The role of ancient human settlements in creating nutrient hotspots in a savanna ecosystem, central Zimbabwe.

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Abstract

Ancient human settlements play an important role in creating heterogeneous African savanna ecosystems through forming nutrient hotspots with increased biodiversity and improved forage quality. However, plant community development and herbivore utilization of these sites after abandonment remain poorly understood. We compared plant and soil parameters in ancient human settlements with off-sites locations. In addition, we set camera traps in ancient settlements and surrounding vegetation to determine their use by herbivores. Grass basal cover, height, biomass and species diversity in ancient settlements had recovered to similar levels with the surrounding landscape. Ancient settlements had small trees (in terms of height and canopy volume), lower tree density and lower species diversity than the surrounding landscape. Soil phosphorus and calcium were higher in ancient settlements than surrounding landscape, while pH, nitrogen, potassium, magnesium and sodium were similar between the two sites. Impala and greater kudu camera sightings were higher in ancient settlements than surrounding vegetation, while warthogs showed no preferential foraging between ancient settlements and surrounding vegetation. We conclude that ancient settlements created functional heterogeneity through altering the structure of savanna vegetation influencing foraging patterns of herbivores such as impala.

Keywords: African savanna ecosystems; camera traps; grass biomass; large herbivores; soil nutrients

1. Introduction

Early nomadic pastoralism in southern Africa was characterised by settlements of huts and livestock enclosures (Kinahan, 1996). Ancient human settlements belonging to early nomadic pastoralists have been identified in southern Africa (Huffman and Du Piesanie, 2011; Huffman et al., 2013). For example, in the Limpopo valley, South Africa and eastern Botswana ancient human settlements, particularly, cattle kraals (corrals, bomas, glades) create nutritive grassy vegetation on dung-modified soils (Huffman et al., 2013). Ancient human settlements create heterogeneous ecosystems (Marshall et al., 2018; Western and Dunne, 1979), that act as nutrient hotspots with increased plant biodiversity and improved forage quality (Scholes and Walker, 2003). They can be identified as open spaces because during occupation human and animal activities destroy vegetation that then takes several years to recover since trees cannot grow in the compacted dung and village immediate surroundings (Huffman et al., 2013; Marshall, 2000). The role of nutrient hotspots is increasingly being recognised in southern African rangelands where plant primary productivity is constrained by factors, such as poor soil nutrients. There is need to identify as many ancient human settlements as possible, explore their legacy effects and assess their roles as nutrient hotspots for their incorporation into rangeland management plans.

Early evidence of the activities of nomadic pastoralist is from excavations and rock shelters (Kinahan, 1986). However, at the time of historic contact the nomadic pastoralists (herders) moved frequently in response to availability of pastures for their livestock and lived in temporary encampments of huts (Kinahan, 1986). The frequent movement of the nomadic pastoralists makes it difficult to easily identify their settlements, particularly in areas where there are no excavations and rock shelters.

Ancient human settlements alter vegetation growth and development through initiating succession. Abandoned settlements, particularly kraaled sites (glades) are quickly colonised by nutritive grasses that attract both domestic and wild herbivores (Veblen, 2013). For example, *Cynodon* species are associated with former settlements and regarded as important forage species (Muchiru et al. 2009). The utilisation of glades by grazers tends to suppress woody plant regrowth with grasses benefitting from improved nutrients released as urine and dung (Muchiru et al., 2008; 2009). There is need for further research to better understand the role of ancient settlements in shaping plant communities.

Human habitation alters soil nutrients through accumulation of organic waste, dung and ash, rich in minerals such as calcium, phosphorous and magnesium (Storozum et al., 2021). Abandoned kraals (glades) accumulate macro- and micro-nutrients through dung deposition (Marshall et al., 2018; Storozum et al., 2021), and thus have elevated pH, calcium (Ca) and magnesium (Mg) levels (Augustine 2003; Muchiru et al. 2009). In addition, kraal fences consisting of tree branches also add nutrients, particularly, Ca and potassium (K) (Huffman et al., 2013). Soil nutrient levels [such as nitrogen (N), phosphorus (P) and K] could be twenty times higher in glades than surrounding landscape (Augustine, 2003; Reid and Ellis, 1995).

