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Resilience modes of an ancient mountain valley grassland in South Africa indicated by palaeoenvironmental methods

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Abstract

Grassland ecosystems supporting wildlife and livestock populations have undergone significant transformation in the last millennium. Climate, herbivory, fire, and people are identified as important drivers of ecosystems dynamics; however, grassland resilience has been rarely explored in landscapes with mixed grazing histories. Here we analyse ecosystems states from a South African mountain valley grassland in the last 1250 years using palaeoenvironmental proxies. Our results suggest that a tallgrass phase maintained by climate, people and fire replaced a shortgrass phase driven by indigenous herbivores after ca. 690 cal BP. Furthermore, the tallgrass phase had unpalatable grasses and disturbed soil. We suggest these ecological changes were linked to climate change and arrival of pastoralists in the region. Therefore, our results indicate that human activities may undermine resilience of grasslands and that reversing some changes may be difficult.

1. Introduction

The earth's grazing systems have undergone significant transformation in the last millennium because of increased human activities (Hempson *et al* 2017). Hunting of indigenous herbivores, agriculture, livestock rearing, and increased human pressure on wildlife resources have compromised key disturbance processes like herbivory and fire (Ripple *et al* 2015, Hempson *et al* 2017). Because climate is another interacting driver of environmental change (Illius and O'Connor 1999), there is growing concern over the resilience of grasslands, i.e. their ability to absorb disturbance without reorganising or transitioning to another phase maintained by different feedback mechanisms (Holling 1973, Scheffer *et al* 2001, Gillson and Ekblom 2009).

Positive feedbacks in dynamic open grasslands cause alternate ecosystem phase states in response to contrasting drivers (Hempson *et al* 2019). For example, tallgrass dominate most open environments as they are good competitors for growing resources (Grime 1977). Because mature tallgrasses are generally unpalatable to most herbivores, they depend on positive feedback with fire to regenerate (Hempson *et al* 2019), but fires also result in palatable post-fire regrowth that attracts grazers (Archibald *et al* 2005, Allred *et al* 2011). Conversely, sustained re-grazing by indigenous and domestic herbivores increases shortgrasses, i.e. grazing lawns (Hempson *et al* 2015), at the expense of tallgrasses. Arid conditions also reinforce the persistence of shortgrasses as they tolerate stressful conditions (Coughenour 1985). However, positive grazing interactions also multiply unpalatable grasses in landscapes and may even lead to soil degradation (Rietkerk *et al* 2002, Vetter 2005). Thus, understanding alternate ecosystem states is an important step for analysing resilience.

Palaeoenvironmental studies are useful for exploring resilience because of records that extend analyses over long timescales (Gil-Romera *et al* 2010). Lengthy records allow changes in vegetation, fire, and herbivory that occur over several decades to be placed in context. For example, pollen has been used to understand changes in woody plants and tree-grass dynamics millennia, with phytoliths focusing
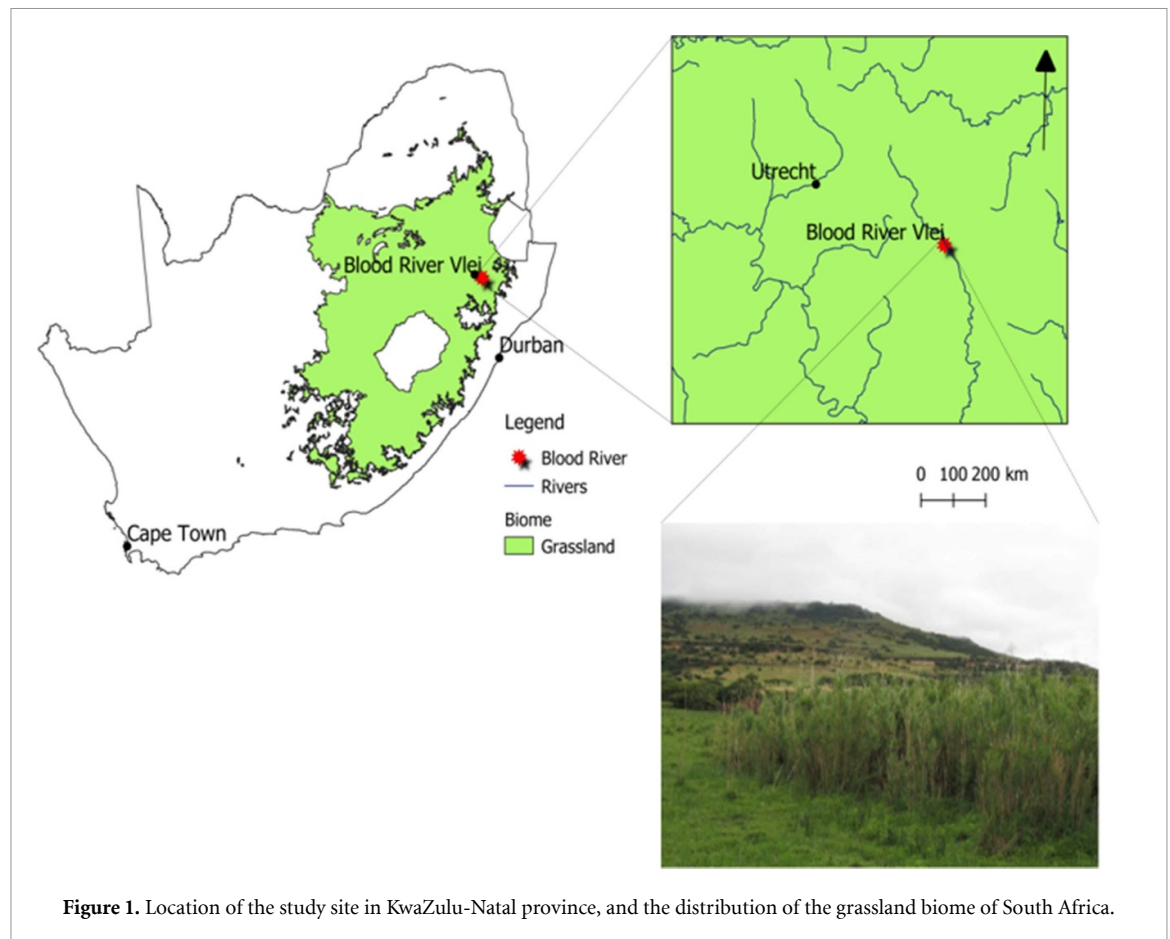
Figure 1. Location of the study site in KwaZulu-Natal province, and the distribution of the grassland biome of South Africa.

