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Using functional groups to predict the spatial distribution of large herbivores on the Palaeo-Agulhas Plain, South Africa, during the Last Glacial Maximum

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ABSTRACT: Throughout much of the Quaternary, lower sea levels in the southern Cape of South Africa exposed a different landscape to what we see today, the Palaeo-Agulhas Plain (PAP). The PAP was dominated by large-bodied and gregarious grazing species contrasting with the small-bodied predominantly solitary species we find in the region today. The distribution of these herbivores would likely have been driven by similar drivers we see in contemporary herbivore ecology. Importantly, the occurrence of early humans and their associated technology would have also influenced the probability of herbivores occurring in an area. Here we create a predictive model for large herbivores using probability of occurrence of functional grouping in relation to environmental drivers and humans. We show how early humans influenced the distribution of large herbivores on the PAP alongside other environmental drivers. In the fynbos biome, probability of occurrence was highest for the medium-sized social mixed feeders' functional group in the thicket for small non-social browsers, large browsers, and non-ruminants and in grasslands for water-dependent grazers. In our models, human influence affected functional groups to varying degrees but had the strongest effect on medium-sized social mixed feeders. © 2022 The Authors. *Journal of Quaternary Science* published by John Wiley & Sons Ltd.

KEYWORDS: environmental drivers; landscape of fear; large herbivores; Pleistocene; probability of occurrence

Introduction

Lower sea levels throughout most of the Quaternary revealed a landscape different to the one we see in South Africa today, driven by the gentle slope of the continental shelf off the current coastline (Fisher *et al.*, 2010; Van Andel, 1989) that was last maximally exposed during the Last Glacial Maximum (LGM) (Cawthra *et al.*, 2020; Compton, 2011; Cowling *et al.*, 2020; Marean *et al.*, 2014). Termed the Palaeo-Agulhas Plain (PAP; Marean *et al.* 2014) this landscape was home to unique vegetation (Cowling *et al.*, 2020) and numerous large herbivores, some of which are now extinct (Brooke, 2021; Klein, 1984; Venter *et al.*, 2020). Although the land surface area fluctuated widely throughout the last 400 ka (Fisher *et al.*, 2010), and even transgressed the current sea level at times (i.e. marine isotope stage (MIS) 5e; Fisher *et al.* 2010), large mammals were always present on the PAP and in the surrounding landscape (Venter *et al.*, 2020). Archaeological (Klein, 1983; Marean *et al.*, 2014) and palaeontological records (Rector and Reed, 2010; Rector and Verrelli, 2010; Williams *et al.*, 2020) and fossil trackways (Helm *et al.*, 2018a, 2018b, 2020) depict species presence and assemblages (Venter *et al.*, 2020), but provide little information

on abundance. These records provide little indication of the species ecology and drivers on this extinct PAP landscape. Records point toward a dominance in grazing species (Copeland *et al.*, 2016; Helm *et al.*, 2018b, 2020; Klein, 1983; Venter *et al.*, 2020), and strontium isotopes show that species likely did not move off the PAP into the interior of South Africa (Copeland *et al.*, 2016). Fluctuations in sea level over the last 200 000 years coincide with the time when anatomically modern *Homo sapiens* (hereafter 'early humans') in the region developed and began a shift toward a diet consuming marine-sourced protein (Marean, 2014, 2016). Further evidence suggests that by ~70 ka early humans had begun using advanced projectile weapons while hunting large animals on the PAP (Bradfield *et al.*, 2020; Brown *et al.*, 2012).

Herbivore distribution is driven by a complex array of biotic and abiotic drivers within the landscape (Redfern *et al.*, 2003) affecting herbivores through bottom-up and top-down processes. Bottom-up drivers are those that are environmentally driven (e.g. vegetation quality and quantity and rainfall) whereas top-down drivers of herbivores are those driven by predation and competition (Grange and Duncan, 2006; Hopcraft *et al.*, 2010). Plant and herbivore biomass increases with increasing precipitation (Chase *et al.*, 2000; Fritz and Duncan, 1994; McNaughton *et al.*, 1989) up to a threshold of ~800 mm annual rainfall in Africa, after which herbivore biomass tends to decrease (Hempson *et al.*, 2015). The

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Table 1. Overview of the five functional groups modelled in this paper, adapted from Hempson *et al.* 2015

Functional group	No of species in functional group	Average body mass (kg)	Diet	Water dependence	Herd size
Small non-social browsers	35	17.9	Browser	Independent	Solitary/pairs
Medium-sized social mixed feeders	18	61.2	Mixed feeder	Moderately dependent	Gregarious
Large browsers	8	354	Browser	Moderately dependent	Gregarious/family groups
Water-dependent grazers	17	137.3	Grazer	Dependent	Gregarious
Non-ruminants	14	789.5	Grazer/mixed feeder	Dependent	Family groups

distribution of resources and predators (top-down and bottom-up drivers) are key factors influencing how herbivores distribute themselves in the landscape (Anderson *et al.*, 2010; Jarman, 1974) through a 'landscape of fear' (Laundré *et al.*, 2010). Herbivores need to balance their acquisition of resources against predation risk and energy expenditure (Fortin *et al.*, 2004; Venter *et al.*, 2019) and the landscape of fear gauges how species infer risk from environmental features and predation (Malone *et al.*, 2020). On the PAP, forage and associated vegetation type, distribution of water, vegetation cover and density (Smit, 2011), pressure from humans (Marean *et al.*, 2014) and animal physical and behavioural characteristics (Searle *et al.*, 2010) all would have played a role in influencing the distribution of herbivores.

Large herbivores (>2 kg; following Fritz and Loison, 2006 and Olff *et al.*, 2002) in South Africa differ widely in size (ranging from the 2.2 kg Cape hare (*Lepus capensis*) to the 3550 kg African elephant (*Loxodonta africana*)), feeding mechanisms, habitat requirements and in their adaptations to environmental conditions (Gagnon and Chew, 2000; Prins and Olff, 1998; Venter *et al.*, 2020). Body mass and feeding mechanisms influence habitat selection and predation risk. In general, smaller-bodied species have smaller gastrointestinal tracts and, as a result, a more selective diet of high quality plant material (Wilmschurst *et al.*, 2000). Smaller herbivores are also prone to increased predation and are preyed on by a larger number of predators (nested effect of predation) under natural circumstances (Cohen *et al.*, 1993; Hopcraft *et al.*, 2012) but may conceal themselves in dense vegetation (Hopcraft *et al.*, 2010). Small herbivores were often not the preferred prey of early humans because they provide less caloric reward relative to the catching effort when compared with larger-bodied species (Lupo and Schmitt, 2016). However, easy capture (i.e. using snares and traps) and complete transport (Monahan, 1998) mean that these species make up a large proportion of the archaeological record, especially more recently (Wadley, 2010; Yellen, 1991). Larger species were preferred prey by early humans (Lupo and Schmitt, 2016) and occasionally mega-herbivores (Ben-Dor *et al.*, 2021). Large herbivores can be less selective and consume larger quantities of lower quality plant material because of their larger gastrointestinal tracts and the ability to extract more nutrients from lower quality forage (Hopcraft *et al.*, 2010; Wilmschurst *et al.*, 2000). Large herbivores are also less likely to be preyed on, and only by the largest predators, and mega-herbivores (>1000 kg) are almost exempt from predation altogether, except for young individuals (Anderson *et al.*, 2016; Hopcraft *et al.*, 2012; Owen-Smith, 1987; Sibly and Brown, 2007). Based on differences in behavioural and physical characteristics, one can group similar species into functional groups. Hempson *et al.* (2015) is one of the best examples of this where they have grouped large African herbivores into five distinct functional groups using trait-based similarities, and a detailed description of factors influencing

functional groups and species can be found therein. (Hempson *et al.*, 2015) and in Table 1.

