



OPEN The role of species interactions in shaping the geographic pattern of ungulate abundance across African savannah

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Macroecologists traditionally emphasized the role of environmental variables for predicting species distribution and abundance at large scale. While biotic factors have been increasingly recognized as important at macroecological scales, producing valuable biotic variables remains challenging and rarely tested. Capitalizing on the wealth of population density estimates available for African savannah ungulates, here we modeled species average population density at 100 × 100 km as a function of both environmental variables and proxies of biotic interactions (competition and predation) and estimated their relative contribution. We fitted a linear mixed effect model on 1043 population density estimates for 63 species of ungulates using Bayesian inference and estimated the percentage of total variance explained by environmental, anthropogenic, and biotic interactions variables. Environmental and anthropogenic variables were the main drivers of ungulate population density, with NDVI, Distance to permanent water bodies and Human population density showing the highest contribution to the variance. Nonetheless, biotic interactions altogether contributed to a quarter of the variance explained, with predation and competition having a negative effect on species density. Despite the limitations of modelling biotic interactions in macroecological studies, proxies of biotic interactions can enhance our understanding of biological patterns at broad spatial scales, uncovering novel predictors as well as enhancing the predictive power of large-scale models.

Keywords Cetartiodactyla, Competition, Perissodactyla, Population density, Predation

The study of the distribution and abundance of organisms over macro-ecological scales has traditionally focused on the role of abiotic factors, such as climate, topography and water availability, assuming these are the dominant determinants (e.g.,^{1,2}). Instead, the role of biotic factors has mostly been considered at local scales^{3,4}.

Although the influential role of biotic interactions in determining local presence and abundance is widely recognized, empirical validation of this role remains limited in literature (e.g.,⁵). Indeed, quantifying representative biotic interaction variables represents a challenge. The scarcity, quality and comparability of data on species interactions has led researchers to resort to geographic proxies, often constraining studies to specific predator–prey relationships or select within unique ecological systems. Consequently, biotic variables are typically represented through measures such as species presence/absence or richness (including competitors, predators, preys, etc.;^{6–8}). For instance, Heikkinen et al.⁹ found a significant improvement in the predictive accuracy of owl species distributions upon incorporation of occurrence and richness data of woodpeckers.

Recent macroecological studies have increasingly embraced the role of biotic factors in shaping broad-scale distribution patterns^{10–12}. For example, Cosentino et al.¹³ observed trophic resource richness to frequently outweigh abiotic factors in predicting the distribution of African bats. However, scant attention has been directed towards studies exploring abundance within the context of biotic factors influencing biodiversity patterns at a large geographic scale^{14–18}. In fact, contrary to species distribution models that rely on occurrence data, studies modelling abundance (number of individuals) or population density (number of individuals/area) generally adopt lower spatial resolution to accommodate the size of the study area over which populations have been

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estimated^{19–23}, which can be extremely heterogeneous when models include species with diverse spatial ecology. It is generally assumed that biotic interactions lose importance at lower resolution. Nonetheless, understanding how biotic interactions influence population abundance and density across species ranges can improve our knowledge in terms of conservation and management plans¹⁸ and our understanding of macro-ecological patterns^{17,24}.

African savannah, which encompasses the Sahel, East Africa and most of Southern Africa, shelters the largest ungulate assemblage of any other biogeographic region²⁵ and the greatest biomass of ungulates on the continent²⁶. This biome hosts roughly 100 species exhibiting a wide range of body masses, from the small dik-diks (*Madoqua spp.*) weighting a few kilograms to the colossal African savannah elephant (*Loxodonta africana*) nearing 6000 kg. Additionally, these species exhibit diverse trophic preferences, from pure grazers such as the oribi (*Ourebia ourebi*) to nearly exclusive browsers like the springbok (*Antidorcas marsupialis*). The abundance of African ungulates is intricately linked to factors such as food availability²⁰, climate conditions²⁷, and water presence^{28,29}. Different trophic guilds (browsers, grazers, frugivores and generalists) exhibit varying food requirements and degrees of reliance on water resources²⁶. Moreover, land use, human activities^{29–31}, and the presence of protected areas³² also influence ungulate populations.