on the grassy layer (Lejju *et al* 2005, Breman *et al* 2019). Phytoliths form when silicates absorbed from the soil by plants solidify inside tissues and are produced by grasses in large quantities (Piperno 2006). Compared with pollen, phytoliths are functionally useful for resolving grass subfamilies, C_3–C_4 photosynthesis pathways, and climate indices (Piperno 2006, Bremond *et al* 2008). Herbivory and fire disturbance processes in vegetation records are explored with *Sporormiella* and charcoal (Ekblom and Gillson 2010). *Sporormiella* are coprophilous fungi that complete their life cycle in herbivore guts and their quantities in sediments indicate past herbivore density or pressure (Baker *et al* 2016).

Despite having long grazing histories with domestic and indigenous herbivores (Veldman *et al* 2015, Hempson *et al* 2017), there are few palaeoenvironmental studies from southern African grasslands analysing resilience. The notable study exploring resilience was at the Kruger National Park, South Africa, but the main focus was on tree-grass dynamics with limited detail about the grassy layer (Gillson and Ekblom 2009). As a result, we have no way of knowing how pastoralists who moved to highland grasslands in the last millennium influenced ecosystem resilience (e.g. Hall 1981, Bousman 1998, Huffman 2004, Schlebusch *et al* 2017), or whether their activities caused degradation. For instance, in lowland savanna grassland, collapse of livestock-keeping

societies in the last millennium is linked to megadroughts and unsustainable resource use (O'Connor and Kiker 2004). At the same time, the persistence of pastoralism in times of climate stress is linked to the productivity of valley grasslands (Hall 1981, Scoones 1991). Since resilience affects both outcomes, it is important to find out how they pan in highlands pastoralists colonised after savannas.

In this study, we analyse grass phytoliths, *Sporormiella*, and charcoal among other proxies from a valley grassland in the highlands using a 1250 year record from Blood River, KwaZulu-Natal Province, South Africa. We are concerned with identifying alternate grass phases and their ecological drivers to assess resilience. Therefore, our study focus is of small spatial extent, i.e. the valley grassland, but it is also influenced by the surrounding landscape and regional climate. Productive valley grasslands are known to support some herbivores in dry seasons and larger indigenous herbivores all year round (Ngugi and Conant 2008, Waldram *et al* 2008, Muthoni *et al* 2014, Fynn *et al* 2015).

2. Data and methods

2.1. Study site
The Blood River Vlei study site (−27.79° latitude, 30.59° longitude) is in the central highland grassland of South Africa near Vryheid (figure 1). Mean

Table 1. Results from ^{14}C radiocarbon dating of the Blood River core.

Analysis ID	Depth (cm)	δ^{13}C	Radiocarbon age (BP)	2σ Calibrated ages (cal BP)	
UBA-26 947	44	−17.2	650 ± 41	543–655	95
Beta—432 462	66	−20.2	730 ± 30	563–601	38.3
				629–677	56.6
Beta—432 461	100	−15.2	780 ± 30	577–583	1.6
				649–728	93.3
Beta—410 175	131	−11	1240 ± 30	988–1022	5.4
				1051–1185	89.5
Beta—379 492	135	−14.4	1640 ± 30	1412–1548	93
				1551–1560	1.9

annual temperature is a mild 17 °C, and annual rainfall averages 800 mm, which is considered wet (Kotze and O'Connor 2000). Seasonal flooding of the grassland happens during the summer rainfall season (November–March), with drying occurring with the onset of dry seasons (Kotze and O'Connor 2000), and droughts.