Here we aim to integrate our understanding of large herbivores, and the biotic and abiotic features of the PAP, to predict what the main drivers of large herbivore occurrence on the PAP were and to create a large mammal 'resourcescape' (a reconstruction of large mammal communities and behaviours that could be used by early humans as a food source) on the PAP. Finally, we model the large mammals of the PAP under two contrasting scenarios, one with high levels of human habitation and the other with low levels of human habitation to determine whether humans did have a possible strong driving effect of herbivore distribution on the PAP.

Methodology

Landscape features

Large herbivore distribution and occurrence are affected by various landscape features. Water-dependent herbivores are constrained by the distances they can travel from water sources (Western, 1980) and are thus more likely to occur nearer to water (see *Distance to water* for details). However, vegetation is often more dense in areas close to water, increasing the direct risk or perceived risk of predation (Hopcraft *et al.*, 2010; Valeix *et al.*, 2009). On the PAP, large herbivores would also have faced risks associated with human distribution on the landscape (Marean *et al.*, 2014) and how humans contributed to the landscape of fear. These proxies along with vegetation density were used to better understand the perceived landscape of fear.

Distance to water

Distance to the nearest permanent water source (coastal rivers and lagoons, Fig. 1, Table 2) (Cawthra *et al.*, 2020) was calculated in ArcMap version 10.5 (ESRI, 2017) using the *Near* tool. We determined the probability of an animal occurring at a certain distance from water from geospatially referenced game census data for Kruger National Park between 2008 and 2017 (South African National Parks, unpublished data). The probability that a herbivore would occur at a certain distance from a water point was calculated using an exponential regression equation ($r^2 = 99.6$, Fig. 2) in *CurveExpert* (Hyams, 2020). Regardless of species or functional group, species tend to aggregate nearer to water when it is available, and for this reason we are not differentiating between functional groups in this paper. Spatially referenced data were binned into 1 km intervals. Additionally, we constrained (i.e. probability of occurrence = 0) the functional groups (already defined as water-dependent, moderately dependent or independent; see Hempson *et al.*, 2015) to foraging within

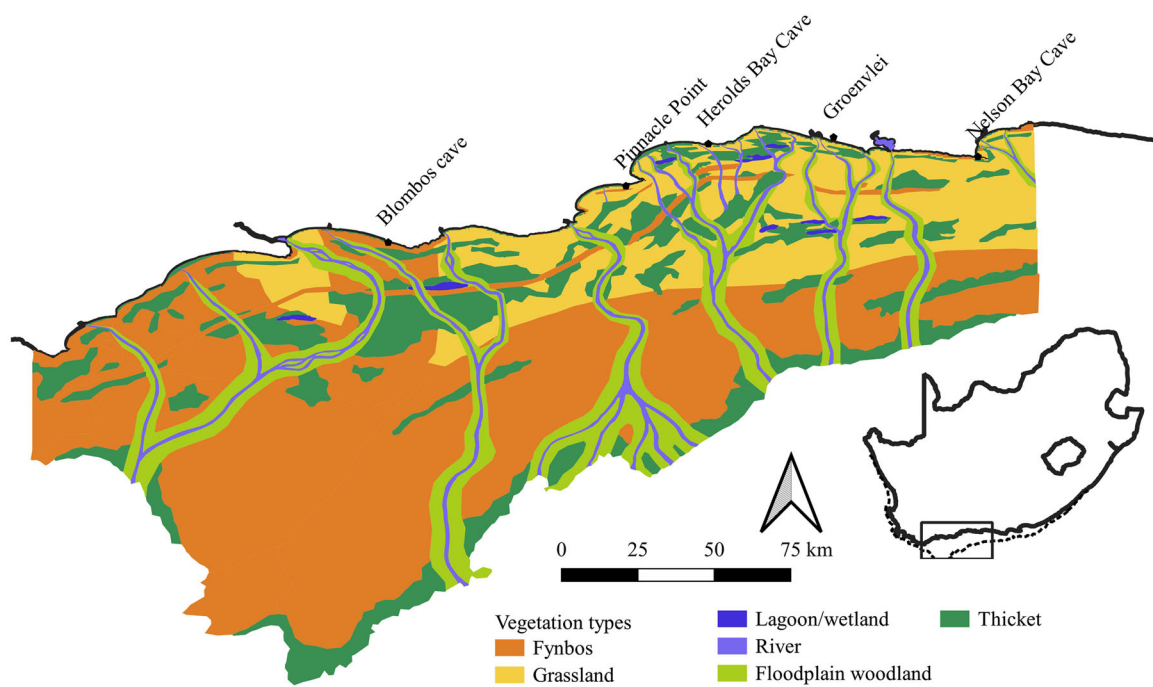


Figure 1. Spatial representation of biomes on the PAP (adapted from Cowling *et al.* 2020) and the availability of permanent water determined from underlying geology (adapted from Cawthra *et al.* 2020) and important archaeological sites (Marean *et al.*, 2014). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

Table 2. Environmental and landscape characteristics for the vegetation types (Cowling *et al.*, 2020) of the Palaeo-Agulhas Plain. Average herbivore biomass is taken from (Brooke *et al.*, 2021).

Biome	Vegetation type	Vegetation density	Average distance to water (km)	Average herbivore biomass (kg/km ²)
Thicket	Dune fynbos–thicket mosaic	Medium	10.6	187
Savanna	Floodplain woodland	Medium	1	207
Fynbos	Limestone fynbos	Medium	17.2	54
Fynbos	Renosterveld	Low	9.3	34
Fynbos	Sand fynbos	Low	2.5	153
Fynbos	Sandstone fynbos	Medium	38	92
Fynbos	Shale fynbos	Low	23	82
Grassland	Shale grassland	Very low	7.4	233
Thicket	Sub-tropical thicket	High	10	150

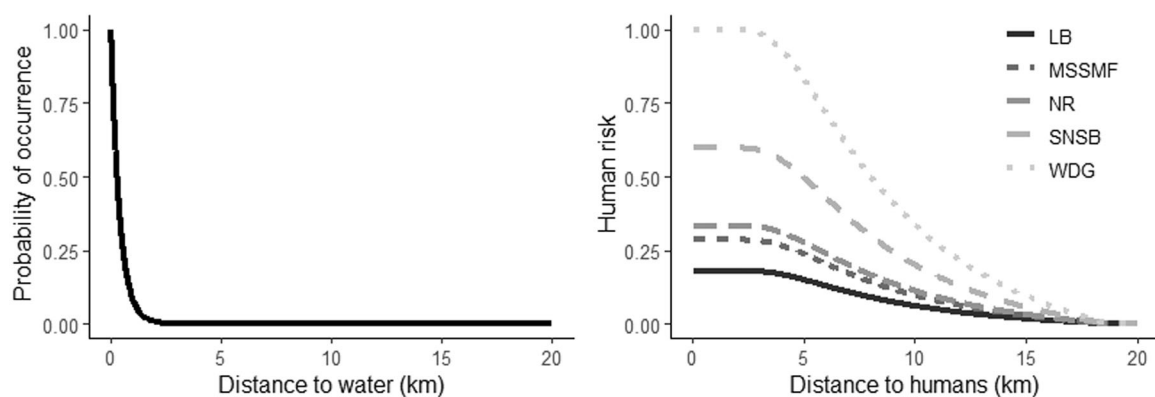


Figure 2. Left: Probability of occurrence of large herbivores in relation to water (unpublished data from Kruger National Park, South Africa). Right: Probability of risk for large herbivores in relation to the human settlements for five large herbivore functional groups. Functional groups are LB = large browsers, MSSMF = medium-sized social mixed feeders, NR = non-ruminants, SNSB = small non-social browsers and WDG = water-dependent grazers (Hempson *et al.*, 2015). Risk became zero after 18 km as average human foraging distances did not exceed this (Pontzer *et al.*, 2015).

predetermined distances from water as water-dependent species were unlikely to move far from a water source.

