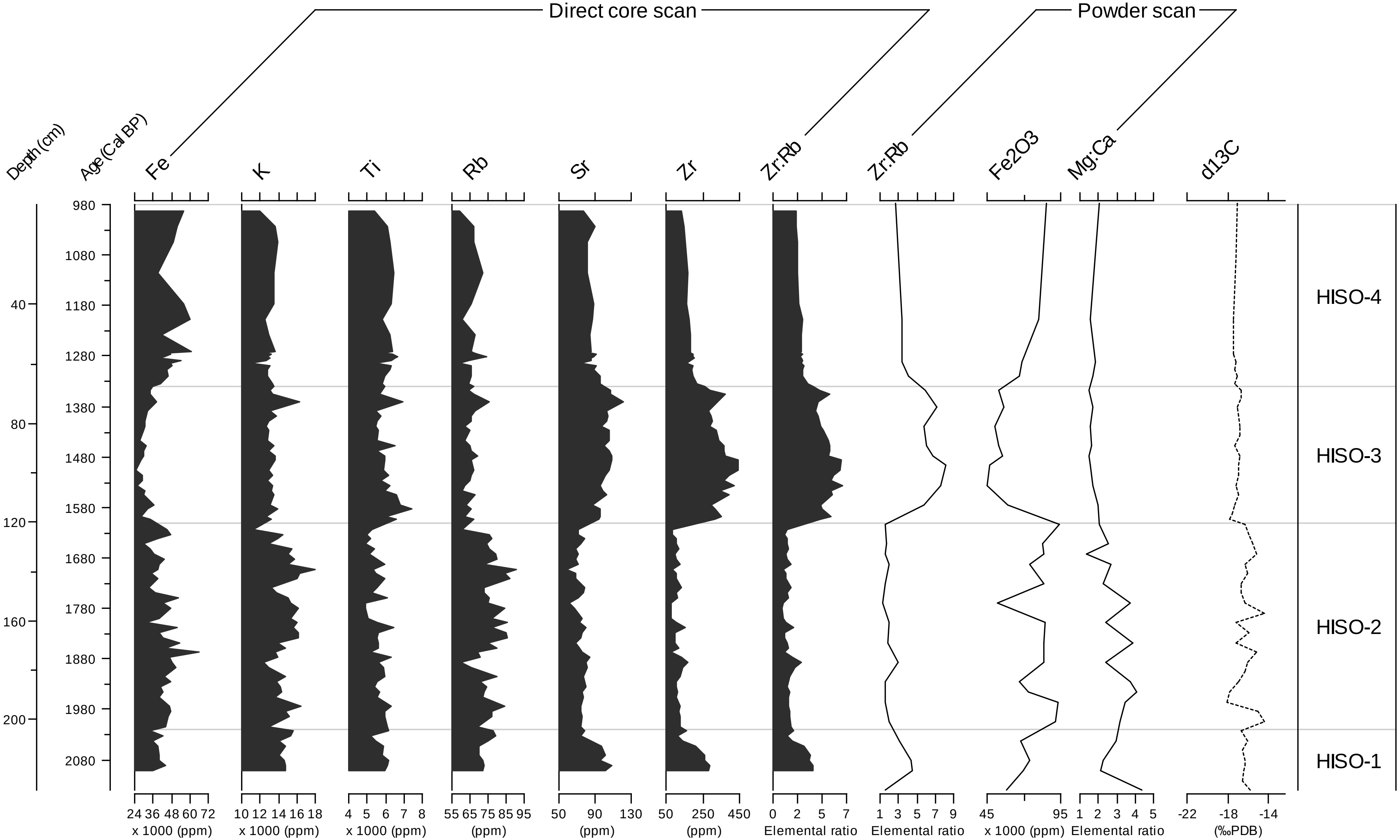


Figure 5.14. Changes in soil elemental concentration and ratios within the stable isotope zones for grass states at Umchachazo Vlei.

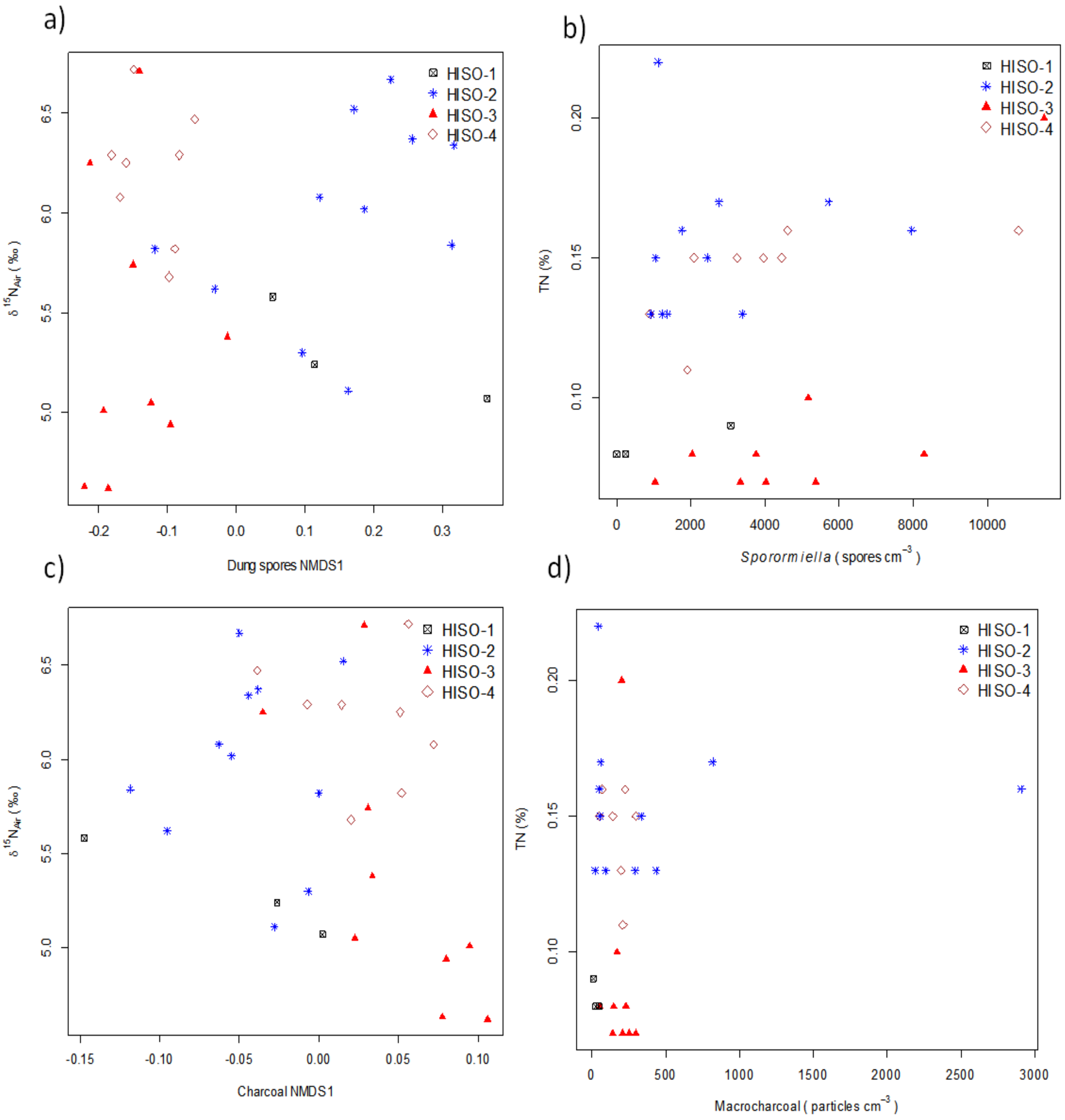


Figure 5.15. Relationships between grass consumers and nitrogen at Umchachazo Vlei. a) Grazing pressure (Dung spores NMDS1) versus nitrogen availability (δ^{15}N); b) Herbivore biomass (*Sporormiella) vs* TN; c) fire activity (charcoal NMDS1) *vs* δ^{15}N; and d) local fire (macrocharcoal) *vs* TN.

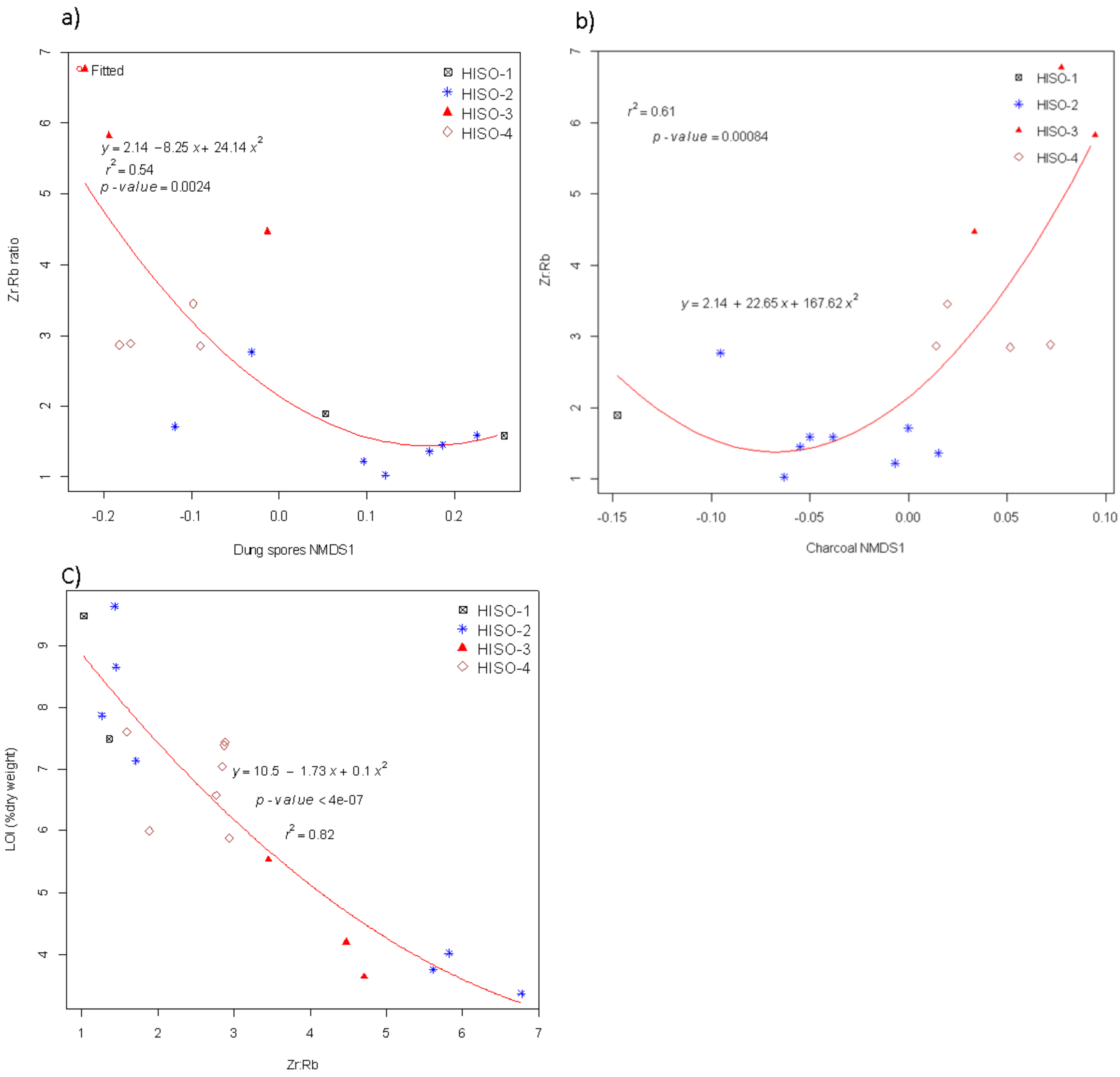


Figure 5.16. Summary of disturbance effects on soil at Umchachazo Vlei. a) Grazing pressure (dung spores NMDS1) versus soil disturbance (Zr:Rb ratio); b) Fire activity (charcoal NMDS1) vs Zr:Rb ratio; and c) Soil disturbance (Zr:Rb ratio) *vs* local grass biomass (LOI).

5.4 Discussion

5.4.1 Resolving vegetation states from isotopes and disturbance proxies

Changes in grass biomass suggesting tallgrass and shortgrass states at the key resource area were deduced from combining local environmental proxies. Four vegetation states were suggested from cluster zones from the multiple proxy stable isotope data (Figure 5.5). The data, $\delta^{13}C$, $\delta^{15}N$, TC, TN, and the C:N ratio, represented changes in the plant photosynthetic signal, nitrogen availability, grass biomass, nitrogen amount, and grass fibre content, respectively. Since combining the proxies can separate local vegetation states and processes (Fredlund and Tieszen, 1997; Ingram et al., 2008; Rietkerk and van de Koppel, 1997), stable states of vegetation were deduced from stratigraphic units. Interestingly, the $\delta^{13}C$ signal was not sensitive, only varying from ca. 2 020-1 610 cal BP. Agreement between the isotopes and LOI (Figure 5.6) improved confidence in the suggestion that zones represented changes in local grass biomass related to grazing (e.g., Ingram et al., 2008). And changes in soil moisture (Ireland et al., 2012; Ireland and Booth, 2011).

Further, changes in fire activity and local grazing pressure pointed out by charcoal NMDS1 and spores NMDS1 (Figure 5.17), suggested changes in states of local grass biomass. Since charcoal amounts representing fire activity are linked with tallgrass patches (Leys et al., 2015), heavy grazing with shortgrasses and more *Sporormiella* (Cugny et al., 2010; Graf and Chmura, 2006), the trade-off between the two represents changes in grass sward heights and biomass in vegetation mosaics (Allred et al., 2011; Fuhlendorf and Engle, 2004; Waldram et al., 2008). Surprisingly, the independent evaluation of the states of grass biomass from isotopes with combined fire and grazing was successful (Figure 5.17).

