Implications of historical interactions between herbivory and fire for rangeland management in African savannas

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Abstract. Herbivory and fire are important drivers of ecosystem processes within African rangelands. We explore whether mid-Holocene African savannas were dominated by herbivory as a means of cycling nutrients, and whether fire perhaps played a lesser role than today. Evidence from savanna ecology, paleoecology, and historical literature indicates higher herbivore densities in mid-Holocene and pre-colonial times compared to present. While fire may increase or decrease forage availability for herbivores, depending on the nutrient status of the environment, herbivory tends to decrease fire intensity and frequency by decreasing fuel loads. Given this competitive relationship between fire and herbivory and the higher herbivore densities of the past, we suggest that some fire-dominated present-day savannas are the product of anthropogenic alterations in herbivore and fire regimes, including the increasing use of fire as a tool for managing ecosystems. We discuss whether managing for an alternative stable state dominated by herbivory could stimulate ecosystem processes such as nutrient cycling and production, and whether this will achieve the same management objectives traditionally satisfied by fire. Management implications may include the adaptive manipulation of herbivore densities over time and space to maintain an appropriate carrying capacity for the rainfall and soil nutrient status of the area, occasional use of fire, and including a diversity of herbivore functional guilds.

Key words: alternative stable states; carbon; ecosystem services; mid-Holocene ecosystems; nitrogen; nutrient cycling; rewilding.

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INTRODUCTION

The notion of extant pristine ecosystems untouched by human influence is false (Denevan 1992). Humans have altered the earth's ecosystems through the alteration of natural fire regimes over the last ~60 kyr (Diamond 2002), domestication and hunting over the last ~13 kyr (Thevenon et al. 2010), and, more recently, through influences on climate change (Voosen 2016). In North America, all mammal species >1000 kg and over half of those >32 kg became

extinct during the Late Pleistocene and Holocene (Koch and Barnosky 2006). This megafaunal collapse is paralleled in Eurasia and Australia and closely tracks human expansion across the planet (Barnosky et al. 2004, Burney and Flannery 2005). Estimates for megafaunal extinction in Africa since the Late Pleistocene range between 14% (Owen-Smith 1987) and 18% (Barnosky et al. 2004); however, looking further back in time (~1–2 mya), it is likely that close to 40% have become extinct (Martin 1966). Although the rate of extinction of African megafauna is lower

than on other continents, key drivers of ecosystem change, fire and herbivory, have been significantly modified by human activities (Archibald and Hempson 2016).

Parallels between fire and herbivory as consumers of biomass and ecosystem engineers have been drawn both globally (Bond and Keeley 2005) and within African savannas (Archibald and Hempson 2016). Reconstructing the past prevalence of fire or herbivory is challenging given limited data. Hempson et al. (2015a) use modeled data to suggest that current-day herbivore densities exceed those of the past where the mean annual precipitation (MAP) is between 500 and 700 mm and that the opposite is true for areas above 1000-mm MAP where soils tend to be leached and require fire to recycle nutrients (McNaughton 1985). Using evidence on the expansion and development of agropastoralism, along with paleocarbon charcoal data, Archibald et al. (2012) suggested that substantial human influence on fire regimes began ~40 kyr BP in closed/dissected landscapes and ~4 kya BP in open landscapes with an increase in fire frequency. These reconstructions contribute valuable baseline information to global change and ecological studies, and their application to rangeland management is yet to be explored.

The recent progress in our understanding of how fire shapes ecosystems and the characterization of "fire-prone" or "fire-adapted" systems (Bond and Keeley 2005, Bond et al. 2005, Lehmann et al. 2014) has informed the adoption of fire as a management tool in African rangelands. For example, fire in the Kruger National Park (KNP) has been actively managed since 1957 (van Wilgen et al. 2003) and is currently being managed to promote biodiversity and structural heterogeneity (van Wilgen et al. 2014). The translation of this understanding to managed commercial rangelands, without adequate consideration of how herbivory can be manipulated to fulfill some of the functions fire does, might result in a bias toward managing rangelands as fire-dominant ecosystems.