Water dependence for each functional group was taken from Hempson *et al.* (2015) and the likely distances that

water-dependent, moderately dependent and independent species would move away from water (i.e. a foraging radius surrounding a water source) were taken from Western (1980). Water-dependent functional groups (Table 1) were unlikely to

move further than 10 km from a water source (Boitani *et al.*, 2008), moderately water-dependent functional groups were unlikely to move further than 15 km from water (Western, 1975) and water-independent functional groups would not be constrained by the occurrence of water in the landscape. As a result, we limited the probability of occurrence in relation to the distance each functional group was likely to travel.

Vegetation density

Using the reconstructed PAP vegetation types of Cowling *et al.* (2020) we scaled vegetation density between one and five (one being the most open and five the most dense). Vegetation density was determined by reviewing the written vegetation descriptions (i.e. whether or not vegetation was open or densely packed) and identifying whether important species formed dense/tall vegetative stands in Mucina and Rutherford (2006). Scaling was carried out by comparing only the vegetation types found on the PAP and not vegetation found elsewhere in South Africa. Rivers and lagoons, although not a distinct vegetation type, were also considered as these areas are generally densely vegetated and have variable topographic features (i.e. steep river banks) (Hopcraft *et al.*, 2012).

Landscape of fear

The landscape of fear encompassed several environmental variables. The density of each vegetation type was predicted and a 100 m buffer was created around water sources. Topography and dense vegetation surrounding water sources influence predation, and so distance to water was also included (Hopcraft *et al.*, 2010). Water-dependent species are also forced to deal with the increased risk of approaching water to drink daily (Valeix *et al.*, 2009). Finally, the risk of encountering early humans was also included as large mammals were an important food source for them. To determine human risk we looked at the exposure to humans in terms of distance from a camp or shelter and a maximum daily human travelling distance of 18 km (Pontzer *et al.*, 2015). Although Marlowe (2005) suggested a maximum foraging radius of 14 km, we opted for the smaller radius as the modelled camps were fixed in the landscape and we did not consider movement between camps. The proportion of risk that humans had on each functional group was calculated using the minimum number of individuals observed in each functional group for 12 archaeological/palaeontological sites (Venter *et al.*, 2020). The proportion of each functional group that made up the entire assemblage was then considered as the likelihood that humans would choose to hunt species from a specific functional group.

We modelled two contrasting scenarios of human risk (Fig. 3) for each of the herbivore functional groups. These were low human density (low human risk model), or high human density (high human risk model). We used estimates from Wobst (1976) whereby low human density was 0.005 humans per km² and high human density was 0.05 humans per km². Additionally, we used the average number of humans per band (camp) to be 25 as is commonly used as the mean band size for hunter-gatherers (*cf.* Kelly (2013) and see Marlowe (2005) for a broader discussion of forager group sizes) and assumed that each camp was surrounded by a territory (Wobst, 1974). Territory boundaries were made hexagonal in shape as this provides a shape that can be bounded on all sides by other territories with the smallest border and no unoccupied space, and in most cases human territories find themselves surrounded by an average of six other camps (Wobst, 1974).

Within each of these territories we randomly placed the camp under the presumption that camps needed to be within 14 km of water (i.e. within the daily human foraging radius whereby humans could travel to a water source and return to camp within a single day, Marlowe 2005). Hexagons that fell outside of this 14 km radius of a water source were excluded.

Vegetation risk was scaled between one and five (one being the lowest and five being the highest risk) using the literature (Hempson *et al.*, 2015; Hopcraft *et al.*, 2010; Laundré *et al.*, 2010). Risk was thus not a direct effect of predation on functional group, but an overall estimation of risk whereby denser vegetation was considered riskier as predators can conceal themselves and smaller species are at greater risk (regardless of vegetation). This was determined based on functional group characteristics (Hempson *et al.*, 2015). Small species are more likely to be preyed on by a larger number of predators due to the nested effect of predation (Cohen *et al.*, 1993; Hopcraft *et al.*, 2010) and are more susceptible to predation in any given vegetation type even though smaller species (i.e. small non-social browsers) are often associated with thick vegetation that they use to conceal themselves (Hempson *et al.*, 2015). Dense vegetation types were still considered more risky as predators would also be able to conceal themselves (Davidson *et al.*, 2012; Hopcraft *et al.*, 2010) regardless of herbivore behavioural selection.

Large herbivore biomass

Large herbivore biomass was calculated using 1 km² grid cells across the PAP for each of the five functional groups based on varying degrees of rainfall and different vegetation types using proxies from extant protected areas across South Africa (Brooke *et al.*, 2021). Brooke *et al.* (2021) calculated the large herbivore biomass for 39 protected areas across the four main biomes found on the PAP. Protected areas were selected across a varying rainfall gradient as rainfall is the best predictor of herbivore biomass in Africa. Using this rainfall gradient and varying herbivore biomass Brooke *et al.* (2021) then predicted the likely large herbivore biomass across the PAP. Their results showed that herbivore biomass was highest in the northern PAP for the water-dependent grazer functional group and lowest in the north for medium-sized social mixed feeders, large browsers and non-ruminants where these functional groups were unlikely to occur. We did not consider body mass of herbivores as this was an explanatory variable in predicting the functional group classification (Hempson *et al.*, 2015).

Statistical analysis

To determine the probability of occurrence of herbivore functional groups we ran general linear models (GLMs) for each of the five functional groups. Models included herbivore biomass (Brooke *et al.*, 2021) as the dependent variable and probability of occurrence in relation to water, vegetation type, vegetation density, and proportion human risk (either low or high risk; both were not included in the same model). We also included two-way interactions between all possible combinations of these variables. Categorical variables (vegetation type and vegetation risk) were included as factors in the GLMs. Continuous variables (probability of occurrence in relation to water and herbivore biomass) were scaled between 1 and 0. For the GLMs, we employed a model averaging approach using the best fitting models (those with a akaike information criterion [AICc] < 2) using the dredge function in the *MuMIn* package (Bartoń, 2020). This process allows for the best-fitted models across all combinations of the explanatory variables and their interactions to be averaged. All statistical analyses