Despite the considerable impact of these abiotic factors, ungulates engage in complex interactions, including both positive (facilitation) and negative (competition) interactions, which can significantly influence their densities and spatial distributions³³. Furthermore, these species face top-down regulation from various large predators^{34,35}, notably lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyenas (*Crocuta Crocuta*), African wild dogs (*Lycaon pictus*), and cheetahs (*Acinonyx jubatus*). The effect of such interactions on ungulate density has been studied locally based on natural experiments (e.g.,³⁴), simulations (e.g.,³⁵), or just speculative discussions (e.g.,³⁶). However, comprehensive assessments integrating these biotic interactions with other ecological drivers at a large spatial scale are lacking. Given this intricate interplay of biotic and abiotic factors influencing their densities, African savannah ungulates present an ideal setting to explore the relative impact of predation, competition, and environmental and anthropogenic factors on species population densities at a continental scale.

In this study, we aim to investigate the relative importance, magnitude, and direction of environmental and biotic variables in explaining gradients of species abundance at large spatial scales. Leveraging on an extensive dataset comprising 1043 density estimates for 60 ungulate species within the savannah biome^{37,38}, we develop variables representing potential competition by accounting for species' similarity in body mass and diet³⁹, and predation by accounting for the distribution of species' primary predators. Subsequently, we model ungulate densities while considering both environmental factors and biotic interactions and assess the relative influence of species' interactions on mammal population density pattern over large spatial scales.

We expect proxies of biotic interactions to play a role in shaping ungulates density. In particular, we expect a negative effect of predators^{34,35} and competitors³³ on African ungulates density. We also expect a positive effect from NDVI²⁰ and protected areas, a negative effect of distance to water resources^{28,29}, and a negative effect of anthropogenic variables³⁰.

Methods

Species data collection

We extracted density estimates for all African ungulates from the TetraDENSITY database³⁷ along with supplementary data in Santini et al.³⁸. Additionally, we complemented with 371 estimates for 45 species sourced from Google Scholar by using combinations of the keywords “ungulate”, “population density”, “savannah”, “aerial survey”, “distance sampling”. Subsequently, we only retained density estimates that were accompanied by clearly delineated sampling methods and periods, and spatial coordinates. To ensure compatibility with covariates (see below), we filtered out estimates predating 1990. To mitigate potential pseudo-replication, we averaged all density estimates for the same species collected at identical geographic coordinates and using the same sampling method. To narrow our study to the African savannah biome, we used the biome layer delineated by Dinerstein et al.⁴⁰.

We finally excluded two species, namely hippopotamus (*Hippopotamus amphibius*) and the African savannah elephant (*Loxodonta africana*), from the final database due to their significant deviation from the general distribution patterns observed in other species. The hippopotamus has a linear distribution along rivers, which produces density estimates that are incomparable with those of other species. The African savannah elephant, being a megaherbivore, occupies an ecologically distinct niche from other ungulates in the dataset. Given their substantial body mass, elephants represent the largest megaherbivores, experiencing minimal competition (and predation) from other species. Conversely, they exert pronounced interference competition on nearly all other herbivores, including other megaherbivores. This ecological segregation justifies their exclusion from the analysis^{41–44}. Following these methodological refinements, our final dataset comprised 1043 density estimates for 60 distinct species (Fig. 1).

Covariates

To model population densities for each species, we considered both environmental covariates and proxies of species interactions. We used the Normalized Difference Vegetation Index (NDVI;⁴⁵) to capture vegetation productivity's influence on savannah herbivores²⁰. We averaged annual layers between 1981 and 2019 (⁴⁵; 0.05-degree resolution) using Google Earth Engine⁴⁶. Climatic variables, known to impact ungulates density by modulating resource availability and mortality rates^{18,19,21,23}, were also considered. However, given the intercorrelation among climatic variables, we conducted a Principal Component Analysis (PCA) on the 19 bioclimatic variables (1-km resolution) within the African savannah biome⁴⁷, and extracted the first two orthogonal axes explaining 72.7% of the cumulative climatic variance in the region. The first PC1 inversely correlates with temperature and precipitation seasonality, whereas PC2 positively correlates with annual mean temperature (Table S1, Fig. S1). From Cosentino et al.¹³, we extracted geographic distances from temporary and permanent water sources (1-km