Ancient human settlements, especially old kraal sites, are an important refugee for large herbivores (Huruba et al., 2017; Muchiru et al., 2008; van der Waal et al., 2011). For instance, impala (*Aepyceros* *melampus*), are attracted to old kraal sites because of short nutritive grasses (Arsenault and Owen-Smith 2008). Interestingly, other large herbivores are not attracted to these old kraal sites (Veblen, 2012), which may be a function of their anatomical traits, especially mouth anatomy (Fynn & Provenza, 2023). Thus, there is need to ascertain the extent of ancient settlements use by different large herbivores.

We studied the effects of anthropogenic activities on vegetation (grasses and trees) and soil nutrient parameters at ancient human settlements at Shangani Holistic ranch, central Zimbabwe (Figure 1). In addition, camera traps were used to monitor wildlife use of these ancient settlements. We tested the following hypotheses: 1) grass parameters (cover, height, biomass and species diversity) recover from human settlements to similar levels to off-site surrounding vegetation, 2) tree growth parameters (height, canopy volume, density and species diversity) do not recover from human settlements impacts to similar levels to off-site surrounding vegetation, 3) human settlements alter soil nutrient parameters (pH, N, P , K, Ca, Mg and Na), and 4) ancient human settlements are preferred wildlife foraging sites than off-site surrounding vegetation.

2. Materials & methods

2.1. Study area

This study was conducted at Shangani Holistic (29˚13'E, 19˚36'S; 1230m elevation), a mixed cattle-wildlife ranch that covers an area of 800 km^2 located in central Zimbabwe (Fig 1). Large mammals found in the ranch include impala (*Aepyceros melampus* Lichtenstein 1812*)*, Burchell's zebra (*Equus quagga* Boddaert 1785), warthog (*Phacochoerus africanus* Gmelin 1788), African savanna elephant (*Loxodonta africana* Blumenbach 1797), northern giraffe (*Giraffa camelopardalis* Linnaeus 1758) and greater kudu (*Tragelaphus strepsiceros* Pallas 1766). The study area is characterized by a catenal vegetation pattern, with most areas consisting of grassed bushland with patches of Miombo woodland (Dunham et al., 2003). The dominant woody species is *Acacia* (*Vachellia*) *karroo* Hayne with the major grass species being *Hyparrhenia filipendula* (Hochst.) Stapf., *Eragrostis curvula* (Schrad.) Nees., *Heteropogon contortus* (L.) Roem. & Schult., *Bothriochloa insculpta* (Hochst. Ex A. Rich.), *Digitaria milanjiana* (Rendle) Stapf., and *Panicum maximum* Jacq. The area receives mean annual rainfall of 612 mm, with a rainy season that runs from November to March and a dry season from April to October (Dunham et al., 2003). Mean annual temperature is 22.6˚C, with October (31.4˚C) the hottest month and July the coldest (8.5˚C). Ancient human settlements on the ranch are characterized by openness due to vegetation clearance during occupation (Figure 2).

2.2 Identification of ancient human settlements

We used archaeological methods to identify four ancient human settlements by checking for the presence or absence of sediments produced by settlers (Shahack-Gross, 2011). Ancient pastoralists are thought to have had a significant environmental footprint, particularly on soil parameters (Storozum et al., 2021). Ancient human settlements had clear demarcations with different soil texture due to vitrified dung compared to surrounding landscape. Excavation trenches measuring 2m x 1m were dug on the ancient human settlements. Archaeological findings included a copper and straw bangle fragment, bones, pottery, slag, pole impressed dhaka, soapstone fragments, charred archatina shell, faunal remains, decorated potsherd, a horn core and carbonized seeds (probably sorghum).