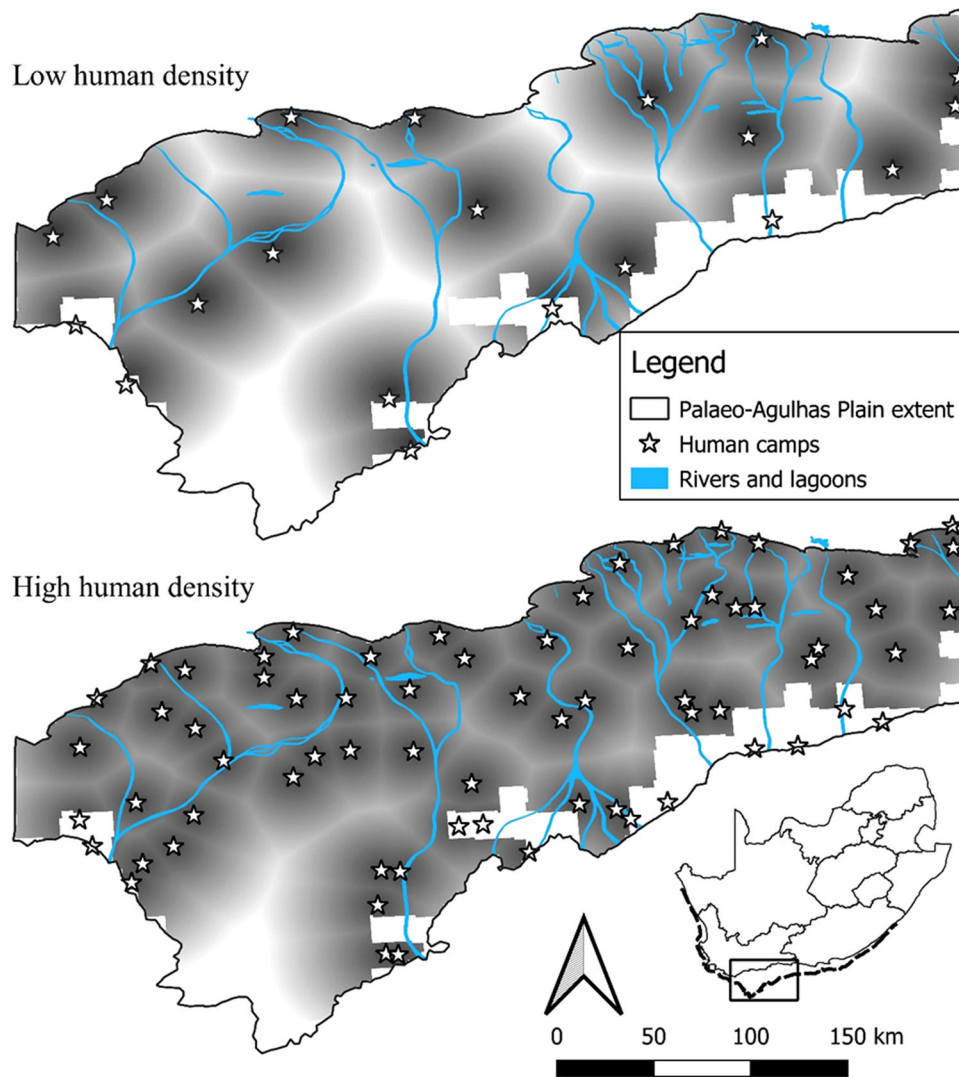


Figure 3. Palaeo-Agulhas Plain showing low densities of human occupation (calculated at a density of 0.005 persons per km² with camp size of 25 people) and high densities of human occupation (calculated at a density of 0.05 persons per km² with camp size of 25 people). Areas shaded darker are closer to human camps. Camps were restricted to within 14 km of a water source as this is the daily human foraging radius (Marlowe, 2005). Blank areas represent areas on the PAP that are not covered by the climate models (Engelbrecht *et al.*, 2019). Additionally, human settlements were still included in these areas as the distance to human settlement still affects the modelled area. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jqs.3430)]

were carried out in the statistical software R (R Development Core Team, 2020).

Results

In the high human density model with humans at a population density of 0.05 persons per km² and bands of 25 people each, we created 70 camps. In the low human density models where humans were at a population density of 0.005 persons per km² and band size was 25 people, we created 20 camps on the PAP (Fig. 3). These estimates were based on hexagons either partly or completely overlapping the PAP and restricted to within 14 km of a water source. In the high-density human foraging model, there was also considerably more overlap between foraging ranges from camps. Of the total human-induced mortalities accounted for in the archaeological record we calculated the risk to large herbivores as 25% for small non-social browsers, 12% for medium-sized social mixed diets, 8% for large browsers, 42% were water-dependent grazers and 14% were non-ruminants (see Fig. 2 for weighted human risk). For the GLMs, model averaging resulted in more than one model being averaged (i.e. all models with an AICc

<2) for all functional groups except the high human density model for small non-social browsers and the low human density model for non-ruminants (Table 3). In these models the strongest model was selected according to the lowest AIC value (-197040.7 and -63545.06, respectively).

For the small non-social browser functional group, the probability of occurrence decreased with both human risk and increased water availability at high human densities on the PAP (Figs 4 and 5). At high human densities the effect of water became stronger, and their probability of occurrence decreased with increased human risk, especially in thicket (Supplementary Fig. 1B). The interactions between biome and probability of occurrence in relation to water contributed significantly at high human densities (i.e. in all the averaged models) in thicket only, but little at low human densities (i.e. the interaction was only in one of the two models). The interaction between human risk and the probability of occurrence in relation to water contributed to only certain models in the model averaging for the low human density models and was not significant in the high human density model. No interactions with vegetation density were included in the averaged models and all other variables contributed to all models (Table 3, Supplementary Table 2). For small

Table 3. Results from the general linear model for the small non-social browser high human density model and non-ruminant low human density model functional group on the Palaeo-Agulhas Plain, South Africa.

	Small non-social browsers (high human density)			Non-ruminants (low human density)		
	Estimate	Standard error	P	Estimate	Standard error	P
(Intercept)	-0.038	0.010	<0.01	0.027	0.002	<0.01
Probability of occurrence (water)	-0.008	0.003	0.027	0.204	0.036	<0.01
Biome						
– Grassland	0.048	0.010	<0.01	0.393	0.003	<0.01
– Savanna	-0.009	0.000	<0.01	0.443	0.002	<0.01
– Thicket	0.054	0.000	<0.01	0.515	0.002	<0.01
Vegetation density risk						
– Low	0.048	0.010	<0.01	0.019	0.002	<0.01
– Medium	0.051	0.010	<0.01	-0.318	0.065	<0.01
– High	0.050	0.010	<0.01			
Human risk	0.013	0.036	0.710	0.061	0.027	0.022
Probability of occurrence (water) × biome						
– Grassland	0.005	0.004	0.170	-0.172	0.039	<0.01
– Savanna	0.007	0.003	0.057	-0.200	0.033	<0.01
– Thicket	-0.013	0.004	<0.01	-0.232	0.036	<0.01
Probability of occurrence (water) × vegetation density risk (medium)						
– Low				0.009	0.049	0.853
– Medium				-87430	31890	0.006
Probability of occurrence (water) × human risk	0.005	0.002	0.039	-0.077	0.034	0.024
Biome × human risk						
– Grassland	-0.013	0.036	0.719	-0.049	0.030	0.109
– Savanna	0.002	0.001	0.227	0.127	0.024	<0.01
– Thicket	-0.027	0.001	<0.01	0.243	0.020	<0.01
Vegetation density risk × human						
– Low	-0.012	0.036	0.736	-0.091	0.029	0.002
– Medium	-0.013	0.036	0.718	1.114	0.661	0.092
– High	-0.017	0.036	0.638			

non-social browsers the predicted probability of occurrence was highest in the thicket biome. For this functional group the thicket biome had the highest associated vegetation density risk, but the dense vegetation would also have provided habitat and cover for small non-social browsers.