The ecotone site shares boundaries with moist grassland, sandy grassland, and 'thornveld' vegetation types (Mucina and Rutherford 2006). The C$_4$ tallgrass landscape mosaic was dominated by *Themeda triandra* and *Hyparrhenia hirta*. Other C$_4$ grasses included *Aristida congesta, Digitaria eriantha, Eragrostis* spp., and *Sporobolus africanus*. Robust C$_3$ *Phragmites australis* and C$_4$ *Cyperus cyperus* reed grasses were prominent at riverine edges. C$_3$ *Leersia hexandra,* and C$_4$ *Cynodon dactylon* shortgrasses were found in the understorey. Forbs typical of grazed sites included *Crinum paludosum, Helichrysum* spp*., Bidens pilosa,* and *Solanum* spp. *Vachellia sieberiana* (formerly *Acacia sieberiana*) trees line the river, and possibly encroached grassland in the last 80 years (Grellier *et al* 2014). Herbivores in the area included cattle, donkeys, and goats; however, cryptic indigenous species may be present. There was evidence of wetland burning to control aggressive reeds, improving pasture, and clearing cropland (Kotze 2013). Also, fire return intervals in the highland grasslands are typically short; less than 3 years (Archibald *et al* 2010).

2.2. Sediment collection and dating

A 135 cm sediment core named BR1 was retrieved from the centre of a section of a floodplain basin next to Blood River using the vibracorer method (Baxter and Meadows 1999). This involved driving a 6 m aluminium pipe into the ground until it stopped at ∼3.9 m, compressing the sediment by 64.4%. Chronology of BR1 was obtained from five sediment samples using ^{14}C radiocarbon dating (table 1). Beta Analytic® (California) and ^{14}Chrono Centre (Belfast) conducted accelerator mass spectrometry radiocarbon dating. Dates were calibrated to years before the present (cal BP) using the Southern Hemisphere 13 curve and the year 1950 was set as year zero. An age-depth model was developed with Clam 2.2 in 'R' (Blaauw 2010). The age-depth model of BRI representing the last ∼1250 years

is shown in supplement 1 (available online at stacks.iop.org/ERL/16/055002/mmedia).

2.3. Response variables: grass dynamics and soil stability

Phytoliths for reconstructing grassland dynamics were extracted from twenty-one 1 cm^3 sediment subsamples from the BR1 core using a standard heavy liquid flotation protocol to simultaneously extract multiple microfossils including diatoms and dung spores (Lentfer and Boyd 2000). The heavy liquid used was sodium polytungstate at specific gravity of 2.3. Microscope slides of each extracted sample were prepared and counted at 1000× magnification. A minimum of 200 phytoliths were counted per sample (Piperno 2006). Phytoliths were classified using a combination of the International Code for Phytolith Nomenclature 1.0 (Madella *et al* 2005) and others (Barboni and Bremond 2009, Cordova and Scott 2010). Diagnostic grass silica short cell (GSSC) phytoliths (figure 2) from the entire morphotype assemblage, (i.e. bilobates, crosses, rondels, saddles, and trapezoids), were used to indicate grass sub-families, functional groups, and environmental indices (Barboni and Bremond 2009, Cordova 2013; table 2).

The aridity index (Iph%) was calculated as the ratio of short cell Chloridoid to the sum of short cell Chloridoid and Panicoid phytoliths (Bremond *et al* 2008). In addition, the aridity index was as an indicator of local grass sward height with higher values pointing to shorter grass swards and vice versa. The relative abundance of C$_3$ vs C$_4$ functional groups of grasses was calculated using short cells of C$_3$ Arundinoid and Pooid to the sum of short cells of Pooid, Arundinoid and C$_4$ (Aristidoid, Chloridoid and Panicoid) (Bremond *et al* 2008). Environmental significances of C$_3$ and C$_4$ grasses are listed below (table 2).

Sporormiella (HdV-113) and intact diatoms counted alongside phytoliths were used as indicators of local herbivory and soil moisture. While diatoms have been used to indicate wetland moisture (Novello *et al* 2015), *Sporormiella* has not been well interpreted.

Soil disturbance around the basin indicated by differences in grain size of accumulated sediment was analysed at 2 cm resolution using an Innov-X Systems DELTA handheld x-ray fluorescence scanner
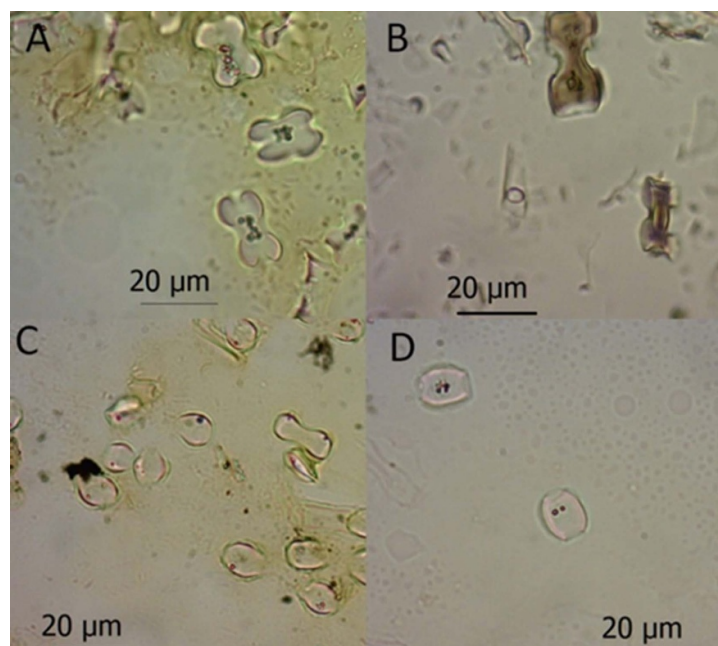
Figure 2. Diagnostic grass silica short cell phytoliths from reference slides. (A) *Panicum coloratum* bilobate and cross shaped cells found in Panicoid; (B) *Themeda triandra* bilobates short cells; (C) *Aristida congesta* bilobates including a diagnostic 'long-shank' at bottom left for Aristidoid; (D) *Sporobolus africanus* squat saddle-types common among Chloridoid.