2.3. Grass basal cover, height, biomass, species diversity and composition

Vegetation assessments were made during the rainy season (February 2021) when grasses and trees could easily be identified to species level. For grass basal cover at each sampling site a 1 m × 1 m quadrat was randomly laid at the centre of the vegetation patch and then four others were located 15 m from the centre point in the four cardinal directions. All basal covers of grasses within the square metre were transferred (drawn) to one corner of the quadrat in order to facilitate the estimation of the proportion of the quadrat covered by the grass bases. The area covered by the grass bases was determined and expressed as a percent of the quadrat area. Only basal cover of living parts was considered. Grass height was measured in five randomly selected points in ancient settlements and off-site (control) locations. We directly measured grass height by placing a ruler vertically from the ground next to the grass plants to the highest apical point. Grass height was expressed in centimetres. Within each 1 m × 1 m quadrat a 50 cm × 50 cm subquadrat was laid at the centre for aboveground grass biomass measurements. All grass was clipped using a pair of scissors and then air-dried in the shade. The grass samples were further oven-dried to a constant weight at 60 °C for 48 h in the laboratory. Aboveground grass biomass was expressed as grams per square metre. Grass species diversity was calculated using the Shannon–Wiener diversity index (Krebs, 1999):

$$H' \text{ (species diversity)} = -\Sigma p_i \, ln \, p_i$$

where p_i is the relative abundance of the grass species.

To determine grass composition all plants were identified to species level in 1m x 1m quadrats and their number recorded. Percent relative abundance of each grass species was expressed as the proportion of the number of a species over the total number of all grasses. The grass species were further classified into three palatability classes (highly, moderately and lowly palatable) and according to life form (perennial or annual).

2.4. Tree height, canopy volume, density, species diversity and composition

A total of ten quadrats (25 m x 25m), five in each of ancient settlement and control site were marked for tree height, canopy volume, density, species diversity and composition determination. The quadrats were demarcated using a string and marked using wooden pegs at each corner.

Tree height was measured for each individual sampled using a graduated nine-meter pole. For trees taller than 9m the pole was raised up by a person whose height was known and the total height determined. Canopy volume was calculated using the formula:

$$\text{Canopy volume} = 2/3 \, \pi \, \text{canopy height} \, (A/2 \times B/2) \qquad \text{(Thorne et al., 2002)}$$

where canopy height is the distance from the base of the plant to the tallest photosynthetically active material and A and B are the diameter readings taken at 50% of plant height with B perpendicular to A.

Tree density was calculated using the formula:

$$\text{Density (number of plants/ha)} = (x * 10000) / (\text{quadrat area})$$

where x = number of woody plants per quadrat, quadrat area = 625 m^{-2}

Tree species diversity indices were calculated using the Shannon-Wiener diversity index:

$$H' = -\Sigma pi \ln pi$$

where *pi* is the proportion of individuals found in the *i*th species, *ln* = natural logarithm.

In each quadrat, woody plants were identified to species level using a field guide (van Wyk and van Wyk, 2013) and their numbers recorded. The number of woody plants in each species was then expressed as a percentage of the total number sampled in both ancient settlements and control sites.

2.5. Soil collection and analyses

We collected soil samples in ancient human settlements and surrounding landscape to compare their nutrient concentrations. Five soil samples each were collected using a 6-cm diameter stainless steel soil auger (0-15 cm depth) in randomly selected positions in ancient settlements and off-sites. Soil cores were collected in the four cardinal directions, bulked, and mixed thoroughly before a composite sample was drawn at each sampling location. Soils were then sieved by passing through a 2-mm mesh before air-drying. The soil samples were analysed for nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) according to Anderson and Ingram (1993) methods at the Department of Research and Specialist Services, Chemistry and Soil Research Institute soil testing laboratory in Harare, Zimbabwe. Total N was determined using semi-micro Kjeldahl procedure of acid-digestion, distillation and titration. Available P was estimated by colorimetry using the ascorbic acid–molybdate method. Extractable K, Ca and Mg were determined using atomic absorption spectroscopy. Soil pH was measured using the water method.