The risk from humans contributed strongly to all models for medium-sized social mixed feeders and was included in all the models (Figs 4 and 5). Importantly, this effect was most observable in the fynbos biome (Figs 4–6) where the variation in probability of occurrence was highest (Fig. 6). Probability of occurrence was predicted to increase closer to water in savanna and thicket, but not fynbos and grassland in both the high and low human density models (Supplementary Fig. 1C and D). In the averaged models only the interaction between vegetation density and probability of occurrence in relation to water was not included and only in the low human density models. In the high human density model the interaction between human risk and probability of occurrence in relation to water only contributed to certain models, and not significantly overall, and this interaction was not included in the low human density models. The interaction between vegetation density and probability of occurrence in relation to water was only included in the low human density model and was not significant (Table 4, Supplementary Table 2). For the four biomes, probability of occurrence was highest in the fynbos and grassland biomes, irrespective of human density and these were also the biomes where vegetation density risk was lowest.

The large browser functional group was the only group moderately dependent on water (i.e. their movement was restricted to within 15 km of the nearest water source). As a result, their probability of occurrence in relation to water increased in both the low and high human models in savanna, grassland and fynbos, but decreased in thicket. For both the

low and high human density models there was little change in probability of occurrence with human risk (Figs 4 and 5, Supplementary Fig. 1E and F), with the greatest observable difference occurring in the low human density model (Fig. 6). All variables and combinations thereof were included in the high and low human density models for large browsers. However, the interaction between vegetation density risk and the probability of occurrence in relation to water and human risk in relation to the probability of occurrence in relation to water did not contribute significantly (i.e. only included in certain models; Table 4). At high human densities the interaction between vegetation density risk and human risk was not included in the models (Table 4, Supplementary Table 2). The highest probability of occurrence occurred in the savanna and thicket biomes; however, these were the biomes with the highest vegetation density risk.

The probability of occurrence for water-dependent grazers increased with water for both the high and low human density models, except in the grassland biome where herbivore biomass is also expected to decrease with increased rainfall (Brooke *et al.*, 2021). Their probability of occurrence changed little and even increased slightly in relation to human risk for both the high and low human density models in all biomes except grassland where their probability of occurrence decreased with increased risk from humans (Figs 4 and 5). Additionally, there was a lower observable probability of occurrence throughout the PAP in the high human density models (Fig. 6), likely as a result of being heavily preyed upon by humans. All the variables and interactions between variables were included in the average models. However, the interaction between vegetation density risk and probability of occurrence in relation to water was not significant in either the high or low human density models (model weight = 0.44 and 0.47, respectively, Table 4). The highest probability of

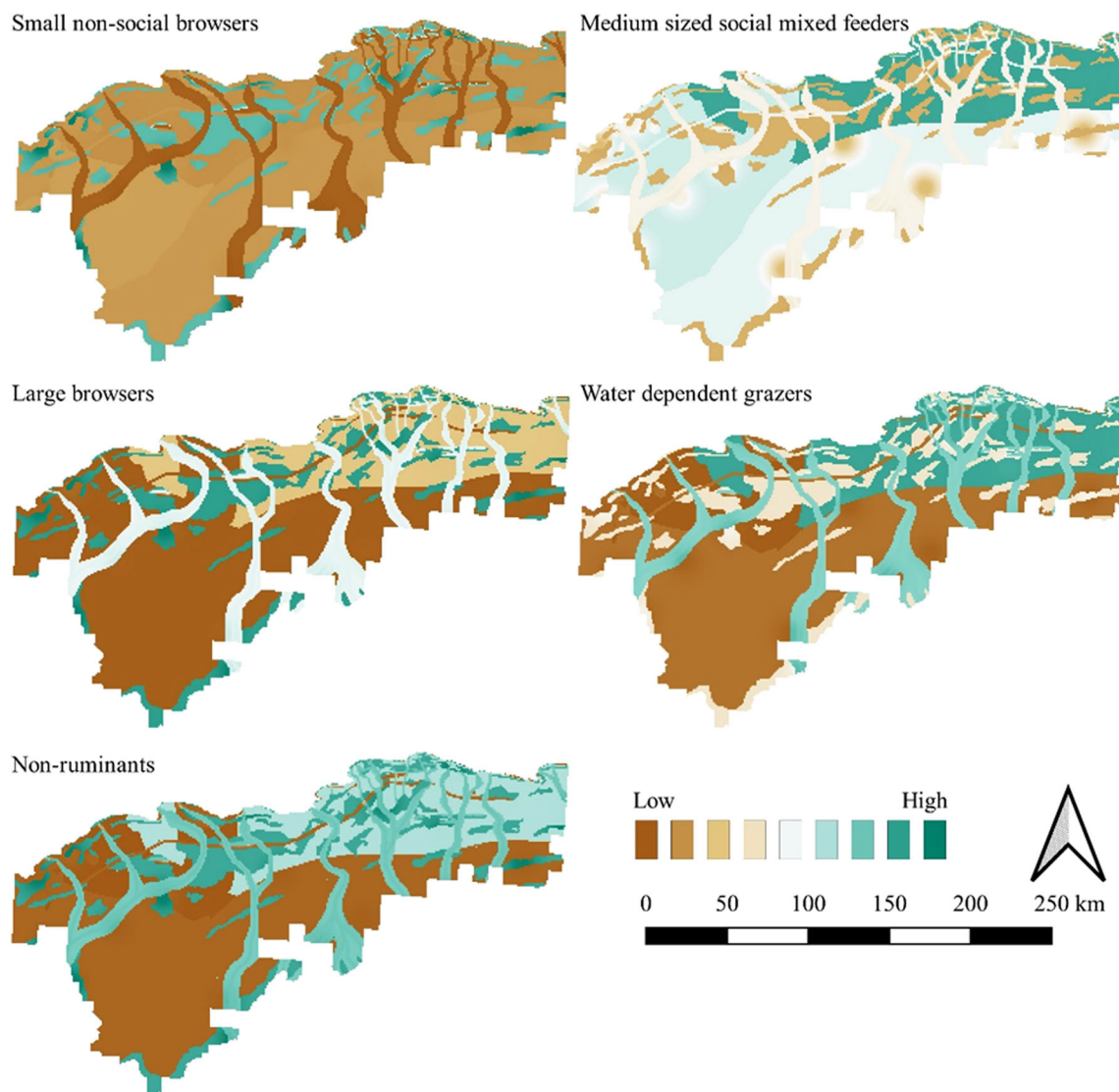


Figure 4. Predicted probability of occurrence for each of the functional groups in the low human density general linear models. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jqs.3430)]

occurrence of water-dependent grazers was in the grassland and savanna biome, and these biomes had the lowest and highest vegetation density risk, respectively. Importantly, grassland and savanna were also the two biomes with the highest grass content (Cowling *et al.*, 2020).

The probability of occurrence for non-ruminants changed little between the high and low human density models, but this difference was most observable around human camps in the low human density models (Fig. 6). This is likely the result of most non-ruminants being large-bodied and affected little by predation (Anderson *et al.*, 2016; Hopcraft *et al.*, 2012). The probability of occurrence in non-ruminants in relation to the probability of occurrence in relation to water increased across both the high and low human density models, most significantly in the fynbos biome (Supplementary Fig. 11 and J). In the high and low human density models the interaction between vegetation density risk and the probability of occurrence in relation to water and the interaction between human risk and probability of occurrence in relation to water did not contribute significantly to the models. The probability of occurrence for non-ruminants was highest in the thicket and savanna biomes regardless of the fact that these two biomes also had the highest vegetation density risk (Figs 4 and 5, Supplementary Fig. 11).