Ecologists have looked to the Pleistocene–Holocene for insights into restoring "lost" biodiversity and ecosystem function such as nutrient cycling, productivity, and resilience. As a result, trophic "rewilding" (Svenning et al. 2016) has been proposed as a restoration strategy that uses species introductions to restore trophic interactions and promote self-regulating ecosystems. Perhaps the most widely known example of rewilding is the reintroduction of apex predators, wolves (*Canis lupus*), to Yellowstone National Park in the mid-1990s with consequences for trophic cascades (Laundré et al. 2001, Ripple et al. 2001). The principle has also been applied to restoring historical disturbance patterns associated with fire and herbivory, which have been dominant evolutionary processes. An emerging management practice, termed pyric herbivory, uses the interactive effects of fire and grazing to promote structural heterogeneity and conserve biodiversity within rangelands (Fuhlendorf et al. 2009). While practices such as pyric herbivory may make implicit assumptions about how prevalent fire and herbivory were in mid-Holocene ecosystems and imply that fire functions as a mega-herbivore (Bond and Keeley 2005), we question the equivalence of fire and herbivory. Furthermore, the interactions and trade-offs between fire and herbivory before colonial hunting and significant livestock domestication in Africa have important implications for current managed rangelands. We hypothesize that herbivory was a more important driver of ecosystem function in mid-Holocene African savannas (~5 kya) compared to present, and use evidence from savanna ecology, paleoecology, and historical literature to substantiate this. We then consider how rewilding of rangelands (defined as savannas and grasslands that are managed under commercial and communal land tenure for meat production) with the type, pattern, and abundance of mid-Holocene herbivory may change rangelands from a fire-dominated to a herbivore-dominated stable alternative state. Lastly, we discuss the implications of a herbivore- versus a fire-dominated stable state for ecosystem processes and thus management of ecosystem services from rangelands.

HERBIVORY AND FIRE INTERACTIONS

A direct and reliable comparison of current herbivore biomass and mid-Holocene herbivore biomass within Africa is confounded by the absence of reliable methods and the difficulty of comparing wildlife biomass of the past with a largely domesticated biomass of the present

(Hempson et al. 2015a). Similarly, past fire regimes are difficult to model due to the complexity of how anthropogenic and natural drivers alter fire ignition frequency and extent (Archibald et al. 2012). However, ecological modeling, paleoecological proxies, and historic records provide some insights.

Hempson et al. (2015a) modeled the past distribution of herbivore biomass across Africa, showing that, since ~1000 yr ago, there has been an increase within agricultural areas, but a decrease in areas with more than 1000-mm MAP. They relate the increase to the disease suppression and resource provision associated with livestock farming. However, the model included census data from wildlife reserves to estimate past densities. Although these reserves presumably approach an intact state, the wildlife populations within these reserves may, arguably, be depressed relative to the past due to colonial and pre-colonial hunting (Spinage 2012), and disruption of migration routes and habitat transformation. Therefore, past herbivore biomass may have been underestimated. Furthermore, global paleoecological studies provide evidence to suggest a decline in megafaunal biomass since the Pleistocene, partially attributing this to the expansion of human populations on the earth and intensified fire regimes (Gill et al. 2009). The proxy for herbivore prevalence in such studies is the presence in lake and cave sedimentary deposits, of spores of the fungal genus *Sporormiella*, which requires herbivore digestion to complete its life cycle (Davis 1987). However, *Sporormiella* spore abundance cannot simply be equated to herbivore biomass since spore abundance is also influenced by climatic and topographic factors (Davis and Shafer 2006).

Nevertheless, early colonial records of herbivore populations, which were already reduced from hunting by indigenous peoples (e.g., Cramer and Mazel 2007, Spinage 2012), suggest higher animal numbers and densities compared to the present. Phrases used by early hunters to describe herds of game in southern Africa ~19th century include "immense numbers," "country swarmed with game," "numbers impossible to estimate," "thousands and tens of thousands," "100,000 seen from a wagon at one time," and "half a million wildebeest within a circle of 12 miles in circumference" (Skead et al. 2007).

Large densities were often reported during large migrations such as that of the "trekbokken" (springbuck) of the Karoo (South Africa). Fraser (1922), writing of a migration observed during 1849 stated "... we were awakened one morning ... by the trampling of thousands of all kinds of game-wildebeest, blesbok, springboks, quaggas, elands, antelopes of all sorts and kinds ... as far as the eye could see covered the whole country, grazing off everything eatable before them ... It took about three days before the whole of the trekbokken had passed." Although such reports may include hyperbole, the consistency between them suggests an element of truth. It would be hard to write similar stories about herbivore herds in reserves today, without the aid of hallucinogens.