2.6. Camera sightings

We deployed Cuddeback Attack/Attack IR digital scouting cameras (n = 16) (Cuddeback Trail Camera company, India) infrared camera traps at eight locations (four ancient settlements and four control sites) at Shangani Holistic ranch in January 2021 for thirty days (Fig 1). Control sites were marked 100m away from ancient settlements. Two cameras were deployed per site. The cameras were mounted on tree trunks at one meter above the ground to detect medium- to large-bodied mammals (Meek et al., 2016). The cameras were set for pictorial (single capture/minute) data capture for diurnal and nocturnal animals at a trigger speed interval of 60 seconds and each image displayed date (dd/mm/yy), time (hh:mm) and camera number(ID). Secure Digital (SD) memory cards and non-rechargeable batteries were replaced after two weeks. The pictorial data was downloaded from the SD cards and stored in folders labelled according to site location. Microsoft Excel version 2016 was used to store the photographic data with the following details: camera location, camera unit identifier, date (dd/mm/yy), time (hours, minutes) and animal species. The number of animal sightings of each large herbivore species was recorded from the camera trap data and expressed as number of animal sightings per day. All successive photographs of a species at the same camera were treated as independent if ten minutes passed with no captures of the particular species (Kolowski and Forrester, 2017).

2.7. Data analysis

Grass (basal cover, height, biomass and species diversity) and soil (pH, N, P, K, Ca, Mg and Na) data were compared between ancient settlements and off-site (control) using Generalized Linear Mixed

Models (GLMMs) in R software (R Core Team, 2020). Settlement vs. off site was the fixed effect and the random effect was sampling site, which accounted for the spatial variation between sites. Tree (height, canopy volume, density and species diversity) and camera trap wildlife (impala, warthog and greater kudu) sightings data were compared between ancient settlements and off-site (control) using the Independent *t*-test with SPSS version 22 (SPSS Inc., Chicago, USA). Tree and wildlife sighting data were tested for assumptions of normality and homogeneity of variance using Shapiro-Wilk test and Levene statistic, respectively.

3. Results

Grass basal cover, height and biomass were similar between ancient human settlements and off-sites, while species diversity was higher in ancient settlements than off-sites (Table 1). The number of grass species was higher in ancient human settlements (15) than off-sites (11) (Table 2). Lowly palatable grass species were only found in ancient human settlements. *Cynodon dactylon* was more abundant in ancient human settlements (4.6 vs 0.8%) than off-sites.

Larger trees (in terms of height and canopy volume) were found off-sites compared to ancient settlements, with tree density and species diversity higher off-sites than in ancient human settlements (Table 3). There were fewer tree species in ancient settlements (5 vs 12) than off-sites (Table 4). Soil P and Ca were higher in ancient settlements than off-sites, while pH, N, K, Mg and Na were similar between the two sites (Table 5).

A total of 239 camera images captured in 30 days were used to calculate the number of impala, warthog and greater kudu sightings per day. Impala and greater kudu sightings were higher in ancient human settlements than off-site, while warthog sightings were similar between ancient human settlements and off-site (Table 6). Other animals captured in the camera traps were waterbuck (*Kobus ellipsiprymnus*), vervet monkey (*Chlorocebus pygerythrus*), bushbuck (*Tragelaphus scriptus*), duiker (*Sylvicapra grimmia*), baboon (*Papio anubis*), zebra (*Equus quagga*), elephant (*Loxodonta africana*), leopard (*Panthera pardus*), giraffe (*Giraffa camelopardalis*), skunk (*Mephitis mephitis*) and cattle (*Bos taurus*). However, there were not consistently captured in both ancient human settlements and off-sites to allow statistical analysis.