Combining the proxies of local grass biomass, fire activity, and grazing pressure suggested four persistent vegetation states. They were the tallgrass I (2 140-2 020 cal BP), tallgrass II (2 020–1 610 cal BP), shortgrass I (1 610–1 340 cal BP), and shortgrass II (1 340–

960 cal BP). The following section discusses the states with context from a regional multiple proxy record for rainfall (Chevalier and Chase, 2015).

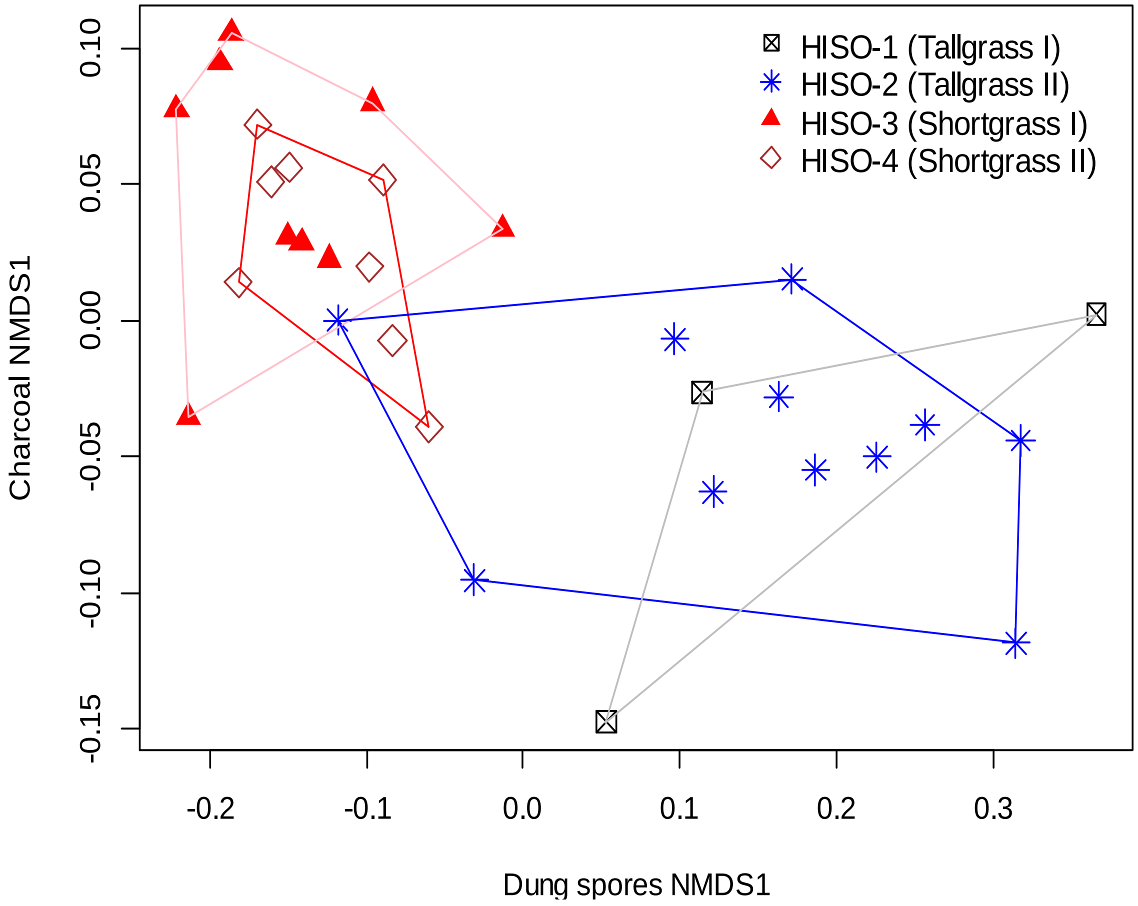


Figure 5.17. Changes in grass states along fire and grazing gradients at Umchachazo Vlei suggested by clusters of charcoal NMDS1 and dung spores NMDS1.

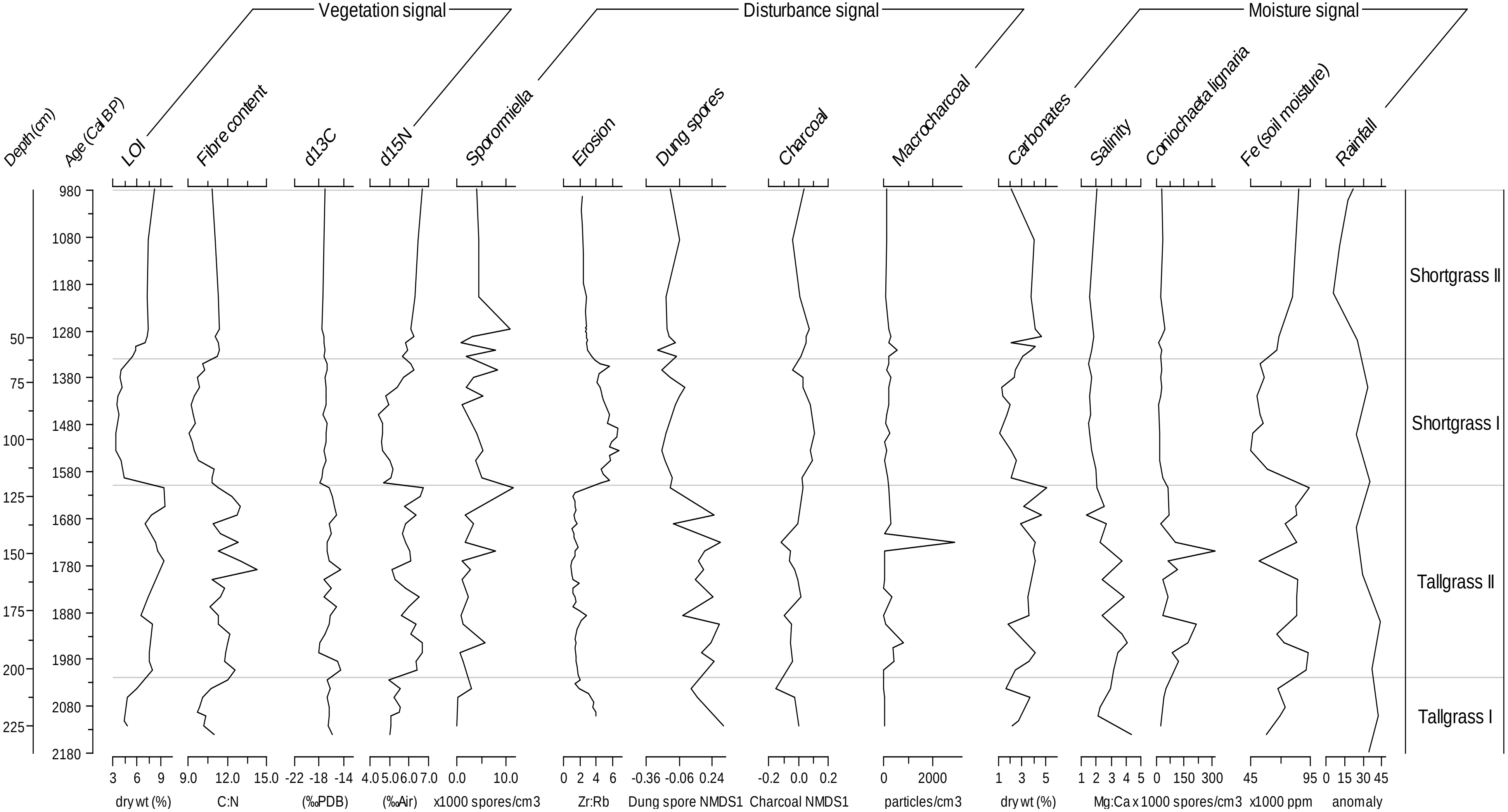


Figure 5.18: Multiple proxy summary of vegetation states, disturbances, local moisture, soil function, and rainfall at Umchachazo Vlei.

5.4.2 Drivers of vegetation states, transitions, and ecological thresholds

Rainfall, people, fire, and grazing were responsible for driving transitions among vegetation states at the key resource area. Here, I discuss grass states and their ecological drivers with stability domains of grass biomass (Figure 5.19).

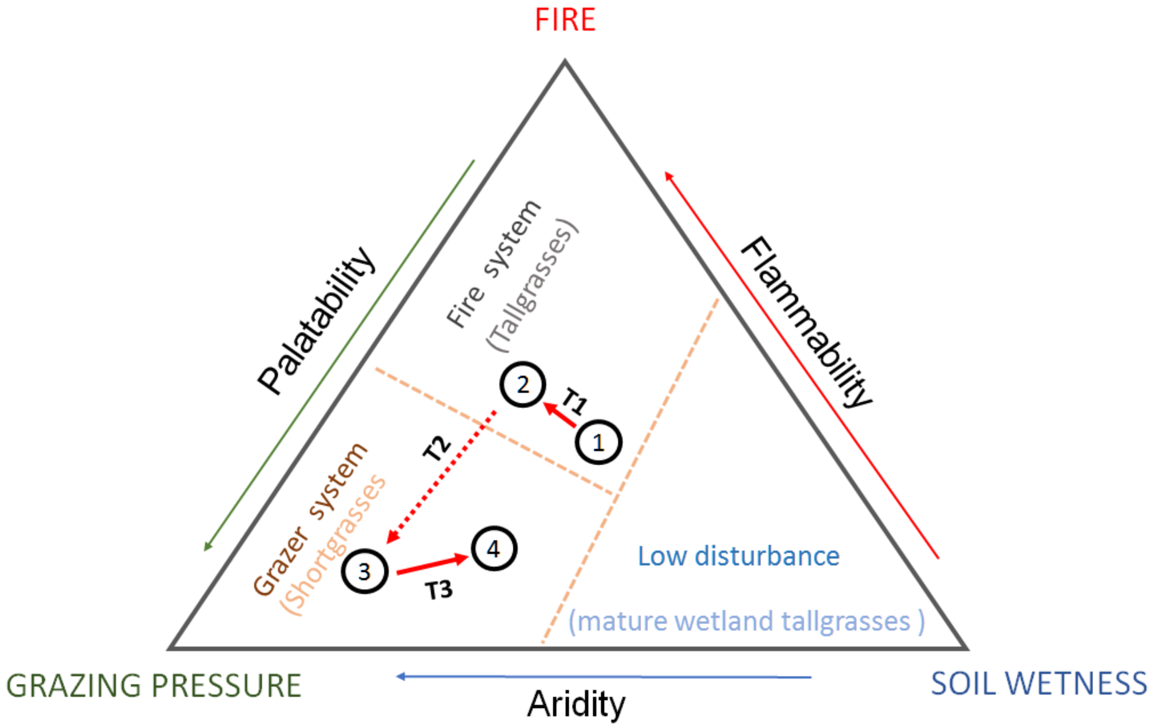


Figure 5.19. Phase space summary diagram of stability domains of grass biomass and vegetation state-transitions at HiP. Ecological drivers included are aridity, palatability, and flammability. State transitions (T_i) without a threshold are shown by solid arrows and the one with a threshold by dashes.

Tallgrass state I, deduced from increasing charcoal and LOI, suggested that an increase in fire activity from ca. 2 200-2 020 cal BP was caused by more grass fuel (Figure 5.18). High concentrations of iron and *C. lignaria* in sediments suggested wet local conditions increased grass biomass (Figure 5.7 and 5.18). Since a wet climate persisted in the region (Chevalier and Chase, 2015), rainfall drove vegetation changes in the landscape. The rise in grass biomass was associated with more stemmy grasses since the C:N ratio was high (Figure 5.5 and 5.6). The data suggests that the presence of tall grasses at wetland margins

(Bell, 1971; Fynn et al., 2015; Vesey-Fitzgerald, 1970), have more structural carbon in their tissue (Anderson et al., 2007; Grime, 1977; Longhi et al., 2008; Ojima et al., 1994).

However, trees and aquatics also contribute to the C:N ratio signal from sediments (e.g., Michener and Lajtha, 2007). Still, grass dominance at most wetland grasslands in the study region (e.g., Fynn et al., 2015; Mucina and Rutherford, 2006; Vesey-Fitzgerald, 1970), suggests that they contribute more to the signal. The dynamic tallgrass state II (2 020–1 610 cal BP) with more grass biomass suggested by TC and LOI, followed the transitory tallgrass state I (Figure 5.18).

Interaction between fire and grazing with the onset of dry climatic conditions suggested a dynamic tallgrass state II, signalled by varying LOI, charcoal, and, spores (Figure 5.18). Changes in LOI from ca. 2 000-1 600 cal BP pointed to heterogeneous grass biomass in the landscape mosaic. The decline in *C. lignaria* also suggested dry local conditions from ca. 1 910-1 770 cal BP, suggests that fluxes in local grass biomass were in response to arid soils and heavy grazing since *Sporormiella* increased (Wood and Wilmshurst, 2012). As *C. lignaria* and *Sporormiella* varied inversely, the increase of the latter signals local heavy grazing and shortgrasses (Figure 5.10a; Graf and Chmura, 2006). Fluctuating biomass suggests tallgrasses resisted grazing. Abundant *C. lignaria* indicated that rebounding of tallgrasses was driven by wet local conditions (e.g., Figure 5.10b; Gelorini et al., 2012; Jarzen and Elsik, 1986). Thus, *C. lignaria* is unsuitable for reconstructing herbivore biomass or density because it is open to several explanations. Thus, many proxies are needed to improve reliability of interpretations.