Climate has been the dominant driver of fire prevalence since the last glacial maximum (Power et al. 2008). However, it is reasonable to conclude that humans have increased fire frequency (Bird and Cali 1998, Mouillot and Field 2005) and that mid-Holocene ecosystems were less fire-driven and more herbivory-driven than present managed rangelands. Indeed, paleoecological studies that use multiproxy analyses associate increased charcoal densities in sedimentary deposits with human expansion across the globe (Thevenon et al. 2010). In Africa, deposits from Masoko lake in Tanzania indicate a major influx of charcoal deposits synchronous with the Late Iron Age and agricultural innovations between 1.8 and 0.6 kyr BP (Thevenon et al. 2003). Apart from increasing fire ignition frequency (Bowman et al. 2011), humans contributed to releasing fire from its competitive relationship with herbivory through increased hunting. For example, in Australia (Rule et al. 2012) and America (Robinson et al. 2005, Gill et al. 2009), vegetation change during the Pleistocene–Holocene has been attributed to the indirect effect of relaxed herbivory pressure induced by human hunting and consequent increases in fire. However, widespread declines in fire over the past century suggest that agriculture and intensive grazing might have reduced fire spread more recently (Archibald et al. 2012, Marlon et al. 2013).

It is thought that the fire and herbivory interactions in near-pristine African wildlife reserves approximate mid-Holocene ecosystems (Hempson et al. 2015a), in contrast to intensively

managed rangelands where the form and function of fire and herbivory have been altered. In wildlife reserves, the interaction between herbivory and fire is partly facilitative, but largely competitive (Archibald and Hempson 2016). Fire non-selectively removes both unpalatable and palatable herbaceous biomass (Spasojevic et al. 2010), thereby excluding herbivory. However, burn scars facilitate nutrient-rich grass regrowth with increased leaf:stem ratios (Van de Vijver et al. 1999), which is of particular nutritive value to herbivores during the dry season (McNaughton 1985). Grazers compete with fire by removing the herbaceous layer that is fuel for fire. However, large browsers, such as elephants, open up relatively closed-canopy woody savannas, thereby promoting herbaceous growth and consequently greater fuel loads (Beuchner and Dawkins 1961, Staver et al. 2009, Bond and Van Wilgen 2012).

African shrub-dominated grasslands and tree-dominated savannas have been shown to exist as alternative stable states driven as much by disturbance regimes, such as fire and herbivory, as they are by climate and soil (Dantas et al. 2016). For example, within a climatic envelope suitable for both grasslands and savannas, any factors acting to reduce fire (e.g., grazing) will increase the probability of a savanna (McNaughton 1984). Similarly, fire-prone tallgrass and herbivore-prone short-grass alternative stable states within the savanna herbaceous layer have been identified and experimentally manipulated (Donaldson et al. 2017). Given that the herbivory–fire interaction is more competitive than facilitative (Archibald and Hempson 2016), we expect these two alternative stable states to be driven by thresholds of herbivory, beyond which fire will be largely excluded from a system, and *vice versa*. The two states are thus likely to contain structurally and compositionally different vegetation in the herbaceous and woody layers.

The herbaceous layer of a herbivore-dominated alternative state within savannas is characterized by herbivory-adapted, perennial shrubs and grasses with low-growth forms (Dublin et al. 1990, Liedloff et al. 2001, Anderson et al. 2007, Asner et al. 2009, Sankaran et al. 2013). The dominant species in this herbivore-dominated stable state are characterized by traits enabling rapid recovery from herbivory such as stoloniferous (e.g., *Digitaria eriantha*) or

rhizomatous (e.g., *Setaria incrassata*) grasses (Diaz et al. 2007, O'Connor et al. 2014). The nutrient-rich regrowth following defoliation encourages repeated herbivory and establishes grazing lawns (McNaughton 1984, Staver et al. 2012, Hempson et al. 2015b). In addition, the lower C:N ratios decrease foliar structural carbon and plant bulk density, thereby inhibiting flammability (Schwilk 2015). A fire-dominated alternative state would promote a herbaceous layer characterized by fire-tolerant taller bunch grass species (e.g., *Hyparrhenia filipendula*) that re-sprout vigorously from stored reserves after a fire (Archibald et al. 2005, Anderson et al. 2007). These grasses are of low nutritive quality (due to lower leaf:stem ratios) and inhibit herbivory, resulting in high levels of standing biomass to fuel fires and thereby enforcing a positive feedback loop, promoting a fire-driven system (McNaughton 1985).