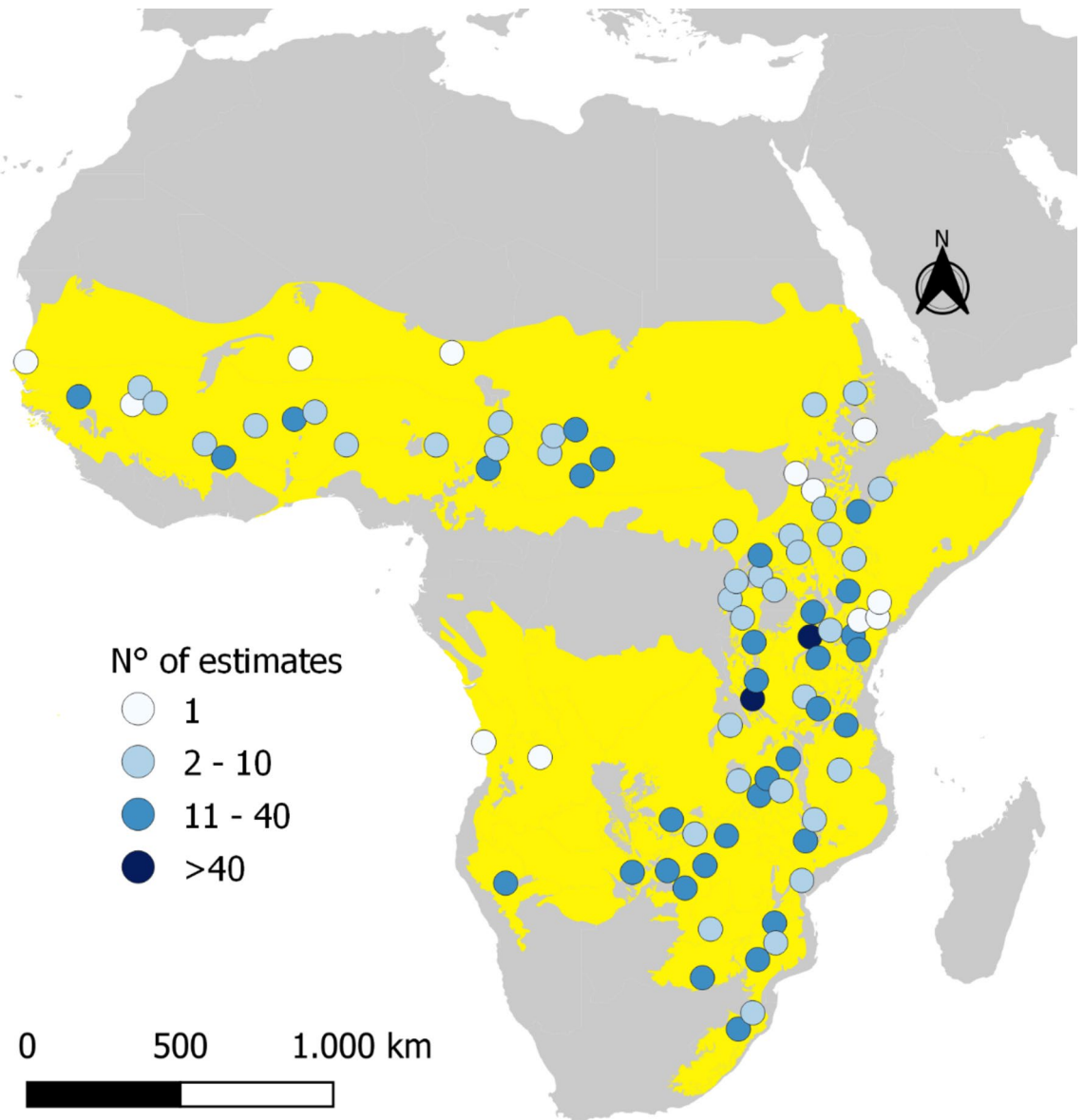


Fig. 1. Spatial distribution of the density estimates in our sample. Darker blue points indicate a higher number of estimates for the same location. African Savannah biome range is visualised in yellow. This figure was produced with R v.4.0.3 (R Core Team, 2020).

resolution), since water often plays an important role in savannahs and water-seeking behaviours (mediated by predation and competition) are crucial²⁸. We also considered the effect of protected areas on wild ungulate densities expressed as a percentage of protected area per grid cell⁴⁸. Lastly, to model the direct and indirect influence of anthropic pressure on wild ungulates, we used cropland data from Copernicus (⁴⁹; 0.1-km resolution) and rural human population density (⁵⁰; ~50-km resolution). For human population density layer, we used the mask provided by SEDAC^{51,52} to extract rural data only.