The positive relationship between macrocharcoal and *Sporormiella* in tallgrass state II, suggested more natural fires or increased burning by people to promote grazing at the key resource area (Figure 5.18). Because wetlands occasionally burn (Just et al., 2015; O’Connor et al., 2011; Vesey-Fitzgerald, 1970), the data support the latter driver of fires. The productive grasses were probably important for Iron Age farmers who arrived in the region from ca. 1 800-1 600 cal BP (Hall, 1981). The wetland supported livestock in dry climatic conditions from ca. 1 900-1 700 cal BP as pointed to by the increase of *Sporormiella* (Chevalier and Chase, 2015; Figure 5.18).

Fire and grazing during the dry period caused the sudden phase transition (T2) to the shortgrass state I. Before the transition, peaks in charcoal and spores happened at ca. 1 730 cal BP and at ca. 1 750 cal BP (Figure 5.18). Sharp declines in grass biomass followed as suggested by the sharp decline in LOI from ca. 1 610-1 590 cal BP (Figure 5.6). Lower C:N values also supported the loss of tallgrass cover as did the increase in soil erosion suggested by the rise in the Zr:Rb ratio (Figure 5.18). Intense fires were the main driver of the reduced stability domain of grass biomass that helped to remove tallgrasses, ushering a shortgrass state from ca. 1 610 cal BP. By reducing grass biomass, herbivores needed less effort to cause a regime shift in consumers (e.g., Perrings and Walker, 1997). Declines in soil moisture indicated by falling iron concentrations happened with the regime shift (Figure 5.18) and fewer *C. lignaria* (Figure 5.7). Thus, the phase transition between shortgrass represented a regime shift from a fire to a grazer stability domain of local grass biomass. However, the phase transition also suggests functional differences in herbivores.

Change from the *C. lignaria* to *Sporormiella* spore cluster suggested functional differences in grazers (Figure 5.7). The transition between clusters at ca. 1 740 cal BP signalled by a sharp decline in *C. lignaria* and more *Sporormiella*, suggested changes in grass biomass marked by LOI that were linked with grazing pressure and/or herbivore biomass (Figure 5.18). Changes in vegetation from c. 2 200-1 610 cal BP have already been discussed. However, reduced local grass biomass and dry soils suggested the importance of indigenous grazers.

Low grass cover and/or biomass and dry soil suggest grazing lawns supported by indigenous grazers (e.g., McNaughton, 1984; Veldhuis et al., 2014). Water-dependent nonmigratory bulk grazers like buffalo and rhino may have moved in to support stable shortgrass patches (e.g., Lock, 1972; Waldram et al., 2008). In the present-day at HiP, more lawns grasses and spores occur where these grazers dominate herbivore biomass (Olsen, 2015). Control of shortgrasses by these herbivores also reduced grass fuels and fires as indicated by low charcoal, supporting results from present-day landscapes (e.g., Waldram et al., 2008).

The gradual increase in local grass biomass leading to the transition to shortgrass state II was suggested by the rise in LOI during a dry climatic period from ca. 1 400-1 200 cal BP (Figure 5.18). Moist local conditions contradicted a dry climate based on increases of iron and *C. lignaria* in sediments (Figure 5.18). Colonisation of previously silted banks by reed grasses increased local biomass after the rise in soil disturbance signalled by a high Zr:Rb ratio from ca. 1 640-1 360 cal BP (Figure 5.18). The contemporaneous increases in the C:N ratio suggests stemmy tallgrasses like *P. australis* that still occupy wetland margins (e.g., Engloner, 2009; Longhi et al., 2008). Intermittent grazing suggested by varying spores increased soil moisture also helped the recovery of tallgrasses in the landscape. Thus, fires returned with more fuel. However, the charcoal and spore data suggest that fire and grazing controlled the continuity of tallgrasses in the landscape since charcoal and *Sporormiella* increased (Figure 5.18).

5.4.3 Alternate stability domains and resilience at a key resource area

Stability domains of grass biomass are useful for assessing the regime shift among alternate consumers and resilience at the key resource area. The clusters of spores and charcoal supported the idea of a gulf in grass biomass and dominant vegetation between tallgrass and shortgrass states (Figure 5.17 and 5.19; Noy-Meir, 1975; Perrings and Walker, 1997). Tallgrass states were associated wet soils indicated by plenty *C. lignaria*. The states also had more charcoal suggesting the importance of fire. In contrast, shortgrass states had fewer *C. lignaria* suggesting dry local conditions. The abundance of *Sporormiella* suggested that heavy grazing reduced grass biomass and soil moisture. At the larger scale, a dry regional climate from ca. 1 600-1 500 cal BP may have triggered the threshold response in local grass biomass by increasing grazing pressure at the key resource area as indicated earlier. This would be consistent with idea that drought and grazing affect the persistence of grasses (Illius and O'Connor, 1999; Owen-Smith, 1996).

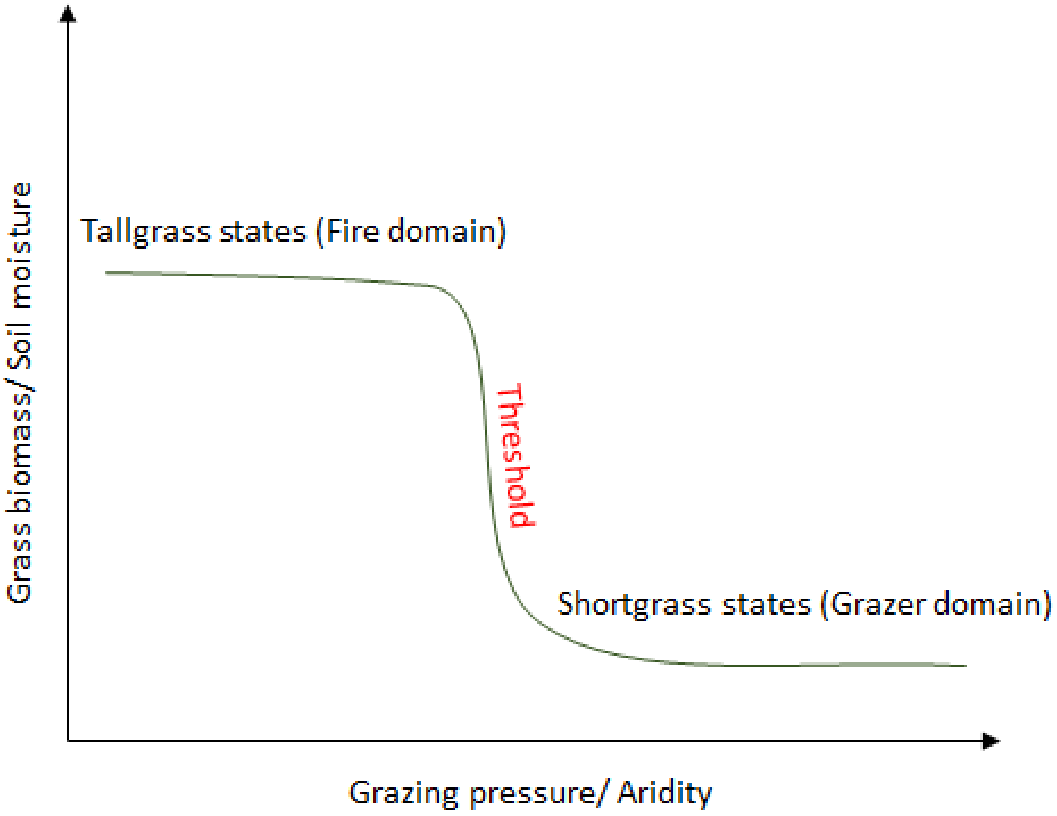


Figure 5.20. A model of alternate consumers states and stability domains at the key resource area.

Changes in fire and grazing among vegetation states suggested alternate consumer stability domains for evaluating resilience. Alternate consumer stability domains are supported by successive tallgrass and shortgrass mosaics separated by a phase transition (Figure 5.17 and 5.20).

Interestingly, phase separation between domains also suggests trade-offs in plant tolerance. Trade-offs have been observed along a single disturbance gradient for tree seedlings at HiP (Staver et al., 2012), and between short and tall grasses in rangelands (Archer, 1989; Augustine and McNaughton, 1998). The data are consistent with state-phase models of ecological resilience (Holling, 1973; Noy-Meir, 1975), and provide evidence of an abrupt regime shift and/or threshold for the savanna. So, these conclusions contribute to advancing debates on the long-term stability and resilience of rangelands (e.g., Gillson and Hoffman, 2007; Illius and O'Connor, 1999; Muthoni et al., 2014; Sullivan and Rohde, 2002; Vetter, 2009b).

However, resilience in current debates from short timescales is synonymous with stability. Research findings from this study suggest the need for separating tallgrass domains that resist combined fire and grazing from shortgrass domains with grazing tolerant species (e.g., Briske, 1996). We cannot rule out degradation for shortgrass state I with high soil disturbance and low grass biomass compared with shortgrass state II, according to grazing catastrophe models. However, shortgrass mosaics lasted for centuries, a surprising result suggesting resilience. In present-day studies, recovery from degraded states may happen within 20 years (e.g., Allington and Valone, 2010; Matchett, 2010). *Perhaps grazing lawn establishment comes at the cost of temporary degradation?* More data are needed to resolve this debate since stability and resilience depend on many local and landscape ecosystem connections.

5.4.2 Fire and grazing effects on soil processes

Soil moisture, grazing pressure, and fire indicated in this study by records of *C. lignaria*, *Sporormiella*, and charcoal affected nitrogen cycling and soil stability (Figure 5.15). Surprisingly, local nitrogen availability represented by the δ^{15} signal increased with grass biomass from shortgrass to tallgrass states (Figure 5.5 and 5.6), and with wet soils indicated by more *C. lignaria* (Figure 5.7). A fall in iron concentrations from ca. 1 610-1 540 cal BP also signalled dry soil. These findings back the idea that heavy grazing suppresses soil nitrogen availability. Trampling alters soil texture, dries soils, and chokes decomposer microorganisms (Elschot et al., 2015; Rietkerk et al., 1997; Schrama et al., 2013). Low-water infiltration rates over trampled soils probably increased soil disturbance based on the rise of the Zr:Rb ratio from ca. 1 640-1 490 cal BP in the shortgrass state I associated with heavy grazing (Figure 5.15). The data suggest dung and urine around at key resource areas are not enough for replacing the undermined soil functioning as argued in other studies (e.g., Cromsigt and Olff, 2008; Holdo et al., 2007).

Support for the idea that water-limitation of nitrogen cycling caused by grazers comes from a grazing lawn vegetation phase from the Kruger National Park savanna (Gillson and Ekblom, 2009a). In this record, the lawn phase had low δ^{15}N and arid conditions. The data suggested a trade-off between water-use efficiency and nitrogen-use efficiency from soils (Gong et al., 2011; Rietkerk and van de Koppel, 1997). However, Stock et at. (2010) argue that midden use by mega-grazers may explain anomalous low soil nitrogen at grazing lawns (e.g., Stock et al., 2010). Nevertheless, results from this study and Gillson and Ekblom (2009a) suggest that fine-textured soils control soil moisture and nitrogen dynamics at wetlands (e.g., Elschot et al., 2015; Kotze and O'Connor, 2000; Rietkerk and van de Koppel, 1997; Schrama et al., 2013).

The decline in local grass biomass with increasing soil erosion indicated by LOI and Zr:Rb ratio respectively (Figure 5.16c), suggests the removal of grass caused by herbivores and a limiting of the nitrogen pool marked by low TN. Nevertheless, some Chloridoideae shortgrasses found in lawns have low resource needs (e.g., water and nitrogen) compared with Panicoideae tallgrasses (Edwards et al., 2010; Grime, 1977).

Changes in grazing in tallgrass mosaics affected soil erosion at vegetation establishment around the wetland. Tallgrasses recolonised the wetland from ca. 1 400 cal BP as indicated by more LOI after high soil disturbance marked by a high Zr:Rb ratio. These data suggest that reed grass dominance around some wetlands are legacies of past disturbance by herbivores (e.g., Hutchinson and Pitman, 1973). Establishment by the grasses stabilised soils as indicated by the drop in the Zr:Rb ratio. Also, local soil moisture increased as evidenced by more *C. lignaria* and iron concentrations (Figure 5.18). These findings suggest resilience because reversing of negative effects on grass cover and soil happened in wet periods with relaxed grazing pressure (e.g., Allington and Valone, 2010; Matchett, 2010; Prince et al., 2007).

5.4.4 Implications for interpreting palaeoecological data

Conclusions from this study suggest that herbivores and vegetation alter conditions around wetlands, may affect the sensitivity of proxies. For example, the support of wetland grazing lawns reduces soil moisture that can affect the preservation of spores, and their interpretation (Wood and Wilmshurst, 2012). Tallgrasses also altered soil and grass biomass at wetlands as indicated above, increased fires in a dry climate period. These two effects suggest the stability domains approach for interpreting multiple proxies is useful for resolving nonequilibrium dynamics at key resource areas driven by local and landscape-regional drivers discussed in sections 5.4.2 and 5.4.3.

5.4.5 Implications of present study on rangeland management

Results of this study suggest that long-term data gives a basis for assessing ecological degradation and nutrient cycling in rangelands. The stable shortgrass mosaics analysed lasted for a long time (i.e., ca. 1 610-960 cal BP). In the present-day, many indigenous grazers (e.g., wildebeest, zebra and warthog) and low rainfall support the grazing lawn (Archibald et al., 2005b; Cromsigt et al., 2017; Veldhuis et al., 2014; Waldram et al., 2008). We do not know whether these lawns are a legacy of past disturbance by indigenous shortgrass grazers like white rhinos and wildebeest (e.g., Waldram et al., 2008). However, this study supports the idea that the wetland grasslands are resilient because the HiP one remains to the present day. The long grazing history and able grazers may have kept lawns tolerant of grazers and drought, which increase local resilience of vegetation (e.g., Cingolani et al., 2005).

Although shortgrass states were resilient, they were susceptible to high soil erosion and reduced nitrogen cycling at the formative stage. This raises the question of the extent of soil effects and whether heavy grazing is sustainable over a larger landscape-scale. Disturbances at HiP were probably local, but if they occurred over a larger area, they would alter the ecosystem. For example, the data suggests that droughts and herbivory may have negative effects on river flow and volume by increasing sediment loads around key resource areas (e.g., Ripple and Beschta, 2003).