The consequences of herbivore or fire dominance for the woody vegetation layer are contested in the debate about the ecological drivers of woody plant encroachment. Relaxing herbivore pressure and increasing that of fire has been proposed as method to prevent woody encroachment (Bond and Midgley 2001, Roques et al. 2001, Wiegand et al. 2005). However, a four-decade fire manipulation experiment in four different savanna ecosystems in KNP found no significant change in woody cover density (Higgins et al. 2007). This may be due to the interactive effects of herbivory and fire on seedling emergence, survival, and recruitment, which can both increase and decrease woody encroachment (van Wilgen et al. 2003). Furthermore, 41-yr herbivore exclusion experiments in KNP, South Africa, resulted in an 11-fold increase in woody canopy cover (Asner et al. 2009). Indeed, herbivory, specifically in the form of browsing, is suggested to have been a key driver in the historical evolution of savannas, suppressing trees and releasing grasses (Charles-Dominique et al. 2016). Herbivory-driven states can reduce woody encroachment if both grazing and browsing act to simultaneously prevent seedling establishment and reduce recruitment of woody plant species (Van Langevelde et al. 2003, O'Connor et al. 2014). For example, Augustine and McNaughton (2004) showed that a community of native browsers ranging from selective species (e.g., dik-diks; *Madoqua* spp.) to large bulk

feeders (elephants; *Loxodonta africana*) can suppress shrub encroachment on commercial rangeland in Kenya.

The transition from one stable state to another occurs when a critical threshold is reached in response to a shift in a climatic or biotic driver (Hirota et al. 2011). The resilience to this transition between fire- and herbivore-dominated stable states might be strongly mediated by spatiotemporal variation in water and nutrient availability (Krawchuk and Moritz 2011). Currently, fire consumes 5.8 times more dry matter than herbivory across sub-Saharan Africa, which equates to 103 g/m^2 (Fig. 1). The median regression line of this relationship changes across the rainfall gradient, where herbivores consume more biomass under ~700-mm MAP. Fire dominance peaks between ~700- and 1500-mm MAP, which are mesic savannas in central and east Africa (Fig. 1). In mesic savannas, leached low-nutrient soils support unpalatable vegetation with high C: N ratios (Bell 1982, East 1984), thereby inhibiting herbivory and promoting fire (Du Toit 1995). Thus, mesic fire-dominated rangelands may be resilient to change and resist switching to a herbivore-dominated alternative stable state (Fig. 2A and red areas in Fig. 1). The opposite is true for arid, less-leached, nutrient-rich savannas with palatable vegetation that sustains an abundance of herbivores, which keep fuel loads down and prevent the occurrence and spread of fire (McNaughton 1984, Du Toit 1995). Consequently, semi-arid grasslands at ca. 700-mm MAP, which are currently neither herbivore nor fire-dominant (gray areas in Fig. 1), may switch faster to a herbivore-dominated stable state (Fig. 2B and light green areas in Fig. 1) under increased herbivore pressure.

REWILDING AND ECOSYSTEM FUNCTION

The principle of rewilding ecosystems with extirpated species (Rosenzweig 2003, Svenning et al. 2016) or evolutionary disturbances (Fuhlendorf et al. 2009, Scasta et al. 2016) has not been directly considered for African rangelands. An obvious commercial benefit of promoting a herbivory-dominant alternative state is potentially greater animal production and profits, whereas benefits to other ecosystem services are dependent on abiotic and edaphic conditions. As we have seen, the effects of herbivory dominance may vary over time and space along nutrient and rainfall gradients (Archibald and Hempson 2016). As an example, we will compare the effects of fire and herbivory on nutrient cycling
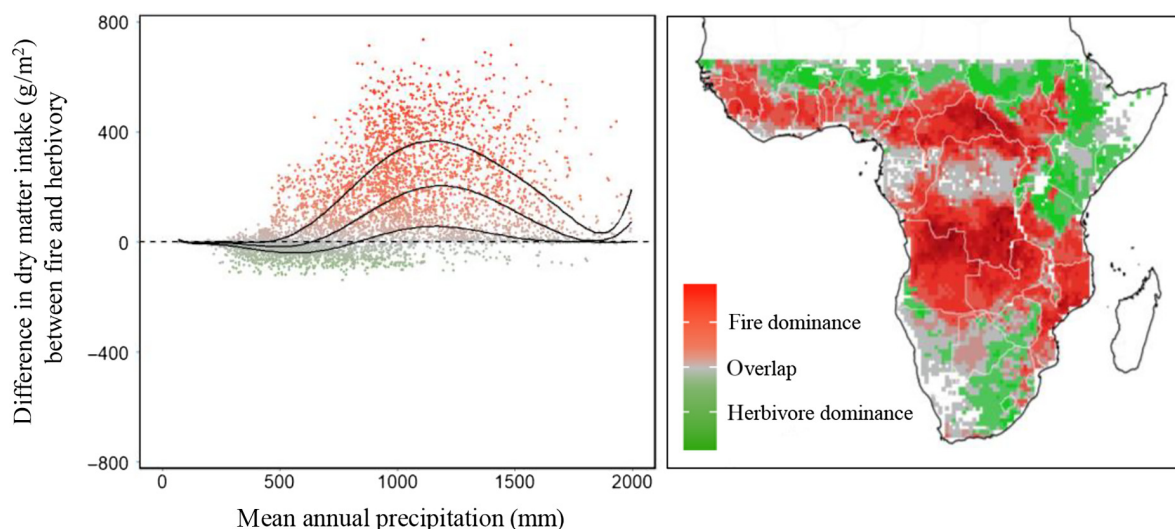