4. Discussion

Our study shows that ancient settlements may alter the structure of savanna vegetation and influence foraging patterns of herbivores. Ancient settlements provide open spaces favoured by herbivores such as impala as foraging and refugee sites due to poor tree recruitment. Ancient human settlements associated with livestock kraaling at Shangani Holistic ranch left behind a legacy of nutrient hotpots after abandonment.

The similarity in grass basal cover, height, and biomass between ancient settlements and off-sites was, presumably, because herbaceous vegetation regrowth in previously cleared settlements had recovered to similar levels to the surrounding landscape. Interestingly, species diversity was higher in ancient settlements than surrounding vegetation (Table 1), presumably, because there was greater grass recruitment in the ancient human settlements. van der Waal et al. (2011) reported aboveground herbaceous biomass to be similar between abandoned kraal sites and surrounding vegetation. Interestingly, there were more grass species in ancient human settlements (15 vs 11) than off-sites, presumably, because herbivores deposited dung rich in various grass seed types. The presence of lowly palatable grass species such as *S. pyramidalis* that are associated with deteriorating rangeland condition could be an indicator of over utilization of ancient human settlements by grazing herbivores resulting in loss of palatable grass species (Dube and Pickup, 2001). For example, *P. maximum* (a palatable grass species) composition was lower in ancient human settlements than off-sites (4.1 vs 12.8%) which can be linked to loss of tree canopy or light shade (van Oudtshoorn, 1999; Heath and Heath, 2009). However, the ancient settlements had higher proportions of the high-quality *C. dactylon* lawns (4.6 vs 0.8%) and the palatable *C. virgata* (17.5 vs 4.9%) than surrounding landscape which is typical of highly nutritious grazing on nutrient hotspots. This shows that ancient human settlements provide good grazing, especially for short-grass grazers. Boles and Lane (2016) reported *C. dactylon* as dominant in glades. *Cynodon dactylon* is adapted to grazing through its prostrate growth habit (McNaughton, 1984), with grazing stimulating new shoot growth (Coetsee et al., 2011). Glades have been reported to support *Cynodon* and other grass species that are rare or absent in surrounding landscape (Veblen, 2012). Thus, the higher composition of *C. dactylon* and *C. virgata* in ancient human settlements than surrounding vegetation could be evidence of the ability of glades to support grass species that are rare in the background landscape.

The low tree density and species diversity as well as small tree size in ancient human settlements was typical of boma-associated savanna glades which have reduced woody plant species growth in favour of nutritive grasses (Muchiru et al., 2009; Veblen 2013). The low tree density in ancient human settlements could also be attributed to the fact that tree seedlings growth was constrained by competition from grasses resulting in low tree recruitment (van der Waal et al., 2011). In addition, the low tree recruitment rates in ancient human settlements could be due to the fact that they attracted herbivores, resulting in increased woody seedling browsing and trampling (Augustine and McNaughton, 2004). van der Waal et al. (2011) reported a lower woody plant density in abandoned kraals than surrounding landscape. In occupied settlements, human and animal activity reduces vegetation in the immediate surroundings (Huffman et al., 2013). It then takes several years for vegetation to recover since most trees cannot grow in compacted village surroundings. *Acacia* (*Vachelia*) species*, D. cinerea* and *G. flavescens* were the woody species found in the ancient settlements. In South Africa former herder settlements were dominated by *A. tortilis* (Blackmore et al., 1990).

The higher P and Ca in ancient settlements than surrounding landscape could be attributed to the accumulation of dung deposits in cattle kraals. Large amounts of P were found to accumulate in cattle resting places over time (Jewell et al., 2007). Augustine (2003) found abandoned kraals to remain enriched with P for several decades after use. van der Waal et al. (2011) also found soil P and

Ca to be higher in abandoned kraal sites than surrounding landscape. However, the accumulation of P in glades depletes the surrounding landscape (Jewell et al., 2007). The similarities in soil pH, N, K, Mg and Na between ancient settlements and surrounding landscape was, presumably, because most of the organic matter from the dung had degraded to levels of the local soil. Dung, which is mostly composed of organic matter, degrades after abandonment in open-air sites due to oxidation (Shahack-Gross et al., 2003). For example, N is readily lost from excreta through volatilization, particularly from urine, and the soil through nitrate leaching (Augustine, 2003). In addition, these settlements may have been used for a limited period. Soil enrichment in abandoned glades was found to be enhanced through reuse of these sites (Porensky et al., 2013; Scholes and Walker, 2003). Studies in Kenya and Tanzania reported ancient anthropogenic soil nutrient enrichment compared to off-site (Storozum et al., 2021).