Table 2. Ecological significance of grasses found at Blood River Vlei.

Subfamily	C_3/C_4	Ecological significance	Local representative species
Aristidoideae	C_4	Intermediate grasses; low palatability in rangelands[a], indicator of heavy grazing and disturbance	*Aristida congesta*
Arundinoideae	C_3	Tall reed grass; moisture and grazing disturbance indicator[b,c]	*Phragmites australis*
Chloridoideae	C_4	Short grasses; indicators of aridity[d]; heavy grazing and lawns[a]	*Sporobolus africanum, Cynodon dactylon*
Panicoideae	C_4	Tall grasses; flammable and palatable when young or burned [a,d]; indicates moist landscapes[e]	*Themeda triandra, Andropogon appendiculatus, Hyparrhenia hirta*
Pooideae	C_3	Intermediate grasses; favour cool moist environments[b,f]	*Poa binata, Leersia hexandra*

Sources:
[a] Hempson *et al* (2015).
[b] Mucina and Rutherford (2006).
[c] Belsky *et al* (1999).
[d] Coughenour (1985).
[e] Bremond *et al* (2008).
[f] Kotze and O'Connor (2000).

2015. Soil elemental ratios of Zr and Rb were used as an increase in heavier Zr compared to lighter Rb indicates more hydraulic energy around basins from poor soil vegetation cover (Dearing *et al* 2012), hence transport of larger soil grains. Meanwhile, organic matter loss-on-ignition (LOI), a method for establishing amount of organic matter was conducted using a standard protocol (Heiri *et al* 2001).

2.4. Explanatory variables: disturbances by fire and herbivores
Charcoal and coprophilous *Sporormiella* for analysing local fire activity (Patterson *et al* 1987) and herbivore pressure (Cugny *et al* 2010) were extracted from thirty 1 cm^3 sediment subsamples along core BR1 using the standard pollen method (Bennett and Willis 2001). We used this independent approach because *Sporormiella* counts from the phytolith method (section 2.3) had significant gaps. Spiking of samples with *Lycopodium* spores allowed the estimation of *Sporormiella* concentrations. *Sporormiella* counts per sample were stopped after reaching 250 *Lycopodium* (Etienne and Jouffroy-Bapicot 2014). Spore slides were counted at $400\times$ magnification. On the other hand, charcoal fragments >150 μm (called macrocharcoal) sieved during pollen preparation were

analysed under a stereomicroscope using the petri dish method (Carcaillet *et al* 2001).

2.5. Data analysis

Herbaceous vegetation phases (zones) were identified based on the relative abundance of grass subfamilies using constrained incremental sum of squares (CONISS) in 'R' (Grimm 1987, Oksanen *et al* 2015). Bayesian changepoint (BCP) analysis of running means of the aridity index (Iph%) was used to explore posterior probability threshold of change above 10% with the 'bcp' package (e.g. Gill *et al* 2012). Changepoints nearly corresponded with breaks in vegetation zones. Finally, correlation between *Sporormiella* and the Zr:Rb ratio (indicators of herbivore pressure and soil stability) were analysed using Pearson's correlation coefficient. All stratigraphic diagrams were plotted using the program C2 (Juggins 2011).

3. Results

3.1. Palaeoenvironmental results

Phytolith morphotypes for vegetation analysis averaged 309 ± 32 grains per sample and diagnostic GSSCs were 137 ± 49 grains per sample, representing a mean of $\sim 44 \pm 15\%$ of the total phytolith sum per sample (figure 3). Though variable, Organic matter loss-on-ignition, macrocharcoal, *Sporormiella*, and intact diatoms increased over time (figures 3 and 5). The C_3/C_4 grass index (Ib%) rose steadily from ca. 960 to 310 cal BP declining thereafter (figure 4).

In the basal GSSC Zone V1 (1250–690 cal BP), Panicoid phytoliths dominated the GSSC assemblage, ranging from c. 35% to 49%, followed by Arundinoid ranging from 17% to 37%. (figure 4). C_3 Pooid abundance increased steadily over time. C_4 Chloridoid were relatively stable, ranging from ca. 1220 to 750 cal BP, averaging c. 15%. Stipa-type phytoliths associated with aridity (e.g. Cordova 2013), reached their highest abundance of c. 14% at ca. 720 cal BP. The aridity index (Iph%) was stable and high from ca. 1220 to 750 cal BP (figure 5(B)), ranging from 28% to 29%, before sharply falling to c. 10% at c. 720 cal BP. There was a changepoint in average Iph with a threshold posterior probability >10% at ca. 750 cal BP (figure 5(B)).

Macrocharcoal and independently assessed *Sporormiella* were low and unchanged throughout the core, averaging c. 115 particles cm^{-3}, and 800 spores cm^{-3}, respectively (figures 5(C) and (E)). After being stable at c.1.3 from 1220 to 860 cal BP, the Zr:Rb ratio peaked to c. 1.5 at ca. 790 cal BP, then fell to c. 1.2 at ca. 720 cal BP. The combination of the above, especially a high aridity index, few diatoms and low macrocharcoal indicate a shortgrass mosaic.