Fig. 1. The difference in dry matter intake (g/m^2) between fire and herbivory for each quarter-degree-square over Africa, represented across mean annual precipitation (left) and spatial (right) gradients. The 25%, 50%, and 75% quantiles are represented by solid black lines (left). The data, supplied by Archibald and Hempson (2016), were derived from satellite imagery, and wildlife and livestock census data.
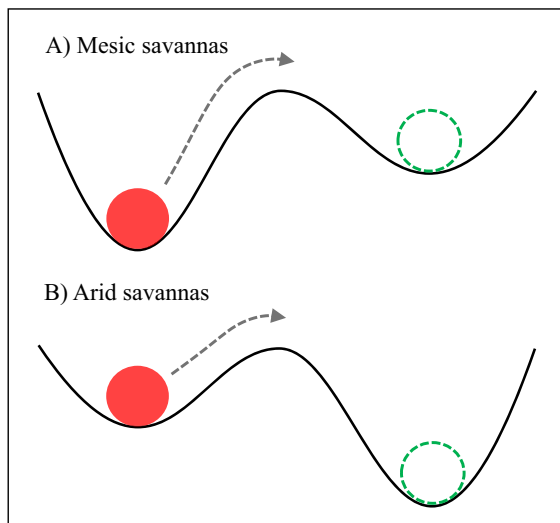
Fig. 2. Two-dimensional ball-in-cup diagrams comparing notional resilience to a shift in alternative stable states within mesic and arid savannas. (A) Mesic savannas contain leached, nutrient poor soils which are prone to fire, and may thus display greater resilience to shifting to herbivore dominance. A greater increase in herbivory is required to push the ball out of the cup. (B) In arid savannas, nutrient-rich soils support higher quality forage which promotes herbivory and consequently reduces fuel for fire. In arid savannas that currently exist as fire-dominated stable states, less change in herbivory is indicated to be required to shift the ball out of the cup into a herbivore-dominated state. Thus, fire-dominated states are more stable in mesic than arid savannas. We suggest that gray and light-red areas on the map, characterizing codominant and slightly fire-dominant states, respectively, can be switched to herbivore dominance through less management intervention than would be required for heavily fire-dominated areas. Management intervention may include adaptive manipulation of herbivore densities over time and space to maintain an appropriate carrying capacity for the rainfall and soil nutrient status of the area, occasional use of fire, and including a diversity of herbivore functional guilds.

in African savannas to explore whether a herbivore-dominant alternative state may improve ecosystem function.

The mechanisms through which herbivory enhances nutrient cycling include dung and urine deposition and trampling (McNaughton et al. 1988, Singh et al. 1991), litter deposition and changes in stoichiometric feedbacks (Krumins et al. 2015), plant physiological responses (Holland et al. 1992), and changes in species composition (Anderson et al. 2007). Plants exhibit compensatory growth after grazing, and after passing through the herbivore gut, this biomass returns to the soil in a form (dung and urine) that enhances substrate decomposition and mineralization rates. Plant litter contributed to the detrital pool through "sloppy" or partial feeding enhances microbial-mediated metabolism and N mineralization (Krumins et al. 2015). This is further mediated through concomitant changes in soil temperature and moisture associated with litter cover, which increases microbial activity and mineralization (Sitters and Venterink 2015). At a larger scale, herbivory has been shown to be associated with higher plant nutritive quality relative to fire, due to a change in species composition favoring lower-biomass species with lower C:N and C:P ratios (Anderson et al. 2007).