Impala mostly foraged on ancient human settlements, presumably, because of the highly palatable *C. dactylon* and *C. virgata,* which are nutritious and digestible and of a favoured height for impala (Arsenault and Owen-Smith 2008). In addition, impala prefer open sites to improve predator detection (Ford et al., 2014; Huruba et al., 2017). Ancient human settlements had very low tree densities compared to off-sites, thus the high impala camera sightings may have been in part influenced by the open structure of the ancient settlements. van der Waal et al. (2011) also found impala to prefer foraging in abandoned kraal site over the surrounding landscape. Consistent with van der Waal et al. (2011) findings warthog showed no preferential foraging between ancient human settlements and surrounding vegetation. The greater kudu preferred foraging on the more open ancient human settlements, presumably, on *A. nilotica* and *D. cinerea*. van der Waal et al. (2011) also reported greater kudu as preferring to forage in abandoned kraal sites over the surrounding landscape. The presence of ancient human settlements created functional heterogeneity which enabled herbivores to forage adaptively between the open ancient settlements and dense surrounding vegetation to meet their intake requirements (Owen-Smith, 2004; Fynn et al., 2016).

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5. Conclusion

Our study demonstrated the importance of ancient human settlements in providing open spaces and nutritive grass such as *C. dactylon* and *C. virgata* for herbivores to forage. Importantly, we demonstrated that ancient settlements are important in soil nutrient enrichment, although over time some nutrients (particularly N) decline to similar levels to surrounding landscape.

Ethical standards

The research involved in this manuscript followed the journal's Code of Conduct for authors contributing articles.

CRediT authorship contribution statement

Allan Sebata: Conceptualization, Methodology, Data curation, Writing – original draft, Visualization, Investigation, Validation.