5.4.4.1 Long-term nitrogen availability

Overall, the results suggest that heavy grazing had negative effects on grass biomass, soil nitrogen cycling, and soil moisture in productive grasslands. The data suggests that continuous heavy grazing may limit nitrogen through direct removal of grass biomass and reduced microbial decomposition of plant matter in compacted soils (Schrama et al., 2013). Although barren, eroded, and sparse shortgrass patches are associated with continuous heavy grazing (Rietkerk et al., 1997, 2000; Schrama et al., 2013), their long-term effects are unknown.

Following wet local conditions, results from this study suggest a decline in soil erosion signalled by the falling Zr:Rb ratio, coincided with an increase in nitrogen (TN) and its availability (δ^{15}N). Grass cover also increased as indicated by more LOI (Figure 5.18). Therefore, shortgrass states and barren zones at key resource areas may be temporary natural features in African rangelands. Persistence of degraded patches depends on climate, grazing, fire, soil moisture, soil texture, and resilience of vegetation. For example, wetland grasslands classified as degraded in the Kruger National Park following droughts and heavy grazing in the 1990s showed remarkable recovery of vegetation and soil in 2006/7, suggested resilience (Matchett, 2010). These areas are cited as examples of irreversible degradation in grazing catastrophe models (Rietkerk et al., 1996; Rietkerk and van de Koppel, 1997; Sinclair and Fryxell, 1985), which, however, discount the importance of resilience. But caution is needed by actively monitoring range conditions to prevent signs of degradation and may include restricting herbivore access to productive grasslands if necessary (e.g.,van Coller and Siebert, 2015).

5.4.6 Reliability of proxies

I have presented a multiple proxy interpretation of vegetation states and their drivers at a key resource area that is considered the best hypothesis based on available data. Although agreement occurred among the proxies examined, grass states and herbivores might be further resolved with grass phytoliths (e.g., Bremond, Alexandre, Wooller, et al., 2008; Finné et al., 2010) and environmental DNA (e.g., Giguet-Covex et al., 2014), respectively. Alternatively, vegetation states and ecosystem processes from proxies used in this study are comparable with many other published records using classification and/or regression approaches or calibration datasets (e.g., Sobol and Finkelstein, 2018). This alternative helps to quantitatively define stability domains. In addition, more dates are needed for improving the dates and for finding instances of sediment mixing (e.g., Ekblom and Gillson, 2010a).

5.4.7 Conclusion

The data suggest that in the savanna, key resource area grasslands are resilient in the face of changing rainfall, grazing, fire, and soil processes. Fast growth and flammability of tallgrasses were considered traits for surviving fire disturbance. In comparison, a short-stature, arid-adaptation, palatability, and positive response to grazing allow shortgrasses to tolerate continuous heavy grazing. Resilience of grass biomass at the local-scale at HiP was maintained by trade-offs in grass tolerance between consumer domains. Fire was important from ca. 2 140-1 610 cal BP when tallgrasses dominated. The period was contemporaneous with the arrival of Iron Age farmers in the park and increased herbivore biomass. Heavy grazing and more fires happened before the abrupt regime shift from fire-driven tallgrass to grazer-driven shortgrass grazer states at ca. 1 610 cal BP. Dry climatic conditions from ca. 1 600-1 500 cal BP may have precipitated the decline, suggesting the importance of climate-herbivore feedback responses, consistent with the key resource area idea.

Heavy grazing in shortgrass state I caused declines in tallgrasses, soil moisture, and nitrogen availability. These results suggest that nitrogen cycling depends on soil function (i.e., texture, porosity) compared with herbivore dung and urine inputs at the key resource area. Continuous heavy grazing promoted shortgrasses development and maintenance. Thus, fire and grazing occupied separate stability domains of grass biomass. Since the phase transition between grazing and fire domain involved an abrupt ecological threshold, this suggests management actions may be implemented beforehand to prevent undesirable vegetation transitions. For example, with herbivore population control or manipulation of grazer movements, especially when there are reliable climate predictions. Also, because the shortgrass state is productive and desirable state for herbivores, trade-offs happen between herbivore management and preserving ecosystem processes provided wetlands.

Chapter Six. **Synthesis and Conclusion**

6.1 Introduction

In this thesis I compared vegetation and soil changes resulting from rainfall, grazing, and fire between a mesic grassland and a semi-arid savanna over millennium timescales. Grass production and nutrients in the ecosystems studied are in constant flux. Thus, there are several ideas proposed for understanding instances of stability. This chapter discusses ideas about grass stability domains, resilience and thresholds, and hierarchy around key resource areas. This study has implications for rangeland management, resilience theory, interpretations of proxies, and future work.

Grass production at key resource areas supported high grazer densities and fires over long timescales. As expected, grass production and soil function declined during dry climatic periods. This suggested the partitioning of landscape into wet and dry climate foraging zones. Herbivore densities were controlled by grass production around wetlands, with weak coupling happening with distance from wetlands (Illius and O'Connor, 1999). However, this contradicted the disequilibrium idea that suggests frequent droughts reduce grazer numbers, minimising negative effects on vegetation and soil (Behnke and Scoones, 1992; Ellis and Swift, 1988).

However, the key resource area idea has not been combined with the multiple stable states and resilience theories at long timescales (e.g., Briske et al., 2017; Gillson and Ekblom, 2009). Also, there is no clarity about the role of fire and its effects on grazing, vegetation stability, and soil processes at key resource areas at long timescales.

In this study, relations among rainfall, grazers and fire on grass biomass and soil fitted into the grass stability domains (Chapter One). Tallgrass and shortgrass states in the domains were independently assessed with fossil grasses, charcoal, and spores. Meanwhile, soil degradation resulting from heavy grazing was signalled by high soil erosion and reduced nitrogen availability. Multiple vegetation states and transitions between them were understood using the thresholds and resilience theory (Gillson and Ekblom, 2009a). The following sections answer questions set-up in Chapter One.

6.2 Vegetation stability and thresholds at key resource areas

I was interested in learning how grass states suggesting stability domains at key resource areas reflected consumers (i.e., fire and grazing) and soil moisture using proxy data. I then arranged the domains by gradients of grass biomass, palatability, aridity, and flammability. In this thesis, the two vegetation states (tallgrass and shortgrass) were used for describing local wetland grass mosaics. Tallgrasses were driven by high soil moisture and mostly consumed by fire. In contrast, shortgrasses depended on arid soils caused by drought and heavy grazing. A summary of vegetation states and their drivers at the grassland and savanna are provided to contextualise this discussion (Table 6.1).

Results from this study suggest that rainfall and soil wetness promote tallgrass states in key resource areas (Figure 6.1). Compositionally, tallgrasses were defined by importance of phytoliths from Arundinoideae and Panicoideae subfamilies. From a consumer perspective, the flammable grasses signalled high fire activity had abundant charcoal except for the *Phragmites*-dominated tallgrass state in the grassland with high soil moisture. However, local soil moisture indicated by *C. lignaria* spores (e.g., Gelorini et al., 2012), was high and variable but not entirely coupled to regional rainfall in savanna from ca. 1 500-960 cal BP (Chapter Four), and in grassland from ca. 600-300 cal BP (Chapter Five).

Interestingly, times when regional rainfall contrasted with soil moisture in tallgrass mosaics were caused by heavy grazing. This suggests swings in moisture were herbivore-driven and related to eating grasses in burned patches. Still, fire was the dominant consumer, supporting the idea of a fire stability domain.

Table 6.1. Summary of relationships among vegetation states, disturbance intensity, vegetation structure and regional rainfall (Chevalier and Chase 2015) at the savanna and grassland key resource areas. Vegetation states preceded by an ecological threshold are shaded.

	Vegetation States	**Chronology**	**Grazing Pressure**	**Fire Activity**	**Patch Structure**	**Rainfall**	**Erosion**
Grassland	Wetland Tallgrass	Present 410 cal BP	Light	Low	Homogenous	Variable, decreasing	intermediate
	Mixed Tallgrass	410 cal BP 690 cal BP	Intermediate/ Heavy	High	Heterogenous	Decreasing	Initially low then high
	Shortgrass	690 cal BP 1 220 cal BP	Heavy	Low	Homogenous	Increasing, recovery from low values	intermediate
Savanna	Shortgrass II	960 cal BP 1 340 cal BP	Intermediate/ Heavy	Low	Homogenous	Initially decrease then increase	intermediate
	Shortgrass I	1 340 cal BP 1 610 cal BP	Heavy	Low	Homogenous	Initial decrease then increase	High
	Tallgrass II	1 610 cal BP 2 020 cal BP	Intermediate/ Heavy	High	Heterogenous	Initially high then decrease	Low
	Tallgrass I	2 020 cal BP 2 140 cal BP	Light	Low	Heterogenous	High	Decreasing

However, tallgrasses were replaced by shortgrasses in the grazer domain in dry periods because fires also increased local grazing pressure (Table 6.1). For example, the vegetation abrupt phase transition (regime shift/threshold) from tallgrasses to shortgrasses from ca. 1 600-1 500 cal BP, was preceded by heavy grazing, a rise in fire activity, and drought in the savanna (5.18). Later, the shortgrass state still in the grazer domain was maintained by heavy grazing and low rainfall. In comparison, the shortgrass state in the grassland dominated by Panicoideae and Chloridoideae from ca. 1 250-690 cal BP, was supported by heavy grazing despite rising regional rainfall. For example, soil moisture in the savanna was low as indicated by few *C. lignaria*. Despite tolerating arid soil conditions, palatable grazing lawns are also highly productive (e.g., Bonnet et al., 2010; McNaughton, 1984).

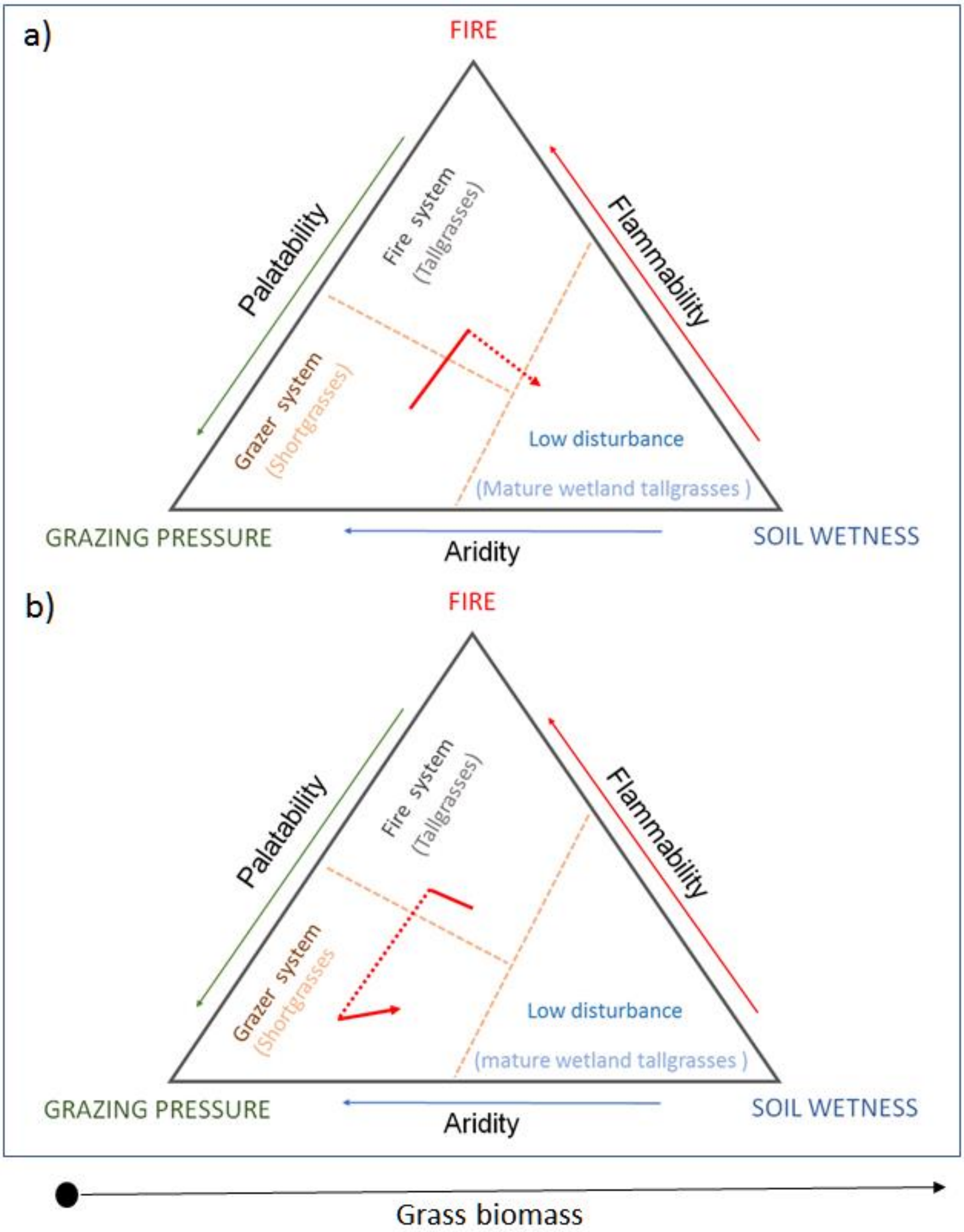


Figure 6.1. Phase space summary diagram tracing state transitions along consumer stability domains in a) grassland; and b) savanna. Evolution of system states depended on initial conditions indicating nonlinearity. Stability or persistence of states is an emergent property of aridity, flammability, and palatability factors. Phase transitions or tipping points can occur when domains are crossed as shown by dotted lines while resilience is assumed when successive states occur in the same stability domain.