The sharp declines in the aridity index and Zr:Rb, and the appearance of Aristidoid phytoliths mark the transition to dynamic Zone V2 (690–410 cal BP). Although Panicoid and Arundinoid tallgrasses increased in this zone, but their abundances are inversely related from 630 cal BP, with the former decreasing and the latter increasing. The low and variable aridity index ranged from c. 5% to 33%, with a sharp rise from ca. 9% to 33% occurring from ca. 550 to 510 cal BP (figure 5(B)).

Independent *Sporormiella* and macrocharcoal were abundant and variable in Zone V2 (figures 5(C) and (E)). The *Sporormiella* reached its highest abundance, ranging from c. 640 to 18 900 spores cm^{-3}. Macrocharcoal also rose significantly from c. 6 to 1970 particles cm^{-3} at ca. 660–610 cal BP, before declining to c. 240 particles cm^{-3} at ca. 450 cal BP. Interestingly, the Zr:Rb and Iph% positively tracked Aristidoid and independent *Sporormiella*. We found a significant correlation between Zr:Rb and independent *Sporormiella* ($r = 0.54$, d.f. $= 26$, p-value $= 0.003$). And Zr:Rb rose sharply from c. 1.2 to 1.5 at ca. 580–510 cal BP, then decreased slowly. Lastly, the mix of tallgrass phytoliths, abundant macrocharcoal, and variable spores indicate a dynamic tallgrass mosaic.

Zone V3 (ca. 410 cal BP to present), the youngest zone, is characterised by the disappearance of Aristidoid phytoliths and increase in Pooid. Arundinoid phytoliths were relatively stable, but abundances of Chloridoids and Panicoids rose from ca. 310 cal BP. These signalled positive changes in the average Iph% from ca. 310 to 260 cal BP.

Like the previous zone V2, macrocharcoal and independent *Sporormiella* changed asynchronously. The *Sporormiella* increased from ca. 360 to 260 cal BP but macrocharcoal decreased. The opposite was true when macrocharcoal increased from ca. 280 to 190 cal BP. Surprisingly, *Sporormiella* and macrocharcoal abundances were low from ca. 110 cal BP. Lastly, Zr:Rb was relatively unchanged at c. 1.3 from ca. 340 to the present. Given the dominance of Pooideae and Arundinoideae, this signals a wetland tallgrass mosaic.