Species interactions included competition (with both wild and domestic ungulates), predation and ungulates species richness. To estimate potential competition between native ungulates, we implemented a novel approach based on mean similarity with other species within a grid cell (Fig. S2). The similarity matrix computed using the Gower metric⁵³, incorporated both body mass and percentage of element consumption in the diet (% of browse, graze, fruit, other), using data manually curated from Kingdon et al.⁵⁴. In some cases, percentages of element consumption in diet had to be interpreted. When species were reported as ‘strictly’ or ‘obligated’ on one diet type, or only one trophic behaviour was reported, we set the percentage to 100%. When a species was reported as feeding ‘primarily’ or ‘almost exclusively’ on a certain diet, we set the percentage to 90% and the remaining 10% was equally allocated to the other categories mentioned in the text. When species were reported as ‘mixed feeder’, ‘generalist’ or ‘omnivore’, or when more than one type of diet was reported, we set the percentages of the cited types at the same level (20 or 30%); then if a diet type among those cited was mentioned as their main or preferred, we added an additional 20% to that diet (subtracting it equally from the others). Diet reported as ‘occasional’ was assigned to 10%, whereas ‘small quantities’ or ‘very low’ was assigned to 5%. We then quantified

competition as the average similarity among co-occurring species in the same grid cell (Fig. S2). We now provide the code to replicate this step at <https://doi.org/10.6084/m9.figshare.25703217.v1>. To account for the diversity of potential competitors, we also included ungulate species richness in interaction with competition.

Predator richness ranged from 0 to 5, making it problematic to treat it as a numeric variable. For this reason, we considered predator species richness in a grid cell as a categorical variable, and grouped it into four categories: 0, 1–2, 3–4, 5 species (Fig. S3). Distribution data for both competitors and predators were obtained from the IUCN Red List (Table S2). We also included livestock density (^{55–57}; 0.083-degree resolution) to account for possible interactions (positive or negative) between wild ungulates and the presence of domestic animals⁵⁸. To combine the densities of different domestic animals (cattle, sheep, and goats⁵⁹), we used the Regional Livestock Units⁶⁰ for sub-Saharan Africa, assigning weights (0.5 for cattle and 0.1 for sheep and goats) and summing up their weighted densities.

All variables were resampled at a 100 × 100 km resolution, deemed appropriate to work at the continental scale, considering the size of the study areas over which ungulate densities have been estimated, and the spatial uncertainty in the coordinates reported in the original studies. We assessed collinearity among all variables and found that none had a Pearson's *r* correlation coefficient >|0.7|, so all variables were retained for the model⁶¹. The distribution of the dependent variable (density) and of some of the covariates (livestock, distance from both permanent and temporary water, PA % and rural human population density) was standardized through natural log-transformation, guided by an examination of their original distributions. All variables were then scaled and centred.

Model fitting

We fitted a linear mixed-effect model using a Gaussian family error distribution and a Bayesian inference⁶². We modelled log-transformed species population density per cell as a function of environmental and biotic covariates. To account for the differences in average densities among species, we included species as random effect. To account for different estimation method of population densities^{18,21}, we included a random effect with five categories: Census, Counts, Distance sampling, Mark recapture and Random Encounters Models (REM). Finally, to address socio-economic factors not captured by fixed effects, we also included country as an additional random effect¹⁸. In addition, we used NDVI as a random slope, as it has already been shown NDVI has different correlation for different species²⁰. Finally, we controlled for phylogenetic relatedness using a variance–covariance matrix based on the phylogeny in Upham et al.⁶³.