It is suggested that grass dynamics at the contrasting key resource areas are described by consumer stability domains of vegetation biomass (Figure 6.1; Perrings and Walker, 1997). Persistent vegetation states in stability domains were linked to dominant growth-forms. Relatively homogeneous biomass was linked with stable/equilibrium states (e.g., Taylor and Woiwod, 1980), supporting part of the nonequilibrium theory (Illius and O'Connor, 1999). Shortgrass states associated with heavy grazing, increased the local extent of grazing-tolerant lawns and reduced grass productivity. The alternative stable state was the wetland mature tallgrass in the mesic grassland with low disturbance. Its absence in the savanna might be linked to low rainfall and heavy grazing that limited grass productivity and stability domains.

In comparison, dynamic tallgrass states with heterogenous biomass persisted in the fire-driven domain. Unlike the homogeneous states, tallgrasses from the landscape was connected to wetland vegetation, resulting in the regular encroachment of wetlands by flammable C_4 tallgrasses (Just et al., 2015). Drought and soil aridity probably increased the flammability of tallgrasses that amplified grazing pressure. These interactions characterised by trade-offs between local grass palatability and flammability (Allred et al., 2011; Archibald and Hempson, 2016; Hobbs et al., 1991), were probably responsible for fluctuating biomass and straddling of neighbouring domains. The straddling behaviour suggests disequilibrium vegetation dynamics or instability (Ekblom and Gillson, 2010b; Ellis and Swift, 1988; Fuhlendorf and Engle, 2004). Importantly, the tallgrass states in the fire and low disturbance domains support contemporary studies showing that grazers struggle to maintain low grass biomass in mesic grasslands without help from fires (e.g., Archibald et al., 2005a; Hobbs et al., 1991; Knapp et al., 1999; Waldram et al., 2008).

6.3 Synthesis

6.3.1 Resilience and hierarchical organisation of ecosystem dynamics at key resource areas

Resilience representing the capacity of ecosystems to absorb disturbance (Holling, 1973), affected stability of grass biomass states of key resource areas at multiple scales. Resilience was considered from the perspective of grazing intensity, on a scale of degraded soil and vegetation or no adverse effects (Illius and O'Connor, 1999). This section discusses results from the two study sites using stability domains (Figure 6.1).

Consecutive shortgrass states in savanna driven by positive feedback responses between low rainfall, heavy grazing, and soil aridity suggested resilience within the grazer stability domain (Figure 6.1b; Table 6.1). In comparison, the preceding tallgrass states in the fire domain that also supported heavy grazing, is an example of resilience as resistance stability (Connell and Sousa, 1983; Holling, 1973). The distinction between resilience in the face of positive feedback and resistance caused by negative feedback responses, not clearly defined by Illius and O'Connor (1999), is demonstrated. Illius and O'Connor (1999) equivalents for susceptible and resistant key resources areas now fall under resistant and resilient, respectively. As expected, the boundary between the stability domains indicated a phase transition (Table 6.1), consistent with predictions from resilience theory (Connell and Sousa, 1983; Folke et al., 2016; Gillson and Ekblom, 2009a; Holling, 1973; Walker and Meyers, 2004).

The hierarchical partitioning of landscapes grazing resources into wet climatic and dry climatic periods forms the basis for synthesis (Illius and O'Connor, 1999; Muthoni et al., 2014). Thus, long-term grassland dynamics depend on interaction among climate, fire activity, grazing pressure, and soil moisture at multiple spatial scales with resilience as an emergent property. Relationships among ideas acting at different spatial and temporal scales are presented using a hierarchical framework (Figure 6.2).

Climate drove ecological dynamics at key resource areas, affecting partitioning of foraging resources, distributions of grazers, and activities of pastoralists (Table 6.1). Water scarcity and grass production increased local grazing pressure, especially at low rainfall. However, changing fire activity in landscapes affected herbivore distributions patterns (Allred et al., 2011; Archibald and Bond, 2004; Hobbs et al., 1991). Lightning, pastoralists, and reserve managers were agents of fire activity. Movements of herbivores to other parts of landscapes relaxes wetland grazing pressure limits the strength of herbivore-vegetation-soil equilibrium(s) (Ripple and Beschta, 2003). Unsurprisingly, disequilibrium dynamics dominate in wider landscapes where grazers control grass biomass in small areas. For example, grazing lawns make up less than three percent in some landscapes of Kruger National Park (Yoganand and Owen-Smith, 2014), and less than 10% of HiP (Archibald et al., 2005a).

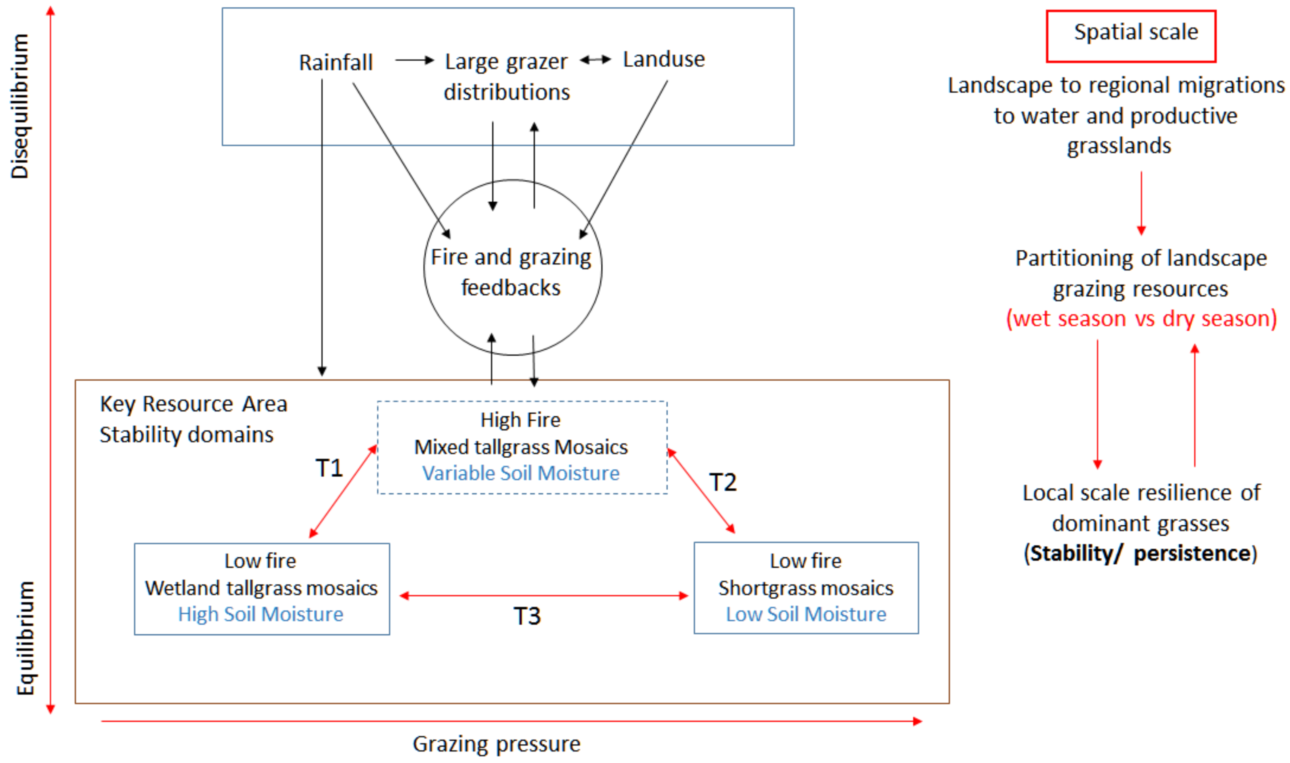


Figure 6.2. Hierarchical framework of climate, land use, intensity of disturbance, equilibrium strength, and stability domains at key resource areas. The stability domain phase space of key resource areas is driven by higher level processes. Transitions between stability domains (Ti) may include ecological thresholds.

6.3.2 Theoretical contributions

This thesis contributes a few ideas to current stability debates in dynamic rangeland grazing systems and to resilience theory. My work suggests that grass production at large spatial scales in grasslands and savannas is at disequilibrium flux with climate, grazing, and fire. However, local-scale islands of stability (equilibrium) occurred in the sea of instability (disequilibrium). I extended Illius and O'Connor's (1999) nonequilibrium theory for key resource areas by proposing a multiple-scale hierarchical framework for thinking about the stability domains of grass biomass. Stability domains included stable and unstable vegetation and soil states, consistent with nonequilibrium theories (Briske et al., 2017; Gillson and Hoffman, 2007; Illius and O'Connor, 1999; Sullivan and Rohde, 2002; Vetter, 2005). Nonequilibrium processes extended to nitrogen cycling. Importantly, disequilibrium dynamics from the tallgrass fire domain suggests instability was caused by coexistence of contrasting growth-forms at large scales. The theoretical equivalent for disequilibrium is HPD (e.g., Gillson, 2004a; Wu and Loucks, 1995).

The thresholds/phase transitions found between stability domains supported ideas from resilience theory (Folke et al., 2004; Gillson and Ekblom, 2009a; Holling, 1973). Evidence for abrupt and gradual phase shifts in grasslands was supported by changes in grass biomass stability domains, consistent with theoretical predictions of multiple stable states (Noy-Meir, 1975; Perrings and Walker, 1997; Scheffer et al., 2009). However, I did not find evidence for permanent grass states in timescales studied as suggested by other studies (e.g., May, 1977; Noy-Meir, 1975). Stability domains of grass fuel may also improve the interpretation of fire regimes palaeoecological data (e.g., Power et al., 2008; Whitlock et al., 2010).

Stability domains also suggest that grass communities in grasslands and savannas are structured along disturbance (Archibald and Hempson, 2016; Chase and Leibold, 2003;

Grime, 1977; Levin and Paine, 1974; Staver et al., 2012), and resources gradients (e.g., light and water) (Grime, 1977; Tilman, 1986c). Dominance of growth-forms along the gradients therefore involve trade-offs related to life-history traits (Chase and Leibold, 2003; Clements, 1936; Grime, 1977; Tilman, 1985). Grazing and aridity representing disturbance and resource control were major drivers of grass biomass dynamics at key resource areas. To my knowledge, no palaeoecological study had been conducted to assess combined resource and disturbance controls on grass dynamics in grasslands. My research shows that there are several spatial levels of interaction depending on rainfall, vegetation, grass consumers, people, and soil that occur over long timescales.

6.3.3 Contrasting nonequilibrium theories

In this thesis, sediment proxy data were used to test the key resource area nonequilibrium theory although there is a competing idea. HPD widely used in rangeland management is an alternative for interpreting changes in grass productivity (e.g., Ekblom and Gillson, 2010; Gillson, 2004). According to HPD, stability of vegetation and herbivore distributions happen at larger spatial scales with instability at local scales. State-phase transitions with HPD suggests changes in scale of processes driving ecosystems (e.g., Ekblom and Gillson, 2010; Gillson, 2004; Wu and Loucks, 1995). This expectation of local-scale instability, despite evidence of persistence grazing lawns, is worth commenting on.

The multiple stable grass states found at key resource areas suggested strong local feedback on resilience. Herbivore and grass fitness clash at wetlands (e.g., Hempson, Illius, et al., 2015; Owen-Smith, 1987; Scoones, 1992; Sinclair et al., 1985; Vrba, 1987), and give clues about conditions of density-dependent resilience (Illius and O’Connor, 1999). Meanwhile, the density-dependent stable states are not predicted by HPD without invoking higher level control by herbivore distributions or soil factors (e.g., Gillson, 2004). Therefore, local stability at wetland grasslands is incompatible with the HPD framework for stability, suggesting that it may not be suitable for assessing key resource areas at long timescales.

Surprisingly, HPD is useful for vegetation in the wider landscape including wet season foraging areas (e.g., Illius and O'Connor, 1999). Since I did not investigate dynamics at wet season foraging areas, I cannot compare the merits of the two approaches. It is safe to assume that the two theories suggest different ideas about stability and scale and are not equivalent between the approaches.

6.4 Implications of this study on rangeland management

Ecological patterns and processes in present landscapes are legacies of past environmental interactions (Fukami, 2015; Gillson, 2009). In terms of managing ecosystems for persistence, palaeoecological insights are valuable (Gillson and Duffin, 2007; Gillson and Marchant, 2014). Ecosystem managers responsible for decision making will, therefore, benefit from palaeoecological records but their scarcity and technical jargon may limit their usefulness (Gillson and Marchant, 2014). Therefore, reflecting on long-term perspectives is necessary because decisions about resource use involve trade-offs regularly leading to unequal results for wildlife and people, often with long-term consequences (Benjaminsen et al., 2009; Conway et al., 2005; Kanga et al., 2013). In this section, I have highlighted insights about the management of bush encroachment, nutrient hotspots, and resilience in social-ecological systems as important contributions arising from this study.

6.4.1 Bush encroachment

The increase of woody plants in open grassy ecosystems is a cause of concern in rangelands where fire, herbivores and rainfall variability interact (Archer et al., 1995; O'Connor et al., 2014; Skowno et al., 2017; Stevens et al., 2016; Watson and MacDonald, 1983; Westoby et al., 1989), and from high atmospheric carbon dioxide (Bond and Midgley, 2012). Mesic regions and riparian areas including key resource areas are vulnerable to invasion by woody plants (O'Connor et al., 2014; Saintilan and Rogers, 2014; Skowno et al., 2017). Loss of grass cover from heavy grazing (Acocks, 1953; O'Connor et al., 2014) and drought (Tinley, 1982), are considered important drivers of encroachment. In this study, a strong relationship was found between grazing pressure and drought (Table 1), supporting the idea that grazing can displace grasses around wetlands.