Fire causes a loss of C and N in soil through volatilization (Kauffman et al. 1994, Bustamante et al. 2006, Chen et al. 2010), and a conservation of Na and P (among other elements) through pyromineralization (Hartshorn et al. 2009). Using satellite-derived estimates, Chen et al. (2010) found that fire emissions in savannas account for a net N loss equivalent to 22% of biological N-fixation. Although some nutrients (e.g., P) are less volatile under fire than others, these may not become available in soils due to wind displacement of ash, leaching, or changes in soil structure (DeBano and Conrad 1978, Anderson et al. 2007, Resende et al. 2011). Consequently, because mycorrhizae are strongly linked to P acquisition in plants, P cycling to plants would be limited (Koide and Kabir 2000). Also, the strong negative relationship between fire frequency and the mycorrhizal colonization of perennial grass roots in African savanna may be due to soil crusting, increased runoff, and decreased moisture following fire (Hartnett et al. 2004).

Long-term decadal studies directly comparing the effects of fire and herbivory on nutrient cycling at different intensities do not exist (Pellegrini et al. 2015). However, in a two-year manipulation experiment in tallgrass prairie, Hobbs et al. (1991) calculated that using herbivory instead of fire to remove biomass saves ~1 g m^{-2} yr^{-1} N that would otherwise have been lost as a result of

volatilization during burning. Assuming that cattle need 0.014 g N per gram of fresh body weight (Berg and Butterfield 1976) and that animals could potentially utilize 50% of standing plant biomass (Cordova et al. 1978) and efficiently convert it to body weight, this equates to 357 kg meat productivity lost per hectare burnt instead of grazed. Apart from N, ~45 million ton of grassland biomass is burned every year in southern Africa (Scholes et al. 1996). Assuming grazing livestock in Africa have a feed-use efficiency of ~1 ton of dry grass matter per kilogram of meat (Herrero et al. 2013), this represents a maximum potential loss of 45 million ton of meat production per year. Even if one assumes that the burnt biomass was likely to be largely unpalatable, particularly in mesic areas and that it would only be moderately utilized (e.g., 25–50%, Hart et al. 1993), this is still a significant economic loss.

Comparing studies on the independent effects of fire and herbivory on soil nutrient pools reveals that herbivory conserves more soil C and N. In a meta-analysis of 115 published studies from around the globe, Zhou et al. (2016) found that livestock grazing decreased soil C and N pools by 10.3 and 13.4%, respectively, relative to ungrazed controls, while increasing N mineralization and nitrification by 22 and 24%. Equivalent meta-analyses for fire effects do not exist, but a 58-yr annual fire experiment in the KNP of South Africa produced soils depleted of C and N by 25 and 62% relative to unburnt plots (Pellegrini et al. 2015). This equates to at least a twofold and fourfold conservation of soil C and N, respectively, when savannas are grazed instead of burnt. Although herbivory and fire both deplete soil nutrient pools relative to an undisturbed control, grazing enhances mineralization whereas fire does not have consistent effects on N (Coetsee et al. 2008) or P (Hartshorn et al. 2009, Holdo et al. 2012) mineralization.

MANAGEMENT IMPLICATIONS

The management implications of rewilding savannas with mid-Holocene herbivore densities are difficult to ascertain because the exact type and spatiotemporal patterns of herbivory that occurred in mid-Holocene ecosystems are unknown. Some resource managers have attempted to derive grazing practices based on ecological principles from observations of supposedly intact ecological systems, for example, pyric herbivory (Fuhlendorf et al. 2009), opportunistic management (Westoby et al. 1989), Holistic Planned Grazing (Savory 1983), and other forms of time-controlled, short-duration rotational grazing (Tables 1, 2). We distill a few basic principles from these management practices, the colonial records, and research within near-pristine wildlife reserves and suggest these principles are necessary to sustain a herbivory-dominant ecosystem state without compromising rangeland productivity and ecosystem services.

Table 1. Summary of existing grazing management systems.