Discussion

Here we have shown how our current understanding of large herbivore ecology and the biotic and abiotic components of the PAP can be used to produce a modelled large mammal resourcescape predicting the probability of occurrence of large herbivores on the PAP, showing how large herbivores distribute themselves around water and the influence that human activity likely had on creating a landscape of fear. We found that in Kruger National Park large herbivores were likely to aggregate near to water, regardless of whether they were water-dependent or water-independent (SANParks, unpublished data, Fig. 2). Likewise, Veldhuis *et al.* (2019) produced similar results indicating an increased availability of prey (herbivore biomass) for lions (*Panthera leo*) closer to water points. In understanding extinct systems such as the PAP, the use of functional groups is beneficial as they allow for simplification of large herbivore communities, by grouping species according to predetermined traits. Here we discuss the significance of our models for each of the five functional groups described by Hempson *et al.* (2015). We also interpret the landscape as temporally static (e.g. variables are constant and not subject to change) as environmental characteristics are modelled (Cawthra *et al.*, 2020; Cowling *et al.*, 2020; Engelbrecht *et al.*, 2019) and predator localities and

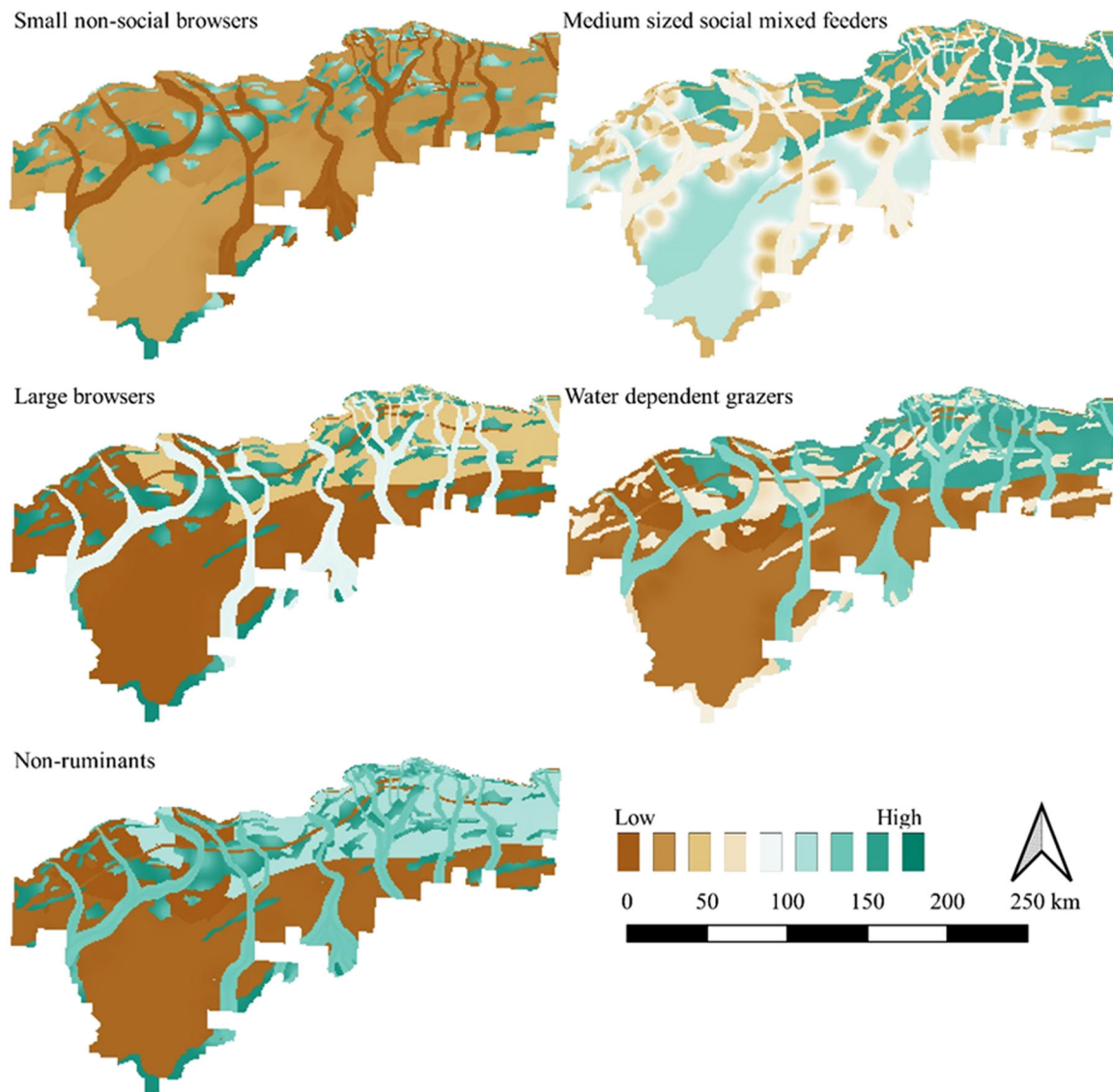


Figure 5. Predicted probability of occurrence for each of the functional groups in the high human density general linear models. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jqs.3430)]

distributions are currently unknown. However, even though we evaluate the PAP as temporally static we do attempt to answer how differing densities of humans affected the probability of occurrence of herbivores by including two contrasting models (high density of human settlements and a low density of human settlements) to compare the influence that humans imposed on the landscape of fear on the PAP.

Small non-social browsers

The probability of occurrence decreased for small non-social browsers, from probability of occurrence in relation to water and increased human risk. Increased human risk is supported by the fact that these species make up a large portion of the archaeological record and are water independent. From these factors small non-social browsers were found throughout the landscape, with their highest probability of occurrence in thicket. In dense vegetation such as thicket it would have likely been easy for humans to conceal themselves while hunting (i.e. tactical landscape use; Marean, 1997) and during sit and wait hunting (Ross and Winterhalder, 2015) but also because small non-social browsers would use these habitats to attempt to conceal themselves. Additionally, these species are limited by fewer environmental factors, but rather are regulated by the

availability of suitable territories and are more self-regulating than many larger species (Estes, 2012; Jarman, 1974). Being regulated by behavioural rather than environmental mechanisms and non-migratory, provides evidence of why small non-social browsers made up a large portion of early human prey as they occurred throughout the year and formed a more predictable prey base than larger gregarious species that would have moved following changes in forage abundance and quality (cf. Merkle *et al.* 2016). Although we predict a relatively low probability of occurrence, our predictions are similar to those of Brooke *et al.* (2021) who predicted a relatively low biomass of small non-social browsers. However, Kiffner and Lee (2019) indicated that small non-social species had the highest population densities because they are less limited by water and other resources within the landscape. Additionally, Hempson *et al.* (2015) showed they are the only functional group to be found at high densities in densely forested areas; however, these areas are not apparent on the PAP.