Global increases in tree cover are also linked to plant physiological responses to the rise in atmospheric CO_2 favouring trees (Bond and Midgley, 2012). More atmospheric carbon dioxide promotes root and stem growth and storage tissue in several common fine (*Vachellia karroo* and *V. nilotica*) and broad-leaved (*Terminalia sericea*) savanna trees, may facilitate the escape of trees from fire and herbivore damage.

Results from this study suggest that local interactions between drought and herbivory helped tree establishment around wetlands by lowering grass biomass, limiting fire, and through seed dispersal from herbivore dung. First, the documented march of fine leaf savanna trees into montane grasslands along riparian zones in the last 80 years are legacies of heavy grazing effects on soil (e.g., Grellier et al., 2012; O'Connor et al., 2014; Roques et al., 2001). Second, low fire return intervals along drainage wetlands (Just et al., 2015; O'Connor et al., 2011) may increase the survival of tree seedlings (Wakeling et al., 2011). This would allow trees to recruit as suggested by the increase in tree phytoliths at grassland site from ca. 410 cal BP to present when fire activity was low.

Last, diverse herbivores probably aided tree invasion by increasing local seed-banks with their dung (e.g., Olff and Ritchie, 1998). Most of deposition would happen in droughts when they range widely in landscapes but depend on wetlands (Redfern et al., 2003). This suggests that networks of key resource areas help savannas to colonise grasslands. The latter is a testable idea with data from comparing tree pollen and genetics around wetlands with the wider landscapes.

Tree encroachment of open environment preferred by grasses has been observed with sediment records (e.g., Gillson and Ekblom, 2009a). Once established, trees are difficult to displace even with fire (Watson and MacDonald, 1983; Westoby et al., 1989), and are therefore considered an alternative stable vegetation phase (Gillson and Ekblom, 2009a; Staver et al., 2011). The stability domains proposed in this thesis are useful for helping landscape managers to halt the encroachment of susceptible landscapes by controlling herbivore densities, fires, and tree seedlings around wetlands.

6.4.2 Management of nutrient hotspots

Soils around wetland margins are valuable mineral nutrient hotspots for large herbivores (Grant and Scholes, 2006; Seagle and McNaughton, 1992). Wetland grazing lawns are high in macronutrient concentrations of nitrogen, calcium and magnesium, and potassium. However, some soils may have low mineral concentrations (Stock et al., 2010), low nitrogen availability (Bakker et al., 2009; Gillson and Ekblom, 2009a; Schrama et al., 2013), with middens associated with the former, and changes in soil structure responsible for the latter. Not much is known about the antiquity of key resource area hotspots despite their importance to herbivore nutrition and survival (Coller and Siebert, 2015; Khomo and Rogers, 2005; Vesey-Fitzgerald, 1970). In this study, wetland soil mineral concentrations were influenced by interactions among climate, soil moisture, fire, and grazing pressure.

Herbivore activity around wetland margins had contrasting effects on soil macronutrients. At the mesic grassland, the shortgrass state was associated with high calcium, potassium, and nitrogen. Heavy grazing was indicated by shortgrasses (Table 6.1), and high nitrogen and calcium typical of grazing lawns after regionally dry climatic conditions. In contrast, high values for nitrogen and calcium were associated with tallgrass state II, compared with low values for shortgrass state I, at the semi-arid savanna. In the tallgrass state, soil moisture and herbivore biomass were high as indicated respectively, by *C. lignaria* and *Sporormiella*. However, shortgrass state I, with low nitrogen and rainfall but with heavy grazing had arid soils caused by trampling by herbivores as suggested by the rise in soil disturbance (Zr:Rb ratio). The decline in soil δ^{15}N, suggests a trade-off in rain water use efficiency and nitrogen-use efficiency in dry soils (Gong et al., 2011), initiated by herbivores affecting the structure of fine-grained soils (Schrama et al., 2013; Veldhuis et al., 2014). Interestingly, shortgrasses from wetlands tend to have higher leaf nitrogen concentrations compared with matrix vegetation (Arnold et al., 2014; Craine et al., 2009), this is despite the variation in soil nutrient concentrations.

Since wetlands are connected to wider landscapes, predicting local nutrient dynamics is complex because mineral concentrations are an emergent property of cross-scale interactions among climate, vegetation, fire, grazers, soil moisture and soil texture. Thus, nutrient pools in grasslands are controlled by nonequilibrium processes as found in other studies (Blair, 1997; Coetsee et al., 2012; Seastedt and Knapp, 1993). Therefore, vigilance has to be maintained by constantly monitoring site-specific factors such as rainfall, herbivore biomass and type, grass composition and biomass, and soil to detect adverse changes (Augustine and McNaughton, 2006; McNaughton, 1983; Rietkerk and van de Koppel, 1997). The good news was that following wet periods and when herbivore pressure was relaxed, soil nitrogen increased, suggesting that degradation signals are temporary and reversible phenomena associated with surviving droughts in natural environments.

6.4.3 Carbon sequestration

Wetland soils and sediments are valuable carbon sinks for managing atmospheric greenhouses gases (Bridgham et al., 2006; Elschot et al., 2015; Kayranli et al., 2010;

McCarroll et al., 2016; Moreno-Mateos et al., 2012). Stability domains of grass biomass explored in this thesis provide a useful benchmark for assessing past soil/sediment carbon fluxes at key resource areas, potentially reducing uncertainties in estimates of carbon dynamics at wetlands (Elschot et al., 2015; Ma et al., 2016; McLauchlan et al., 2014). For example, estimates of burned biomass and atmospheric carbon for Africa have high uncertainty compared to other continents (Brucher et al., 2014). However, wetlands also release carbon when they dry because increased decomposition rates release more methane (Cao et al., 2012; Davidson and Janssens, 2006; Kayranli et al., 2010; Mitsch et al., 2012).

Disturbance of wetland vegetation by herbivores and fire influence the storage of carbon in sediments (Elschot et al., 2015). In this study, tallgrass states had more organic carbon in sediment and experienced high fire activity compared to shortgrass states maintained by heavy grazing or drought. Technically, there is potential for relating contrasts between *Sporormiella* and *C. lignaria* that point to herbivore biomass and soil moisture respectively (Gelorini et al., 2012), for assessing local herbivore effects on vegetation and build-up of carbon stocks. Interestingly, *C. lignaria* may be used as indirect signals of local grass productivity and fire activity. So, multiple proxies approaches promise to improve accountability of past and present wetland carbon stocks at herbivore landscapes for the benefit of carbon sequestration.

6.4.4 Soil erosion

Rangeland managers manipulate herbivores density and grazing pressure that drive undesirable soil losses in grazing systems (Bestelmeyer et al., 2017; Briske et al., 2005; Illius and O’Connor, 1999). In this study, soil disturbance increased during periods of heavy grazing pressure (Figure 6.1). Thresholds in grass cover were associated with positive feedback between heavy grazing and drought that hastened soil erosion. Hence, thresholds in grass cover used to monitor range vegetation and soil condition in rangelands (Briske et al., 2005; Illius and O'Connor, 1999; Read et al., 2016), may be linked to those found in this sedimentary study.

Following periods of high soil disturbance, it was interesting to find that the wetland tallgrasses dominating wetland margins stabilised soils (Figure 6.1). In the montane grassland, unpalatable *Phragmites* reed grass cover associated with low soil disturbance signalled a shift in ecological function suggesting reduced grazing potential. This discovery suggests that invasive *P. australis* dominance are linked with heavy grazing and erosion. Alternatively, this study also suggests that in some contexts, interaction among drought, fire, and indigenous grazers can control reed grasses. Therefore, droughts are an important time for controlling hardy reeds, especially with continuous and unselective heavy grazing (e.g., Cornelissen and Vulink, 2015; Deursen and Drost, 1990). But it happens at the cost of soil loss.

However, recent studies of carnivore-herbivore interactions at HiP suggest that grazers below 1 000 kg avoid areas with tallgrasses where large carnivores can hide (Le Roux et al., 2018). This suggests infrequent use of tallgrass-dominated key resource areas. Therefore, soil erosion is expected to be negligible at these areas except when fires attract grazers. By killing herbivores or keeping them on the move, carnivores relax local grazing pressure, and promote vegetation and soil recovery. For example, reintroducing wolves (*Canis lupus*) to control elk (*Cervus elaphus*) populations halted degradation at riparian areas in Yellowstone National Park, caused the recovery of trees and improved water quality (e.g., Ripple and Beschta, 2003).

The recovery of vegetation and soil condition during wet periods in this study did not support the claim of irreversible degradation at key resource areas (e.g., Illius and O'Connor, 1999; van de Koppel et al., 1997). This highlights challenges in the current degradation paradigm (e.g., Allington and Valone, 2010; Prince et al., 1998, 2007), suggesting that a long-term perspective to ecosystem functioning that considers the resilience of grazing systems is necessary.

6.4.5 Resilience in social-ecological systems

Wetlands provide important ecosystem services supporting agriculture, livestock production, and wildlife resources for people in grassland and savanna in drylands (Scoones, 1991; Vetter, 2009a). Because of their persistence, wetlands have social (Adams, 1993; Benjaminsen et al., 2009; Conway et al., 2005; Thebaud and Batterbury, 2001), economic (Adams, 1993; Okpara et al., 2016; Scoones, 1991), and ecological consequences (Adams, 1993; Conway et al., 2005; Sinclair and Fryxell, 1985; Varis and Fraboulet-Jussila, 2010). In this study, the savanna protected area and montane grassland previously occupied by farmers and/or pastoralists are two extremes of social and ecological objectives in resource management. Grass production and water at both wetlands, varied with climate and soil, which affected grazing patterns.

Coexistence of indigenous and domestic herbivores, and multiple uses of wetland resources for agriculture and livestock production persists to the present day in sub-Saharan Africa (Ingram, 1991; Scoones and Cousins, 1994; Sitters et al., 2009). Food security ensured by water provisioning, soil nutrients, and grass productivity, is an important ecosystem service driven by hydroclimatic (i.e., soil moisture and rainfall) variability (Conway et al., 2005; Okpara et al., 2016; Scoones, 1992). While I found that rainfall, fire, and low rainfall affected soil grass biomass and soil stability at both sites, both herbivore types may have been responsible for ecological changes since they cannot be distinguished with spores (e.g., Baker et al., 2013). While I cannot speculate about how resources were used in the past, present patterns of use suggest that pastoralists migrate their herds over great distances and rely on wetland grasslands (Benjaminsen et al., 2012; Scoones, 1991; Sinclair and Fryxell, 1985).

Although fire is a natural phenomenon in grassy ecosystems (Archibald et al., 2011), people purposely light fires at occasional wetlands to increase pasture for their livestock. Therefore, people caused more fire activity in landscapes.

The balancing of social and ecological needs practised by pastoralists and farmers is inherently political (Benjaminsen et al., 2009; Maconachie et al., 2009; Scoones, 1991), and is the responsibility of reserve managers (Kanga et al., 2012; Somers and Hayward, 2012), makes up connected social-ecological systems (Gillson and Marchant, 2014; Holling, 2001). This suggests resilience of vegetation at key resource areas discussed in the preceding sections is important for peoples livelihoods because of the direct effect on livestock production (Scoones, 1991; Sullivan and Rohde, 2002), agricultural production (Ingram, 1991; Jogo and Hassan, 2010; Scoones, 1991), wildlife management (Owen-Smith, 1996; Redfern et al., 2003; Sinclair et al., 1985; Yoganand and Owen-Smith, 2014), and political stability (Adano et al., 2012; Benjaminsen et al., 2009; Scoones and Cousins, 1994; Thebaud and Batterbury, 2001).

Ecological restoration, conservation, and social justice are three areas where palaeoecological data has relevance (Gillson and Marchant, 2014). The paucity of long-term sediment data limits the setting-up of suitable environmental benchmarks for managing these three factors. Stability domains of grass mosaics are useful for assessing changes with sediment data. Since grass states were related to ecosystem functioning, in this case grazing and soil conservation, they signalled changes in range condition (Briske et al., 2005; Šmilauer et al., 2015; Teague et al., 2011). Importantly, the findings are presented in an accessible form for ecosystem managers and policy-makers (e.g., Gillson and Marchant, 2014).

For example, the transition between the tallgrass state II and shortgrass state I at the savanna in response to increased grazing pressure and drought could set up a *critical* *threshold* related to degradation (e.g., Briske et al., 2005; van de Koppel et al., 1997), and a *functional threshold* (e.g., Briske et al., 2005), associated with the development of grazing lawns preferred by herbivores (e.g., McNaughton, 1984; Waldram et al., 2008).

Distinguishing among thresholds is important as some changes are easily reversible, while other changes like bush encroachment are hysteretic. Last, livestock herders have been blamed for degrading rangelands (Illius and O'Connor, 1999; Lamprey, 1983; Rietkerk et al., 1996; Sinclair and Fryxell, 1985), and this harsh view is continued by some governments and aid agencies (Prince et al., 2007; Sullivan and Rohde, 2002). However, degradation occurs during droughts in communal and protected areas with recovery happening when wet conditions return (Matchett, 2010; Prince et al., 1998). The harsh opinion remains (Prince et al., 2007). In a sense, long-term research outlined in this thesis may restore herder's dignity by shifting the focus from perceived causes to building resilience and adaptation as droughts are certain.

6.5 Alternative interpretations of proxies

We depend on proxy data to understand ecosystem processes that happen in past and present landscapes. My research findings suggest proxies are not always faithful and perform poorly in nonequilibrium systems. Therefore, I combined many proxies to present a faithful picture of past changes in stability domains grass biomass. I tested a novel method using coupled fire and grazing disturbance from charcoal and spore assemblages to define grass stable vegetation states. The approach helped me to find shortgrass and tallgrass states that represented levels of fire and grazing intensity (Chapter Four, Figure 4.18; Chapter Five, Figure 5.17). However, the approach raises questions about the use and interpretation of charcoal and dung spore records, and climate proxies traced from grasses.