System	Description	Reference
Continuous grazing; season-long grazing	Access to all or half of grazing areas for at least a full season. Particularly common in communal rangelands and wildlife areas.	De V. Booysen (1967), Tainton (1999)
Rotational grazing	Grazing area divided into multiple paddocks to create reoccurring periods of grazing and rest. Generally managed according to a fixed or adaptive rotation plan.	Merrill (1954), Tainton (1999), Briske et al. (2008)
High- and ultra-high-density grazing; cell grazing; Holistic Planned Grazing™; short-duration grazing; non-selective grazing	A variant of rotational grazing with higher stocking densities (more camp divisions and shorter grazing durations) of hundreds or thousands of animals per hectare. Often associated with an adaptive management approach.	Acocks (1966), Savory (1983), Voisin (1988), Briske et al. (2008)
Opportunistic management; pyric herbivory	A non-equilibrium approach where grazing management decisions are made in response to spatiotemporal patterns in resource availability at varying scales. Fire may be used to create a shifting mosaic of heavily grazed burnt patches among taller undisturbed patches. Water points may be moved to achieve similar effects.	Westoby et al. (1989), Illius and O'connor (1999), Vetter (2005), Fuhlendorf et al. (2009), Laca (2009), Limb et al. (2011), Fynn (2012)

Table 2. Summary of existing grazing management systems (continuation of Table 1).

System	Claimed benefits	Criticisms
Continuous grazing; season-long grazing	Increased grazing selectivity for palatable plants and subsequent increased animal production; low management inputs	Increased woody plant encroachment through reduced competition from grass; overgrazing and loss of palatable species
Rotational grazing	Increased forage utilization; reduced grazing selectivity and subsequent loss of palatable species; sustained species diversity	Lack of empirical evidence; existing evidence displays large variation and is often confounded by other variables; reduced selection for palatable plants results in animal weight losses
High- and ultra-high-density grazing; cell grazing; Holistic Planned Grazing™; short-duration grazing; non-selective grazing	Increased forage utilization; reduced grazing selectivity and subsequent loss of palatable species; increased trampling and subsequent enhanced water infiltration and soil nutrient cycling; reduced woody plant encroachment through seedling mortality	Lack of empirical evidence; increased trampling damages biological soil crusts and increases soil compaction; higher infrastructure costs; potential for increased animal stress and reduced fecundity
Opportunistic management; pyric herbivory	Results in functional heterogeneity and consequent resilience to environmental stresses; conservation of biodiversity; increased forage quality on post-burn grazing patches	Adaptive approach makes experimental testing difficult; lack of empirical evidence for increased production; loss of species and soil erosion on heavily grazed patches

Diversifying the type of herbivory through introducing mixed livestock herds has not been directly accounted for in the dominant rangeland management strategies (Tables 1, 2). Mixed herbivory may approximately imitate the large variation in herbivore functional types that would have been present in mid-Holocene savannas (Du Toit and Cumming 1999). Currently, higher rainfall savannas support a much lower herbivore biomass than in the past (Hempson et al. 2015a). This is largely due to the loss of large browsers in farmed rangelands, which has also been identified as a contributing factor to the widespread woody plant encroachment across southern Africa (O'Connor et al. 2014). Furthermore, a comparison between domestic cattle herbivory and wildlife herbivory in the KNP of South Africa found that mono-specific herbivory led to increased tree cover and lower grass foliar N content relative to multispecies herbivory (Baumgartner et al. 2015). A possible improvement could involve introducing a combination of grazers, browsers, and generalist livestock along with wildlife (Augustine et al. 2011, Fynn et al. 2016) onto rangelands to sustain a productive herbivore-dominant stable state.

The strong herding behavior of wild herbivores, which evolved in response to predatory pressures and the need for migration (Savory 1983), is perceived to be less evident in domesticated livestock, and this may have significant effects on foraging patterns and soil and vegetation responses. It may be effective to increase herbivore density per unit time through intensive rotational grazing management (Tables 1, 2). Claims that the rotational grazing strategies will increase productivity while maintaining ecosystem processes have been contested and are currently both supported (e.g., Teague et al. 2013) and contradicted (e.g., Briske et al. 2008, 2011). Savory (1983) and others propose increasing grazing densities to increase animal "hoof impact," which will promote nutrient and water cycling through litter cover, soil surface chipping, and dunging. However, other studies have shown that high grazing densities can cause soil compaction, reduce water infiltration, and damage biological soil crusts (Warren et al. 1986, Du Toit et al. 2009, Carter et al. 2014). The effects of animal densities on soil are minor compared to the defoliation effects (Greenwood and McKenzie 2001), and the rotational grazing debate has largely centered around grazing selectivity and the resulting long-term changes in species composition. Species composition responds strongly to stocking rate (O'Reagain and Turner 1992), but is largely unaffected by grazing management system (Morris and Tainton 1996, Hickman et al. 2004, Dowling et al. 2005). This may be because it is difficult to reduce animal selectivity at the feeding station scale (Kirby and Webb 1989, Walker et al. 1989, Morris and Tainton 1996). However, at the patch and landscape scale, rotational grazing can reduce selectivity and shows potential to reduce loss of palatable species (Teague et al. 2004). Thus, introducing a variety of