Medium-sized social mixed feeders

The risk associated with both vegetation density and humans features in all the averaged models but is likely driven more by

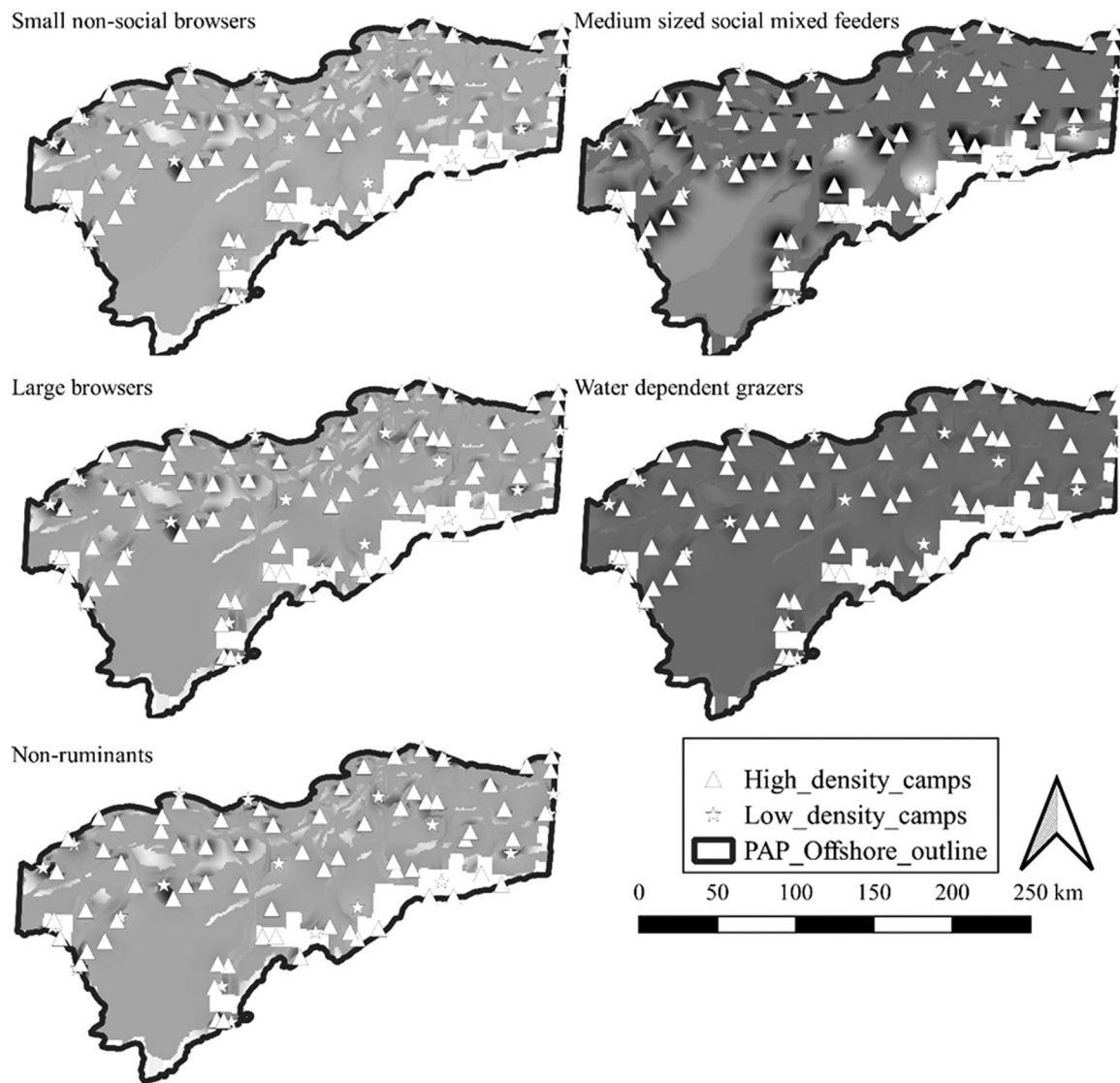


Figure 6. The difference between the high and low human density models for each of the functional groups. Here the high and low human density models were subtracted from one another highlighting where variations occur between the two models.

Table 4. Variables and their associated weights in the general linear model averages for the environmental variables on the Palaeo-Agulhas Plain, South Africa. Results are only for the four functional groups where model averaging occurred. A full list of model estimates and their relative weights can be found in Supplementary Table 2.

Herbivore functional type Human presence	Small non-social browsers		Medium-sized social mixed feeders		Large browsers		Water-dependent grazers		Non-ruminants	
	Low	High	Low	High	Low	High	Low	High	Low	High
Number of models	4	1	2	2	4	4	2	4	1	4
Model weight										
Biome	1		1	1	1	1	1	1		1
Vegetation density risk	1		1	1	1	1	1	1		1
Human risk	1		1	1	1	1	1	1		1
Probability of occurrence (water)	1		1	1	1	1	1	1		1
Biome × human risk	1		1	1	1	1	1	1		1
Biome × probability of occurrence (water)	1		1	1	1	0.82	1	1		1
Vegetation density risk × human risk	0.51		1	1	0.52		1	1		1
Vegetation density risk × probability of occurrence (water)			0.36		0.48	0.57	0.47	0.44		0.32
Human risk × probability of occurrence (water)	0.3			0.35	1	0.57	1	0.68		0.34

the interaction between the two variables. The predicted probability of occurrence figures (Supplementary Fig. 1) show a somewhat negligible effect of humans on the medium-sized social mixed feeder functional group which was expected as only 12% of the archaeological record is made up of these species (Venter *et al.*, 2020; Venter and Brooke, 2019). However, in areas surrounding camps, especially in the fynbos biome, large disparities between the high and low human density models were apparent (Fig. 6). There is also an apparent increase in probability of occurrence in relation to water in savanna and thicket. This is surprising as grasslands were generally closer to water and had a high biomass of large herbivores (Table 2). In the south-west PAP (predominantly fynbos), this functional group had a higher probability of occurrence than all other functional groups. This is important as many of the species (i.e. *Antidorcas marsupialis*) are adapted to arid environments (Lehmann, 2015) and would not have been limited by water on the PAP. Even though medium-sized social mixed feeders are not water dependent, their highest probability of occurrence was in the grassland biome. High probability of occurrence in grasslands may be a result of being able to switch between browse and graze (Hempson *et al.*, 2015; Lehmann, 2015) by moving between the grasslands and floodplain woodlands where nutrients would have been higher than in fynbos (Cowling *et al.*, 2020). The average distance to water on the PAP was ≤ 10 km in all biomes except fynbos (19.2 km), suggesting that dependence on available water would have little influence on all functional groups except those in fynbos.

Large browsers

For large browsers there was little change in the probability of risk associated with humans in either of the models, but this was expected as they were the least preferred species and made up the lowest proportion of the archaeological assemblage (Venter *et al.*, 2020; Venter and Brooke, 2019). The largest disparity between the high and low human density models occurred in the fynbos biome in areas where low human density camps were situated. The decrease in probability of occurrence in relation to water in thicket only for large browsers may have been attributable to thicket occurring on average within their daily foraging radius from water (i.e. thicket was on average ~ 10 km from water sources, Table 2). Large browsers were also the only moderately water-dependent functional group (Hempson *et al.*, 2015). Aggregation into groups (Hempson *et al.*, 2015) and behaviour characterised by sensitivity to disturbance by humans may have in part allowed these species to avoid predation (Riggio *et al.*, 2018). Large browsers are widespread throughout Africa (Hempson *et al.*, 2015), but at a low predicted biomass for the PAP (Brooke *et al.*, 2021), which in part accounted for the relatively low predicted probability of occurrence in all biomes except thicket. The effect of humans was also most apparent in the high human density models in the thicket biome; however, this relationship may be slightly exaggerated resulting from the highest probability of occurrence (Fig. 5). Alternatively, the high probability of occurrence may also have resulted from there being adequate food in the thicket biome and their relatively large body mass might have negated the effect of predation somewhat.