First, charcoal and spores are signals of the grass structural states at wetland margins and not just burned area or herbivore biomass as traditionally argued. By considering them as coupled consumers, tallgrass states supported by high productivity were more susceptible to fire compared with grazing, hence more charcoal. In contrast, shortgrass states persist under heavy grazing or drought that reduce fine fuels. Since grazers have marked effects on grass composition and structure through suppression of grass biomass (Augustine and McNaughton, 2006; Fuhlendorf et al., 2001; Milchunas et al., 1988), stability domains give faithful representation of past resource use by herbivores compared to direct interpretation of spores whose abundance is affected by soil moisture (Wood and Wilmshurst, 2012). Therefore, additional layers of proxies are needed for interpreting spore signals. At best, the signals reflect local patch disturbance instead of grazer biomass or density.

Second, in wetlands used by indigenous herbivores in Africa, using grasses as climate proxies needs revision. Herbivores have the potential to override the grass-derived climate signal since they affect both vegetation composition and structure (Muthoni et al., 2014). In particular, grazers increase lawns at the expense of mature tallgrasses (Lock, 1972; Owen-Smith, 1996; Rietkerk et al., 2000; Vesey-Fitzgerald, 1970; Waldram et al., 2008). At the grassland site, Chloridoideae and Panicoideae phytoliths may have been be related to lawn grasses like *Cynodon dactylon, Urochloa mossambicensis, Sporobolus nitens,* and *Panicum coloratum* among other species (e.g., Archibald et al., 2005b; Waldram et al., 2008), found at HiP savanna lawns with high herbivore biomass (Olsen, 2015). The climate aridity proxy comparing the ratio of Chloridoideae to Panicoideae grass phytoliths and the grass water stress (Barboni et al., 2007; Bremond et al., 2005; Bremond, Alexandre, Wooller, et al., 2008), may have to be interpreted carefully due to positive feedback between drought and grazing. However, there are productive mesic grasslands where herbivores cannot suppress grasses and that may increase confidence in applying climate indices (e.g., Hempson, Archibald and Bond, 2015; Sinclair, 1975; Slobodkin et al., 1967).

Last, the resilience of grass states within stability domains suggests that a direct interpretation of proxies without context is doubtful. For example, there is no direct relationship between herbivore biomass increase and S*porormiella* since resilient shortgrasses promoted by herbivores are associated with dry conditions that affect spore preservation. Fortunately, stability domains and resilience framework outlined in this thesis could address this type of problem with multi proxies. Also, stability domains allow comparison of records from other regions where herbivores rely on wetland grazing resources to survive dry climatic periods.

6.6 Limitations of the study

The current study provided new insights on interactions among climate, disturbance, and vegetation stability at key resource areas at multiple spatial and temporal scales. Although the key resource area idea was tested successfully using multiple proxies and stability domains of grass biomass, calibration of fire and herbivory with charcoal and spores is necessary to assess the possibility of non-analogue ecosystems dynamics. Also, the multiple proxy approach could be improved by uncovering strengths of ecological relationships with advanced mathematical approaches like structural equation modelling as a first step (e.g., Anderson et al., 2010), and machine learning classification algorithms (e.g., Sobol and Finkelstein, 2018), see future studies below.

Low taxonomic resolutions of grass phytoliths and spores are areas of method development. Grass taxonomic bias is widely acknowledged in phytolith classification. Although there has been significant progress (e.g., Barboni and Bremond, 2009; Cordova, 2013; Fahmy, 2008; Neumann et al., 2017; Novello et al., 2012; Rossouw, 2009; Twiss et al., 1969), there is variability in identification protocols that hamper the comparing of datasets (Barboni and Bremond, 2009; Neumann et al., 2017; Twiss , 1969). Therefore, the multiple proxy approach including spores was satisfactory because it provided interpretable results despite known limits.

More dates along the cores and high resolution rainfall records will allow Bayesian (probabilistic) analyses for comparing regional rainfall and key resource area ecological dynamics (e.g., Gill et al., 2012). However, financial constraints limited the number of dates processed. Despite this limitation, the closest and coarsely sampled regional multiple proxy rainfall record was useful. The Past Global Changes Africa 2k working group is at present compiling regional palaeoclimate records from the last 2 000 years that when online, may be of higher spatial and temporal resolution.

6.7 Future studies

Grassland and savanna ecosystems cover large parts of Africa, South America and south Asia and support diverse herbivore communities and human cultures. This research incorporated multiple levels of ecosystem analysis and can be improved in the following ways:

1. An expensive but useful approach is environmental DNA to identify vegetation and herbivore assemblages that are comparable with phytolith and fossil dung spore profiles. This may help if patterns of vegetation disturbance or persistence depend on plant or herbivore species/genera. However, the method is limited to lakes with good preservation of proxies compared with the variable wetland conditions in most savanna and grasslands.
2. Several field calibration studies of fire activity and grazing pressure from charcoal and dung spores are needed at wetlands with different vegetation, herbivore densities,

herbivore guilds, fire regimes, and soil disturbances. At present, published studies are from Europe and North America (Etienne et al., 2013; Gill et al., 2013; Graf and Chmura, 2006; Parker and Williams, 2011; Raper and Bush, 2009), but they do not have the range of herbivore diversity found in Africa or South Asia. An area requiring attention is the separation of local grazing pressure and herbivore density. This is critical since spores are locally deposited while herbivore densities are decoupled from vegetation in wider landscapes. Another area to explore are relationships between spores and the build-up of organic carbon at wetlands in an area with herbivores (e.g., Elschot et al., 2013, 2015).

3. Stability domains are open to investigation with mathematical modelling approaches like structural equation modelling (SEM) and machine learning that simplify complex ecosystem relationships. For example, multiple stable vegetation states or domains summarised as shortgrass and tallgrass and their ecological drivers could be represented using an ecological network (Figure 6.4). The SEM approach is particularly useful for measuring strengths of ecological connections using correlations and has been applied in similar contexts (e.g., Anderson et al., 2007; Eby, Anderson, et al., 2014). However, more multiple proxy records are needed, giving many opportunities to explore data compared with SEMs.

In this thesis I demonstrated relationships among vegetation units obtained from grass phytoliths and coupled disturbances The data suggest machine learning algorithms including classification, clustering and regression tree methods are applicable to palaeoecological data and are useful (e.g., Sobol and Finkelstein, 2018). Rigorous and computationally derived grass stability domains for key resource areas will reduce uncertainties in classifying grass state and stability domains. One way of doing this is by incorporating calibration studies that are used for training and validation purposes. Still, there remains the problem of non-analogue ecosystems.

However, the success of machine-learning will depend on the ability to profile wetland grass mosaics across landscapes and regions for reconstructing grazing histories and herbivore functional types (Hempson, Archibald and Bond, 2015). The profiles will lead to mapping of past herbivore distributions, especially herbivore relationships with grass productivity and climate. Since sediment records deal with the survival and fitness of herbivores, the data is useful for refining models of herbivore evolution by extinction processes driven by climate (Bobe et al., 2002; Faith and Behrensmeyer, 2013; Vrba, 1987, 1992).

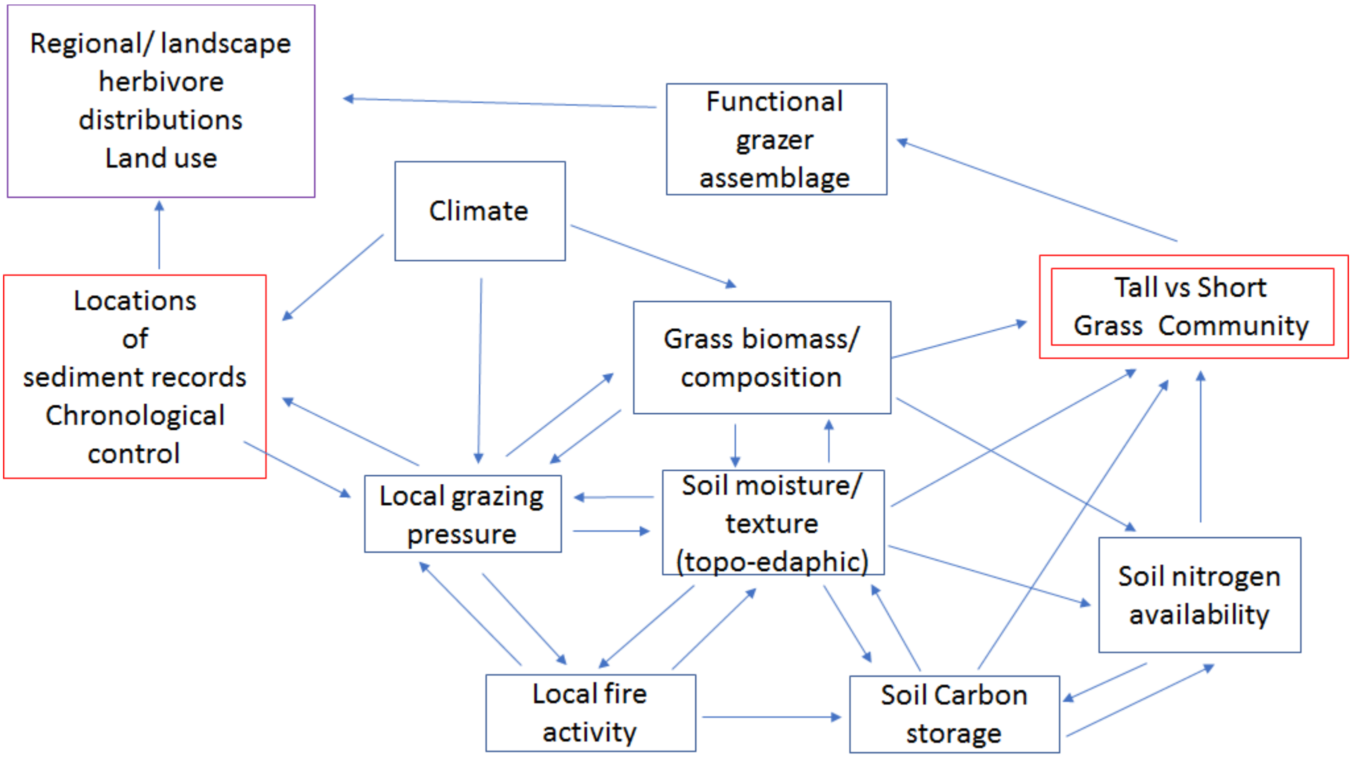


Figure 6.3. A representation of ecological factors used in this thesis and their connections at key resource areas.

6.8 Conclusion

Reconstructing ecosystem dynamics in dynamic grasslands using proxies is complex. Climate, vegetation, fire, grazing, soil, and activities of people are interconnected at wetland boundaries. Thus, a tension exists between the scale of action of equilibrium and disequilibrium ideas used for understanding ecosystem stability. Long-term sedimentary proxy records were useful for understanding vegetation and soil dynamics from two South African wetland grasslands with contrasting consumer dominance. There was a semi-arid herbivore-dominated savanna and a mesic fire-driven montane grassland.

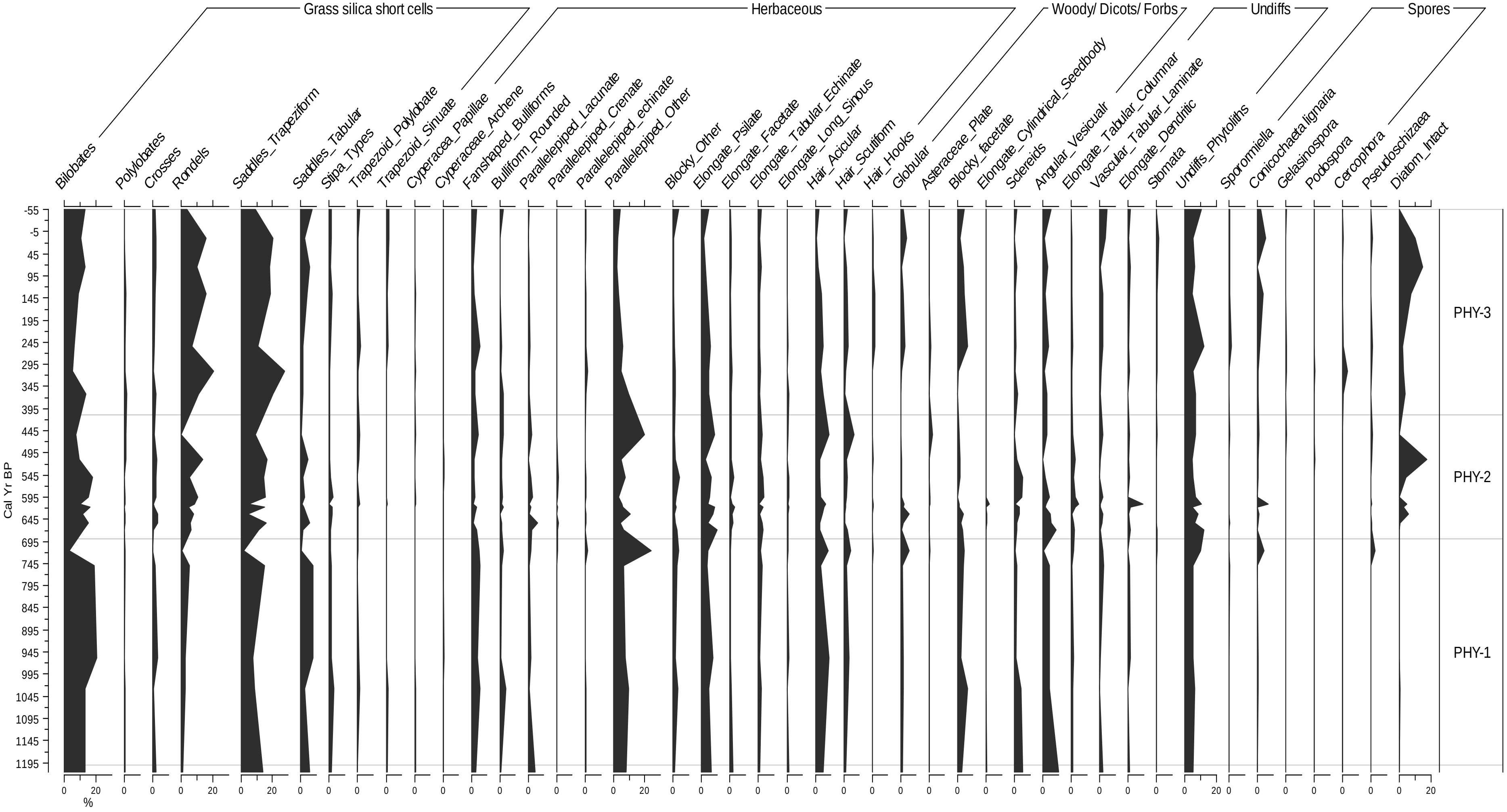
The key resource area idea was useful for assessing stability and resilience of stable grass states at multiple scales. At local scales, feedback among grazing pressure, soil moisture, and fire activity were important for organising grass states into stability domains. Stability depended on bounded vegetation changes with time. In comparison, resilience was suggested by multiple states within a stability domain. The domains in order of increasing biomass were grazing, fire, and low disturbance. At landscape scales, positive feedback between low rainfall, grazer densities and fire caused changes from tallgrass to shortgrass (grazing lawn) states and soil damage at local scales.