4. Discussion

4.1. Climate history

Palaeoclimatic records from Southern Africa suggest spatial variability of rainfall conditions in the last millennium (Hannaford *et al* 2014). However, Chevalier and Chase's (2015) multiple proxy record showed that pooled southeast African records agree. This gave us confidence to compare it to the Blood River aridity index. Interestingly, the aridity index tracked the regional rainfall record (figures 5(B) and (F)) and changes in the mean aridity index closely matched the vegetation transitions (figure 5). Mesic conditions began from ca. 800 to 600 cal BP as indicated by a low aridity index and rising diatom counts. Furthermore, the aridity index was high from ca. 1220 to 750 cal BP when regional rainfall was low. Agreement between the regional rainfall record and aridity index could be
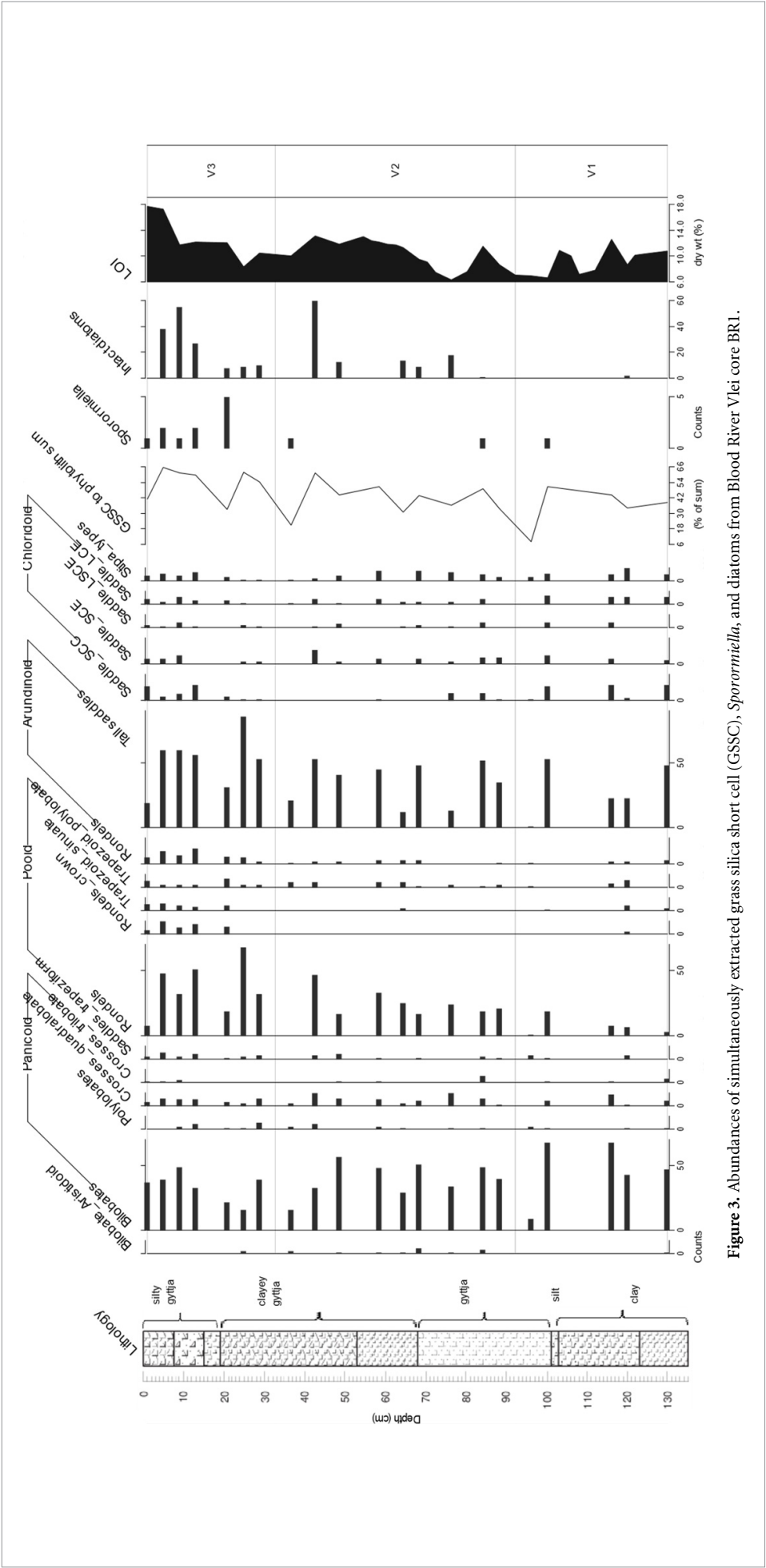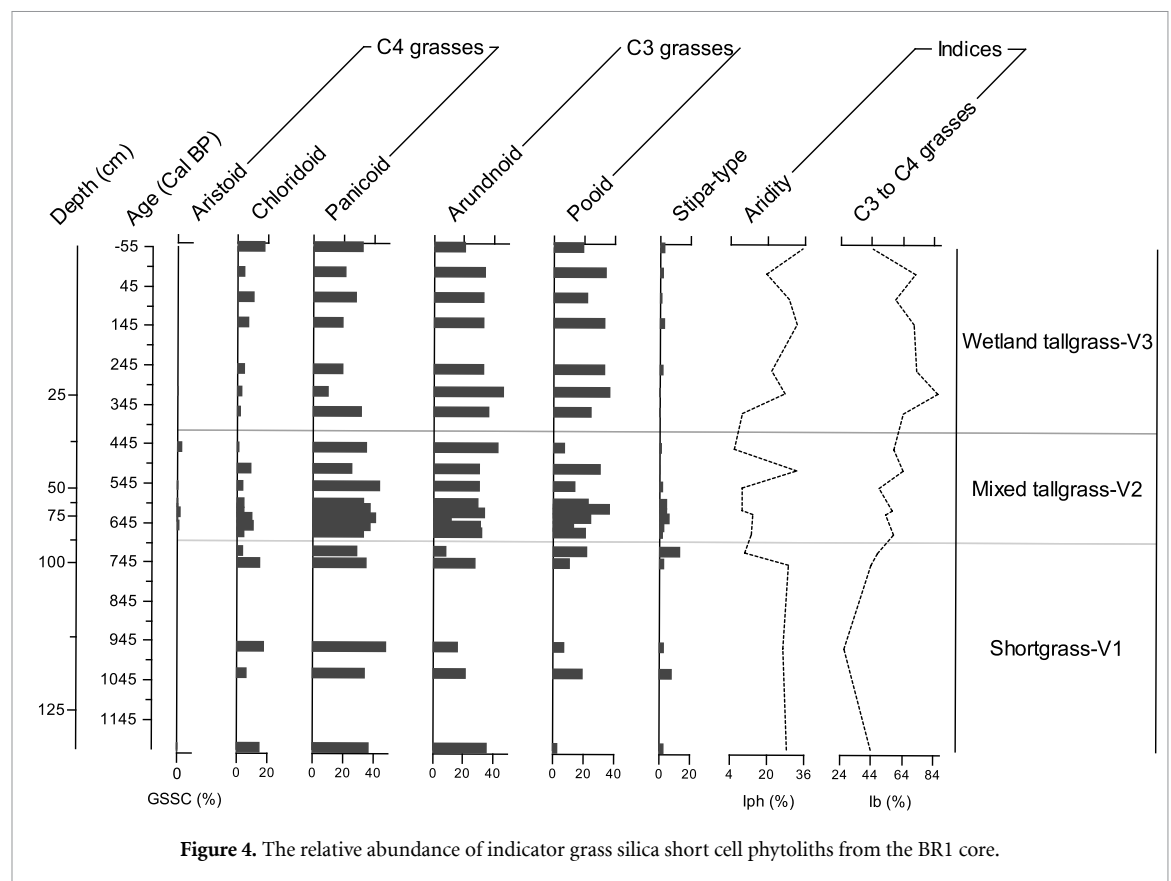
Figure 3. Abundances of simultaneously extracted grass silica short cell (GSSC), *Sporormiella*, and diatoms from Blood River Vlei core BR1.