Water-dependent grazers

Water-dependent grazers were at the highest risk of predation by humans on the PAP as they made up the greatest proportion of remains at the archaeological sites (Venter *et al.*, 2020;

Venter and Brooke, 2019). However, this was not reflected in our models where there was little change between the high and low human density models (Fig. 6). Additionally, human risk alone was not significant in either model (Table 3, Supplementary Table 2). However, there was a significant interaction between human risk and probability of occurrence in relation to water, the interaction between biome and human risk and the interaction between human risk and high vegetation density. Together these interactions account for the importance of human risk in our models. The high proportion of water-dependent grazers in the archaeological record is likely the result of these sites occurring close to both water and grasslands where water-dependent grazers had the highest probability of occurrence (Cowling *et al.*, 2020; Marean *et al.*, 2014). Water-dependent grazers are characterised by species that are generally gregarious (Hempson *et al.*, 2015) and these behaviours may have increased the likelihood of being killed by humans. The dilution effect (i.e. many animals congregating decreases the risk to an individual) through aggregation would have decreased the likelihood of an individual being killed (Hamilton, 1971), but not necessarily decreased the rate of predation. Additionally, species in this functional group also showed high levels of sensitivity to humans (Riggio *et al.*, 2018) and may have been the result of targeted predation as indicated by the archaeological record (Venter *et al.*, 2020). Here we support this supposition as water-dependent grazers had a higher probability of occurrence throughout the PAP in the low human density models where pressure from humans would have been less, and the highest probability of occurrence in the grassland biome where vegetation would not have supported a landscape of fear (Burkepile *et al.*, 2013; Hopcraft *et al.*, 2012).

Non-ruminants

Increases in the probability of occurrence for non-ruminants in relation to water was expected as these species were water dependent (Hempson *et al.*, 2015), especially in the low human density model where humans had little effect. In the high human density models, decreased effects from humans were the likely cause for the lower probability in relation to water of non-ruminants in all biomes except fynbos. The probability of occurrence of non-ruminants in fynbos was low and likely results in the high average distance to water (Table 2). Our model averaging for the high human density models did not support the relationship between increased risk to non-ruminants near to water (model weight = 0.34); however, this was significant in the low human density models ($P < 0.05$, Table 4). The species in this functional group were generally large-bodied (Hempson *et al.*, 2015) and gregarious. This is supported by Jarman (1974) who produced a positive relationship between herbivore body size and group size. Large body mass may also have influenced sensitivity to humans (as shown in the high human density model) (Riggio *et al.*, 2018). Venter *et al.* (2020) assumes there may be an underestimation of the effect of humans on these large species as carcasses of large species are hard to transport and as a result are often consumed or butchered at the kill site to enable transportation.

Distance to water

The three functional groups that included large amounts of browse in their diets (small non-social browsers, medium-sized social mixed diets and large browsers) were the functional groups that were moderately or fully water independent (Hempson *et al.*, 2015). In the context of the

PAP, they would have maintained a higher dietary intake of water (Veldhuis *et al.*, 2019) which would have allowed them to exploit woody habitats further from water (certain fynbos and thicket habitats on the PAP). Areas directly surrounding rivers on the PAP were also dominated by such dense woody vegetation that changes little seasonally (du Toit, 2003; Smit *et al.*, 2007). It is also these areas that are associated with an increased risk of predation (Hopcraft *et al.*, 2010).

Effect of early humans

We have created a human-induced landscape of fear for PAP ungulates by looking at the risk from humans in relation to distance from a camp or settlement (Fig. 2). Avoidance of potentially dangerous areas may form a key antipredator strategy for large herbivores (Laundré *et al.*, 2010). The presence of humans (direct or from other cues, i.e. sound) can significantly affect animal behaviour. For example, in badgers (*Meles meles*), the sound of humans affected every measure of fear (Clinchy *et al.*, 2016). Bonnot *et al.* (2013) showed that in roe deer (*Capreolus capreolus*) an increase in daytime use of habitats was apparent with an increasing distance from humans, except in woodland environments where adequate protection (allowing roe deer to remain undetected) was available. Finally, Brooke *et al.* (2020) indicated that herbivores would not maximise their intake of energy through forage in areas where the poaching risk was higher. There is no question about the fear that humans cause in wildlife (Clinchy *et al.*, 2016; Riggio *et al.*, 2018). In effect, humans are potentially more frightening and lethal than other predators and often termed a super-predator (Darimont *et al.*, 2015), especially since the development of tools and projectile weaponry (Bradfield *et al.*, 2020; Brown *et al.*, 2012). In analysing this relationship between humans and large herbivores, it is conceivable that we have underestimated the effect of humans somewhat, even though we have distributed humans throughout the PAP at high densities (0.05 persons per km²; Wobst 1974). In a contemporary context, Darimont *et al.* (2015) showed that mean mortality caused by humans was 1.9 times that caused by all other predators. Interpreting this in our analysis proves to be quite complicated as we do not perceive the direct effect of either human or natural predation; rather, we infer these characteristics based on landscape characteristics. This increased risk associated with human predation can be attributed to the cognitive development of humans, allowing them to use more effective technology to increase their chances of hunting success and to target more naive prey (Darimont *et al.*, 2015; Ripple and Van Valkenburgh, 2010). In addition to changing the landscape of fear, humans may also have altered the landscape through fire (Kraaij *et al.*, 2020; Marean *et al.*, 2014) and other means. Fire may have been influential in mitigating some of the negative effects associated with a human-induced landscape of fear, especially close to camps. For example, if fire was used in areas close to human settlements, herbivores may have increased their predation risk to use these recently burnt areas, because of the increased vegetation palatability (Brooke *et al.*, 2020) and an open landscape promoting vigilance (Burkepile *et al.*, 2013).

Conclusion

Here we have shown how environmental variables, a landscape of fear and the risk associated with early humans influence the probability of occurrence of large herbivore functional groups on the PAP. Additionally, we have successfully shown how changes in human densities (high and low

human density models) influence different functional groups across biomes. Water-dependent grazers were the species most preyed upon by early humans on the PAP, but medium-sized social mixed feeders were most affected by the presence of humans. We have provided some of the first comprehensive models depicting herbivore probability of occurrence using functional groups on the PAP in relation to these environmental factors. Finally, we have shown this under two contrasting human density models. Small non-social browsers predicted their highest probability of occurrence in the thicket biome; medium-sized social mixed feeders in grassland; large browsers and non-ruminants in the savanna and thicket biomes; and water-dependent grazers in the savanna and grassland biome.

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Conflicts of interest—To the best of our knowledge there is no conflict inhibiting the publication of this manuscript.

Data Availability Statement

Data related to this article are stored privately and can be made available by contacting the corresponding author.

Supporting information

Additional supporting information can be found in the online version of this article.

Supplementary Figure 1. Predicted graphs showing the relationships between five large herbivore functional groups and probability of occurrence in relation to water, probability of occurrence in relation to human risk and probability of occurrence in relation to vegetation density risk. Data is compiled for the high and low human density models separately.

Supplementary Figure 1. Predicted graphs showing the relationships between five large herbivore functional groups and probability of occurrence in relation to water, probability of occurrence in relation to human risk and probability of occurrence in relation to vegetation density risk. Data is compiled for the high and low human density models separately.

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