Richard W.S. Fynn: Conceptualization, Methodology, Data curation, Visualization

Tshephang Keemekae: Methodology, Data curation, Visualization

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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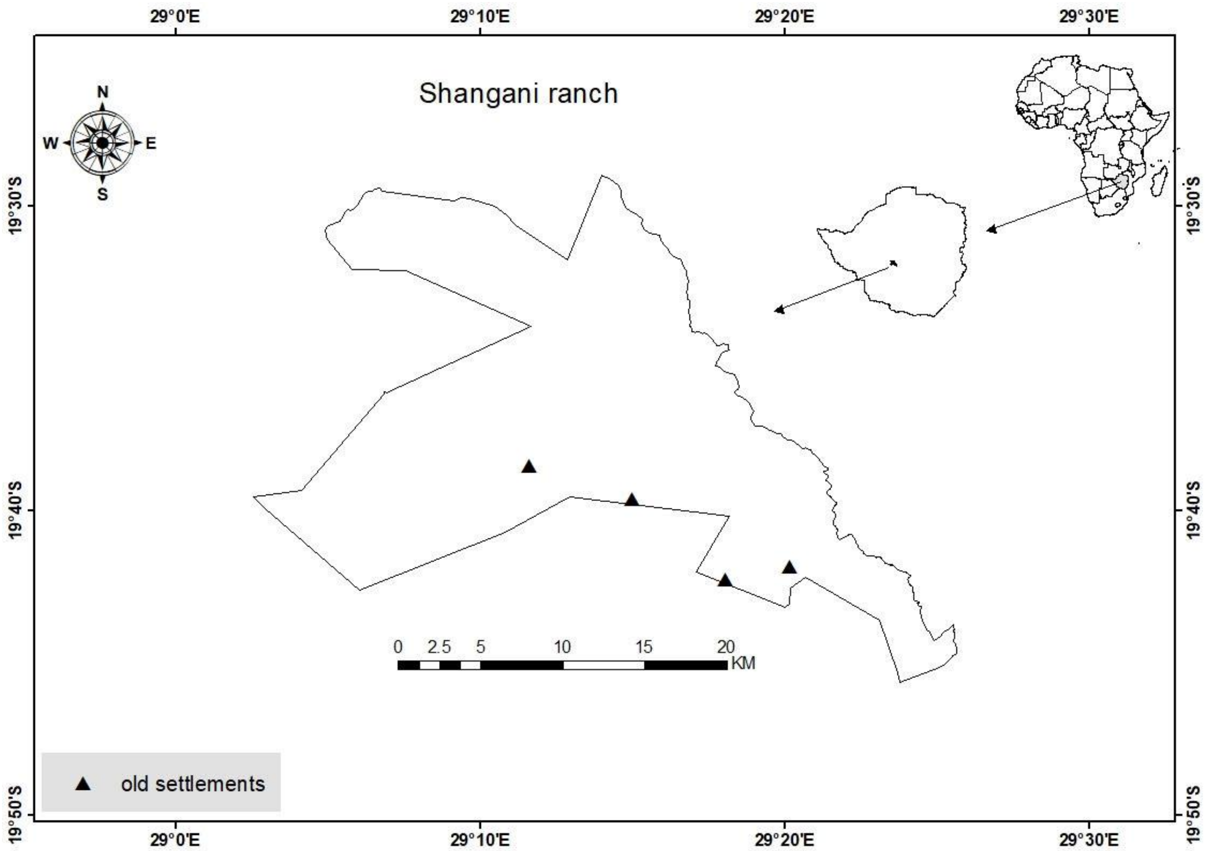

Figure 1 Location of ancient (old) human settlements at Shangani Holistic ranch.

Figure 2a An ancient (old) human settlement covering an area of 0.15 ha at Shangani Holistic, central Zimbabwe

Figure 2b An off-site adjacent to ancient (old) human settlements at Shangani Holistic, central Zimbabwe

Table 1 Mean (±SE) grass basal cover, height, biomass and species diversity in ancient human settlements and off-sites (*n* = 20) at Shangani Holistic.

Grass parameter	Ancient settlements	Off-sites	*F*- values	*p*-value
Basal cover (%)	31.95 (± 2.22)	26.10 (± 3.56)	1.95	0.17
Grass height (cm)	25.90 (± 3.17)	22.65 (± 2.42)	0.66	0.42
Biomass (kgm^{-1})	0.29 (± 0.03)	0.25 (± 0.03)	1.08	0.31
Species diversity	0.80 (± 0.08)	0.66 (± 0.06)	9.12	< 0.01

Table 2 Grass species composition (%) at ancient human settlements and off-sites at Shangani Holistic ranch.

Species	Life form [perennial (P) or annual (A)]	Ancient settlements	Off-sites
Highly palatable species			
Cynodon dactylon (L.) Pers.	P	4.6	0.8
Digitaria eriantha Steud.	P	0.5	-
Panicum maximum Jacq.	P	4.1	12.8
Themeda triandra Forssk.	P	-	1.1
Moderately palatable species			
Chloris virgata (Kunth) Stapf	A /P	17.5	4.9
Dactyloctenium aegyptium (L.) Willd.	P	-	1.1
Eragrostis superba Peyr.	A / P	1.9	2.2
Eragrostis barrelieri Daveau	A / P	-	0.8
Heteropogon contortus (L.) P. Beauv. ex Roem. & Schult.	P	14.2	10.7
Hyparrhenia tamba (Hochst. ex Steud.) Andersson ex Stapf	P	1.9	3.0