Figure 4. The relative abundance of indicator grass silica short cell phytoliths from the BR1 core.

considered coincidental because of differences in spatial and temporal scales of the reconstructions; however, the index is robust hence successful use in other grassland studies from the region (Finné *et al* 2010, Breman *et al* 2019).

4.2. Disturbance history
Disturbance histories of African landscapes are complex because of the overlap between indigenous and domestic herbivores, and differences in flammability of valley grassland plants (Dabengwa 2019). Also, these functionally different grazers are difficult to separate using fossil *Sporormiella*. However, in this study we have combined phytolith, *Sporormiella*, macrocharcoal, soil disturbance, and archaeological evidence to make the distinction.

The vegetation phase V1 from ca. 1250 to 690 cal BP with low macrocharcoal and few *Sporormiella* at first glance suggests fewer fires and low herbivore densities (figures 3 and 5). However, high local abundances of landscape Chloridoid and Panicoid phytoliths plus low diatom counts indicate a different story. It is one of heavy grazing in the valley grassland owing predominance of landscape C4 grasses and dry soils. Positive feedback between indigenous herbivores and palatable shortgrasses may have lowered grass cover leading to arid soil conditions (e.g. McNaughton 1984), and resulted in fewer tallgrasses for fuelling fires (e.g. Waldram *et al* 2008). Therefore, the effects of herbivores on vegetation
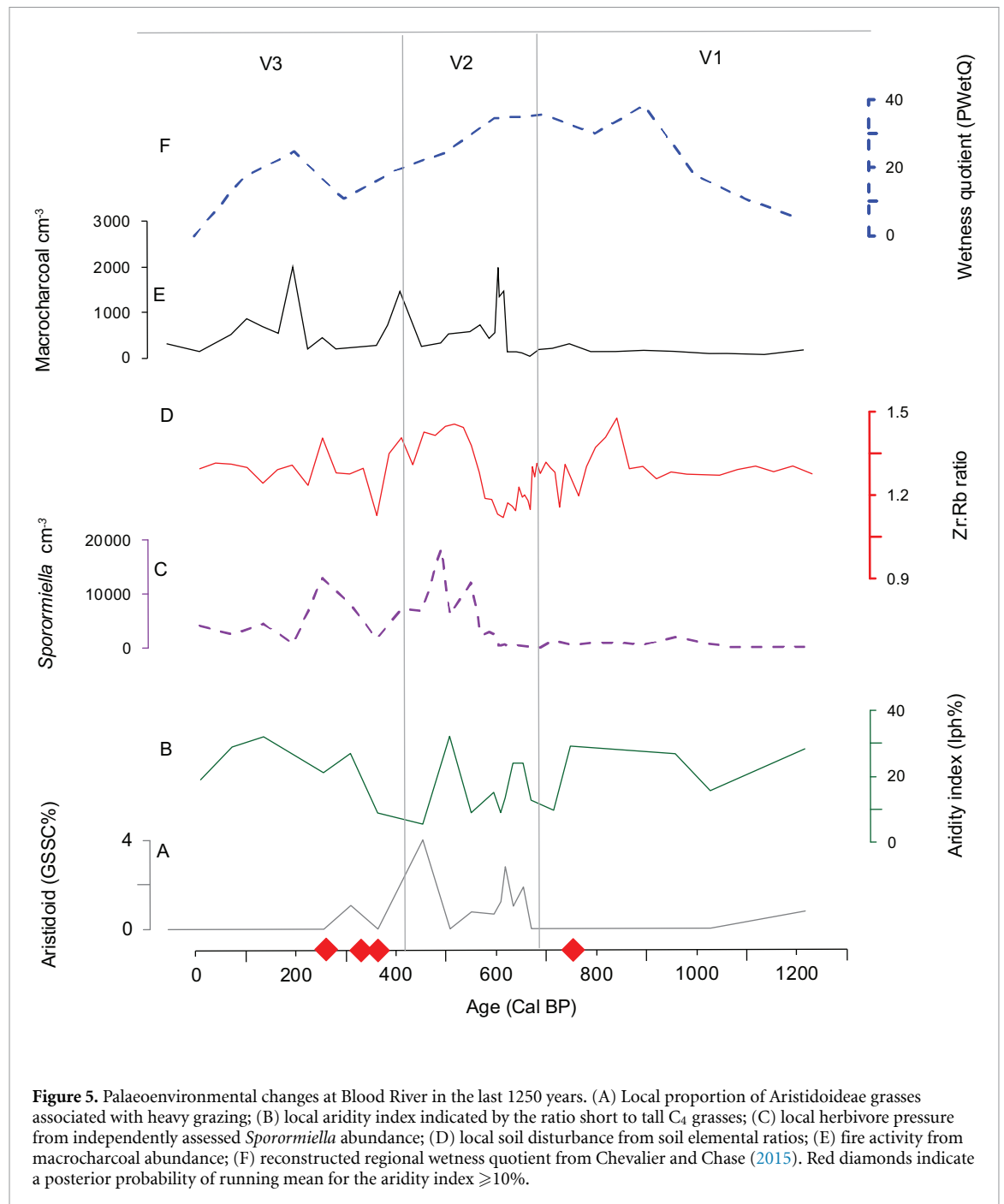
and soil negatively affected *Sporormiella* preservation (Wood and Wilmshurst 2012).