animal densities through rotational grazing to imitate the herding behavior of wild herbivores may benefit long-term rangeland production.

Alternatives to traditional rotational grazing strategies (Tables 1, 2) that attempt to reduce selection and vegetation heterogeneity are emerging primarily in the rangeland conservation literature. The maintenance of ecosystem function and biodiversity in historical ecosystems have often been attributed to landscape heterogeneity (Christensen 1997). Diversifying disturbance patterns to change vegetation structure over the landscape may imitate the high levels of ecosystem function and biodiversity that were present in mid-Holocene ecosystems (Fuhlendorf and Engle 2001). This might involve adopting an adaptive and opportunistic management framework that implements variable herbivore pressures over time and space to shift non-equilibrium rangelands into desired alternative states (Westoby et al. 1989). Movable watering points can achieve something similar through imitating ephemeral water resources that characterized mid-Holocene savannas. Small fires may also be used in this regard to create a mosaic of nutrient-rich regrowth patches over the landscape, possibly leading to grazing lawns (Archibald et al. 2005). Manipulating grazing return-periods from a day (as would be the case on grazing lawns) up to a year or longer (as would be the case with seasonal migrations) depending on the vegetation composition present will utilize the suite of plant phenotypes that evolved during the mid-Holocene.

There is a balance to be found between the competing equilibrium and non-equilibrium paradigms in ecology and rangeland management (Vetter 2005). The density-dependent regulation of livestock numbers (equilibrium theory) should be adaptable to stochastic factors such as rainfall and fire (non-equilibrium theory). For example, de-stocking during drought and re-stocking in high rainfall years imitates the natural fluctuation in wild populations and prevents over-utilization of forage (Skovlin 1987, Westoby et al. 1989, Jakoby et al. 2014). Instead of managing for livestock numbers to be in equilibrium with the ecological carrying capacity, there is potential for rangeland managers to maintain equilibrium dynamics within alternative stable states (Briske et al. 2017). John Acocks once remarked that African rangelands might be "understocked and overgrazed" due to a perceived lack of grazing management leading to high selectivity for, and consequent overgrazing of, palatable species (Hoffman and Cowling 2003). Altering the spatiotemporal pattern of herbivory may afford an increase in overall abundance and stocking rate over a landscape without causing rangeland degradation. Although matching the stocking rate to the carrying capacity (forage base) of an area remains, and should remain, a guiding principle in rangeland management (Briske et al. 2017), a landscape can be maintained under a mosaic of animal densities leading to multiple fire- and herbivore-dominant stable states depending on the rangeland manager's objectives. The resilience of current fire-driven systems to a shift to herbivore dominance will determine the lag-time for the change to take effect, and the intensity with which the above-mentioned practices should be implemented. For example, in a mesic, fire-dominant system, more intense herbivory and fire suppression might be required over a longer time to shift the system to herbivore dominance (Fig. 2). In arid rangelands, the shift might be faster.

Conclusion

We thus question the widespread assumption that frequent fires are a necessary and "natural" management tool to address ecosystem problems such as woody plant encroachment, induced by reduced diversity and density of herbivores. Prolonged rewilding of some African rangelands with mid-Holocene herbivory pressure and diversity may shift a system into an alternative stable state, which, relative to a fire-dominant state, may enhance nutrient cycling, conserve soil nutrient pools, and benefit productivity. The conservation of nutrients and alteration of vegetation communities might have long-term consequences on the global carbon budget and climate change. Although briefly considered here, the conversion of biomass, that would otherwise have been burnt, into meat may have economic and societal impact of global significance. Sustaining this intense herbivory may involve diversifying livestock feeding guilds, increasing herding densities and spatiotemporal herbivory patterns, and promoting adaptive heterogeneous management practices.

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