This novel long-term study suggests that grazers control wetland vegetation and soil dynamics, especially in dry climatic periods when degradation is likely. Positive feedback responses between grazing and drought were major drivers of vegetation change and signs of soil disturbance at wetlands. Grazing lawns sometimes associated with degradation, depended on multiple scale relations among rainfall, land use, grazing pressure, plant tolerances of fire and grazing, and soil moisture. So were soil nutrients pools. Fire and grazing increased the loss of grass cover and speeded up soil instability. Although signs of degradation appeared in dry periods at both sites, they vanished following wet periods when local grazing pressure relaxed, showing recovery and resilience at long timescales. These conclusions have the potential to change discussions of degradation because they cast doubt on claims of irreversible changes (e.g., van de Koppel and Rietkerk, 2000).

The stability domains idea is important in rangeland ecosystems because it allows the simultaneous testing of equilibrium ideas. For example, the nonequilibrium and resilience theories that were assessed in this thesis. Support for multiple equilibriums suggests rangeland stability debates are driven by competing social and ecological agendas (e.g., Briske et al., 2003, 2017; Gillson and Hoffman, 2007; Illius and O'Connor, 1999; Lamprey and Yussuf, 1981; Vetter, 2005). Stability domains may therefore give rangeland managers a template for manipulating vegetation at long timescales in semi-arid regions by changing fire or grazing intensities. Therefore, findings from this thesis are relevant in grassland ecology, savanna ecology, and resilience theory.

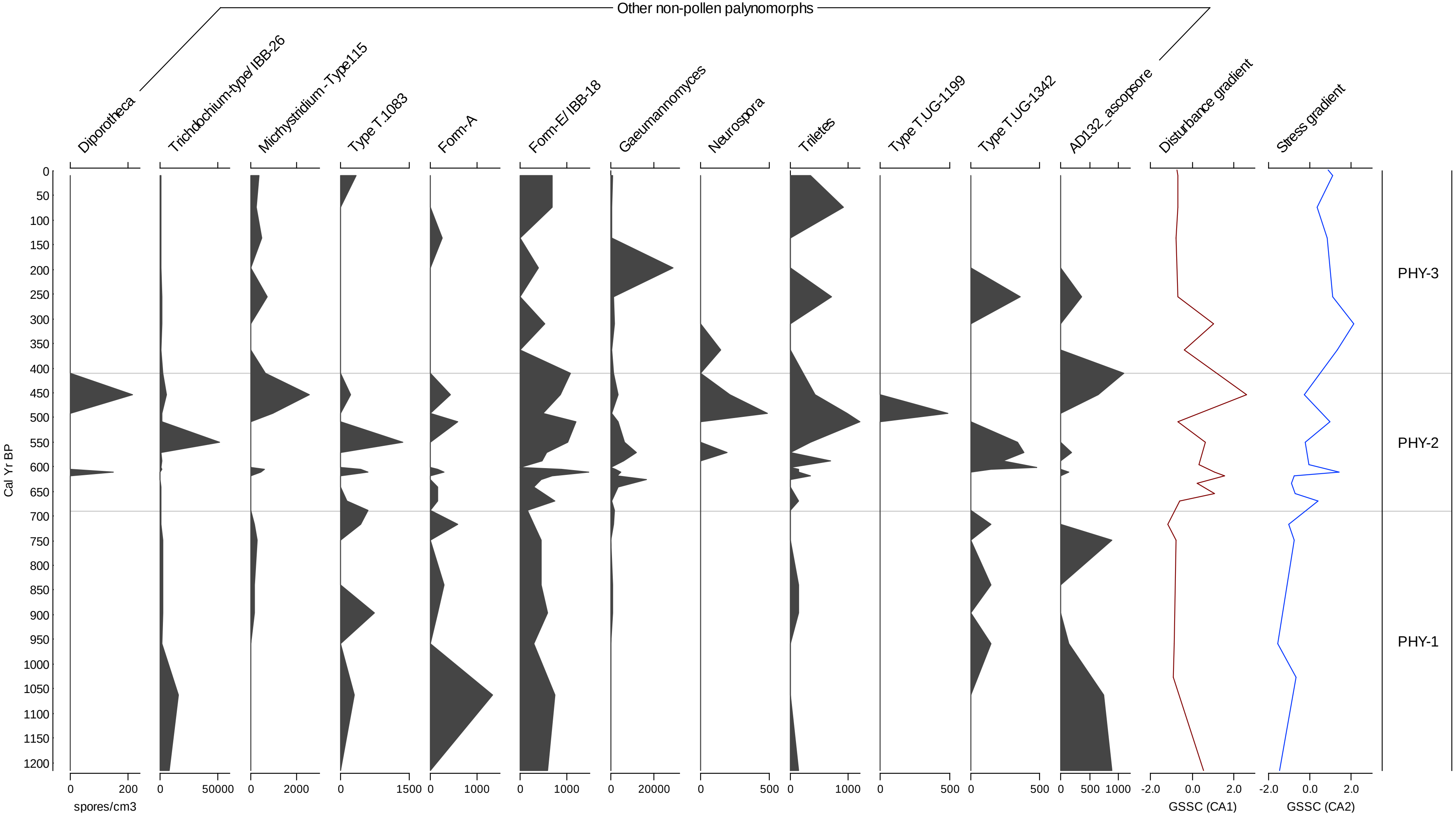
Recurrent droughts in sub-Saharan Africa affect plants, animals, human livelihoods, and ecosystem functioning. Droughts effects on food may modify populations over long timescales. Degradation remains a pressing concern in these rangelands. However, understanding ecosystem resilience is important for resolving the concerns. Stability domains were valuable ways of assessing the persistence and resilience of key resource areas. Therefore, this thesis shows the value of proxy studies and their contribution to nuanced understanding rangeland equilibrium.

Appendices



Appendix One. Multiple proxy summary of vegetation indicator phytolith types, dung fungal spores and diatoms in the Blood River Vlei proportional counts from samples prepared using the heavy liquid flotation.

Appendix Two. Other non-pollen environmental indicators plotted alongside GSSC CA ecological gradients at Blood River Vlei



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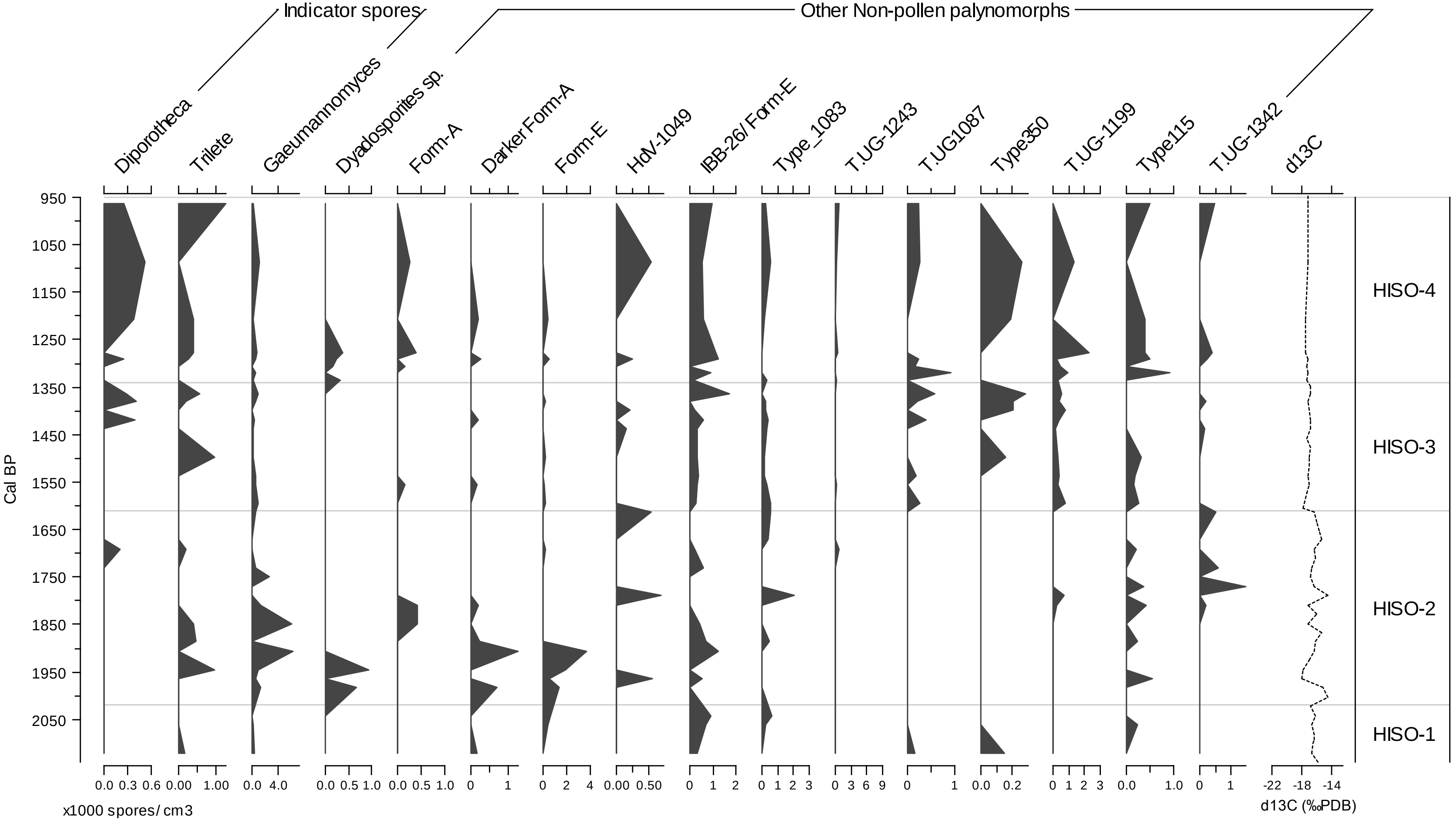
There was a continuous presence of Form-E, *Gaeumannomyces* and ascospore IBB-26 types while other non-pollen types did not regularly appear in the sequence (Figure 7.11). Trilete spores increased in abundance with time, with peak concentration c. 1 199 x10^4 spores cm^{-3} occurring at ca. 510 cal BP in GSSC zone PHY-2. The Form-E spore was present throughout the sequence but exhibited its highest abundance of 1 487 at ca. 610 cal BP in GSSC zone PHY-2. The disturbance indicator spores *Neurospora* and *Diporotheca* were only found in GSSC zone PHY-2 where trilete spores and Form-E were frequently present.

Appendix Three. Pearson's correlation for direct core scan XRF elemental concentrations from the Blood River Vlei (*p-values* are in parenthesis, with the significant ones in bold and *d.f.* = 61)

	Fe	K	Sr	Ti
K	-0.182 (0.153)			
Sr	-0.109 (0.393)	0.527 **(<0.000)**		
Ti	0.082 (0.523)	0.575 **(<0.000)**	0.580 **(<0.000)**	
Zr	-0.075 (0.557)	0.360 **(0.004)**	0.827 **(<0.000)**	0.374 **(0.003)**

Appendix Four. Other spores and non-pollen palynomorphs at Umchachazo Vlei.



The CONISS zonation of the stable isotopes was used to reference the changes in other non-pollen types (Figure 8.5). Compared to the dung spores (Table 8.4), spores not associated with herbivores were found at low abundance (Table 8.5). Spore abundance was higher in zones HISO-2 and HISO-4 compared to the other zones. However, there was a notable presence of T.1199, Type 350, Form-E and Triletes in in zone HISO-3. Except for Form-E, most spores were not reliably present throughout the sequence. *Gaeumannomyces* and Trilete spore abundances co-occurred and *Diporotheca* featured more prominently from ca. 1 440 cal BP. G*aeumannomyces* abundance was high from ca. 1 960-1 850 cal BP, with peak abundance of c. 6 190 spores cm^{-3} at ca. 1 610 cal BP.

Appendix Five. Pearson's correlation for the direct core scan elemental concentrations of the 86 samples from the Umchachazo Vlei core (*p-values* are in stars below the respective correlations)

	Fe	K	Rb	Sr	Ti
K	0.015				
Rb	0.053	0.894 ***			
Sr	-0.466 ***	-0.394 ***	-0.571 ***		
Ti	0.000	-0.119	-0.254 **	0.424 ***)	
Zr	-0.622 ***	-0.382 ***	-0.565 ***	0.895 ***	0.439 ***

Significance codes: < 0.05 = ‘* ‘, < 0.01 = ‘**’ ; < 0.001 = ‘***’

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