The subsequent vegetation threshold phase transition at ca. 690 cal BP was characterised by more fire, suggesting the development of a new herbivore regime. Increased *Sporormiella* and more phytoliths of unpalatable Aristidoid and Arundinoid grasses from ca. 670 to 310 cal BP propose the new herbivores were selective grazers as Panicoids slightly declined. Furthermore, as *Sporormiella* increased after macrocharcoal peaks, this may imply herbivores relied on fire to suppress tallgrass biomass (e.g. Archibald *et al* 2005). It is worth noting that archaeological records pin these ecological changes happened when pastoralism began to spread into the highland grassland (Hall 1981, Bousman 1998, Huffman 2004, Schlebusch *et al* 2017), and may possibly indicate the introduction of livestock within the area. Pastoralists using fire to manage pastures were presumably responsible for maintaining the new herbivore regime. However, owing to the low temporal resolution of our core, indeterminacy of *Sporormiella*, and lack of environmental DNA (e.g. Giguet-Covex *et al* 2014), it is not possible to constrain when the transition between indigenous and domestic herbivores that likely happened over several decades.

4.3. Resilience of the grazing system
We assessed local and landscape drivers of ecological resilience of the two herbivore regimes that we

Figure 5. Palaeoenvironmental changes at Blood River in the last 1250 years. (A) Local proportion of Aristidoideae grasses associated with heavy grazing; (B) local aridity index indicated by the ratio short to tall C$_4$ grasses; (C) local herbivore pressure from independently assessed *Sporormiella* abundance; (D) local soil disturbance from soil elemental ratios; (E) fire activity from macrocharcoal abundance; (F) reconstructed regional wetness quotient from Chevalier and Chase (2015). Red diamonds indicate a posterior probability of running mean for the aridity index ⩾10%.

identified for the Blood River core. As mentioned earlier, the shortgrass phase or regime was driven by positive interactions between indigenous herbivores and possibly grass quality. However, climate was another positive interaction as the aridity index in this phase was high. This coupling of climate, herbivory, and vegetation at the Blood River valley grassland may have contributed to the persistence of a shortgrass phase in an otherwise tallgrass landscape because of strong positive equilibrium forces (e.g. Illius and O'Connor 1999).

By comparison, tallgrass phases were likely driven by positive feedbacks among climate and grass production, and grazing and unpalatable grasses. We

arrived at this conclusion because of the generally low aridity index from ca. 720 to 360 cal BP, which also indicates a high proportion of flammable Panicoid tallgrasses in the landscape (figure 5(B)). Macrocharcoal representing mostly local fires increased by several magnitudes compared to the shortgrass phase, alluding other positive interactions among rainfall, grass productivity, and fire (Pausas and Ribeiro 2013, Hempson *et al* 2019).

On the other hand, positive feedback between herbivory and unpalatable grasses was cause for concern in this tallgrass phase influenced by pastoralists. For example, the concomitant rise in phytoliths of unpalatable Aristidoid and Arundinoid grasses from

ca. 610 to 510 cal BP was linked with increases in Zr:Rb and macrocharcoal and *Sporormiella* (figure 5), indicated possibly that livestock overgrazing and poor fire management lowered grass cover, causing soil instability (Illius and O'Connor 1999, Vetter 2005). Dry climatic conditions in the region from ca. 600 to 300 cal BP may have increased use of the valley grassland by pastoralists to sustain livestock. A similar pattern of parallel increases in *Phragmites* and coprophilous spores was observed at higher elevation in the region though temporal resolution for the last millennium was poor (Neumann *et al* 2014). Still, it is unclear how extensive or destructive soil erosion and heavy grazing were, but pastoralism could be directly linked to the expansion and establishment of less flammable *P. australis* stands in valley grasslands, similar to what ranching caused along North American rivers (e.g. Belsky *et al* 1999).

4.4. Conclusion

The long-term palaeoenvironmental evidence from Blood River suggested two distinct vegetation phases with different climate and herbivore regimes for the last 1250 years. The valley grassland system transitioned from a shortgrass phase supported by positive interactions between aridity and what we perceive to be indigenous herbivores, to a tallgrass phase controlled by interactions among climate, pastoralists, and fire. Owing to changes in soil and unpalatable grasses during the dry climatic phase from ca. 600 to 300 cal BP, and the persistence of the tallgrass phase, our results suggest that ecosystem dynamics in valley grasslands used by pastoralists may be compromised, lending support to the idea that droughts pose severe threats to grazing systems (Illius and O'Connor 1999) and human societies they support (O'Connor and Kiker 2004). Our study also supports to the use of resilience theory (Holling 1973, Dearing 2008, Gillson and Ekblom 2009, Buisson *et al* 2019), because the grazing system under consideration appears to have reorganised under different drivers (Holling 1973, Dearing 2008, Gillson and Ekblom 2009).

Natural grasslands worldwide are under threat from global environmental changes and this will have consequences on the wellbeing of wildlife and human populations. By combining insights from resilience theory and palaeoenvironmental archives, we may better understand our fragile ecosystems, our past actions and what we need to do to secure our future.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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