Setaria pumila (Poir.) Roem.& Schult	A	5.2	2.5
Setaria verticillata (L.) P. Beauv.	A	1.1	1.1
Less palatable species			
Aristida congesta Roem. & Schult.	P	0.5	-
Aristida junciformis Trin. & Rupr.	P	2.7	-
Eragrostis cilianensis (All.) Vign. ex Janchen	A	1.1	-
Eragrostis cylindriflora Hochst.	A / P	1.4	-
Pogonarthria squarrosa (Roem. & Schult.) Pilg.	P	1.4	-
Sporobolus pyramidalis P. Beauv.	P	1.4	-

Table 3 Mean (±SE) tree height, canopy volume, density and species diversity in ancient human settlements and off-sites (n = 20) at Shangani Holisitic.

Tree parameter	Ancient settlements	Off-sites	Independent *t*-test	*p*-value
Tree height (m)	1.27 (± 0.13)	2.50 (± 0.15)	- 4.00	< 0.001
Canopy volume (m^3)	0.67 (± 0.23)	4.51 (± 0.77)	- 2.47	0.02
Density (number of trees / ha)	10.98 (± 2.12)	58.95 (± 9.18)	-27.73	< 0.001
Species diversity	0.35 (± 0.09)	1.24 (± 0.20)	- 4.07	0.01

Table 4 Woody plant species composition (%) at ancient human settlements and off-sites at Shangani Holistic.

Species	Family	Ancient settlement	Off-site
Acacia (Vachellia) erioloba (E.Mey.) P.Hurter.	Fabaceae	0.94	2.83
Acacia (Vachellia) karroo Hayne.	Fabaceae	-	4.72
Acacia (Vachellia) nilotica (L.) Willd. ex Delile	Fabaceae	9.43	9.43
Acacia (Vachellia) tortilis (Forssk.) Galasso & Banfi.	Fabaceae	0.94	4.72
Carissa edulis Vahl	Apocynaceae	-	3.77
Combretum hereroense Schinz	Combretaceae	-	6.60
Combretum molle R. Br. ex G. Don	Combretaceae	-	2.83
Dichrostachys cinerea (L.) Wight & Arn.)	Fabaceae	7.55	22.64
Euclea divinorum Hiern	Ebenaceae	-	5.66
Grewia flavescens Juss.	Tiliaceae	0.94	-
Peltophorum africanum Sond.	Fabaceae	-	5.66
Terminalia sericea Burch.	Combretaceae	-	1.89
Ziziphus mucronata Willd.	Rhamnaceae	-	9.43

Table 5 Mean (±SE) soil pH and nutrient concentrations in ancient human settlements and off-sites at Shangani Holistic.

Soil parameter	Ancient settlements	Off-sites	GLMM	
			F- values	*p*-value
pH	5.91 (± 0.07)	5.74 (± 0.07)	3.62	0.07
Nitrogen (ppm)	25.00 (± 2.35)	23.50 (± 0.87)	2.50	0.13
Available P (ppm)	18.50 (± 1.71)	14.75 (± 1.80)	8.04	0.01*
Potassium (me per 100 g)	1.09 (± 0.06)	0.96 (± 0.09)	2.16	0.16
Calcium (me per 100 g)	7.74 (± 0.85)	5.62 (± 0.25)	19.61	< 0.001***
Magnesium (me per 100 g)	4.15 (± 0.27)	3.76 (± 0.21)	2.37	0.14
Sodium (me per 100 g)	0.76 (± 0.05)	0.66 (± 0.05)	2.92	0.10

Table 6 Mean (±SE) impala, warthog and greater kudu camera sightings per day in ancient human settlements and off-sites at Shangani Holistic.

	Ancient settlements	Off-sites	Independent *t*-test	*p*-value
Impala	3.05 (± 0.37)	0.19 (± 0.03)	7.78	0.001
Warthog	0.25 (± 0.03)	0.36 (± 0.05)	- 1.99	0.09
Greater kudu	2.63 (± 0.17)	0.23 (± 0.03)	13.66	< 0.001