We used weakly informative priors using a normal distribution with a standard deviation of 10 for the intercept, and a standard deviation of 1 for all slope coefficients, thereby limiting the range to a plausible gradient of variation considering the scaled coefficients⁶⁴. We used 5 Markov Chain Monte Carlo (MCMC) chains, each comprising 6000 iterations to achieve convergence. The first 1000 iterations were utilized as warm-ups in the model. To minimize storage demands, we implemented a thinning factor of 5. Visual assessments, along with the R-hat diagnostic, were employed to ensure chain convergence and parameter identifiability. We also tested for spatial autocorrelation in the model residuals using the Moran's I test.

Quantifying the relative importance of each predictor was achieved by partitioning the variance explained across predictors. This involved estimating the squared correlation coefficient between model predictions with one variable set at its mean and the observed data. The full variance explained was then subtracted from each estimate to determine the relative importance of each variable, expressed as a percentage.

The standardized effect sizes and contribution to the variance can both be intended as measures of variable importance but can give complementary information and should be interpreted differently. A strong effect indicates that the variable has a strong effect on the response variable, yet this may contribute very little to the overall variance if the gradient in the training dataset is limited. So variable importance estimated using the variance explained returns a more comprehensive view of intensity of the effect, and entity of the effect over the total.

All analyses were conducted in R v.4.0.3⁶⁵. The 'brms' package⁶⁶ was used for model fitting, while 'raster'⁶⁷, 'psych'⁶⁸ and 'ape'⁶⁹ supported data manipulation. Similarity was extracted with the 'cluster' package⁷⁰. Model fit assessments and covariates effect visualisation were conducted using the 'bayesplot' package⁷¹ and the 'ggplot2' package⁷². Model diagnostics were tested and visualised using the 'DHARMA' package⁷³. The code to replicate the main analysis is provided at <https://doi.org/10.6084/m9.figshare.25703217.v1>.

Results

The MCMC chains of the model converged well (R-hat convergence diagnostic ≤ 1.01 for all coefficients). Our model successfully explained 46.04% of the variance, as validated by the Moran's I test, which confirmed the absence of spatial autocorrelation effects on the residuals (Observed = 0.0006, Expected = -0.0045, sd = 0.0208, *p*-value = 0.8008). Diagnostic plots further confirmed the model fit's robustness (Fig. S4).

Ungulate population densities were influenced by both environmental and biotic covariates (Fig. 2). Densities were higher in non-seasonal climates (PC1, Table S1) and lower at higher mean temperatures (PC2, Table S1). Densities were also positively associated with the proportion of cropland per cell, but negatively associated with areas characterized by high human densities. As expected, densities were strongly negatively associated with distance from permanent water sources, while surprisingly, positively associated with distance from temporary water sources. NDVI and the percentage of protected areas showed weakly positive and negative effects, respectively.

Among our sets of species interaction proxies, average competition with other wild ungulates had a negative influence on ungulate density, while species richness and livestock density showed a clear positive effect. The interaction between competition and species richness had no significant effect on density. The presence of predators yielded the strongest effect on species densities, leading to lower densities where multiple predator

species are present. Despite the magnitude of this effect, uncertainty remains high since very few estimates were associated with no predators.

Despite the limited individual effect sizes, some variable explained a particularly high portion of the variance. Among environmental variables, NDVI, human population density and distance from permanent water had the highest importance, while among biotic interactions Livestock competition and competition with other wildlife species had the highest importance. Species interactions alone explained about 25% of the overall variance (Fig. 3).

Discussion

In this study we modelled African ungulate density in savannah at the continental scale considering both environmental and biotic interaction variables. We showed that the continental pattern of density is jointly shaped by both types of variables, with biotic interactions constituting a large portion of the variance explained. Our results corroborate the role of biotic interaction variables in large-scale models of species density.

Environmental drivers

Savannah ungulate densities mirrored environmental gradients shaped by climate, vegetation, land use, and human presence, consistent with prior research. Densities were notably higher in non-seasonal climates, a trend observed across mammalian species^{21,22}. Seasonality in precipitation impacts resource availability, leading to periods of scarcity that limit reproduction and potentially increase mortality. NDVI had a mild positive effect on species densities, but overall, explained a substantial part of the variance in observed densities (~24%). This aligns with expectations, highlighting the importance of resource abundance for herbivore populations²⁰. Areas characterized by a high proportion of cropland were associated with high ungulate densities. Indeed, this pattern is not new and has been observed across mammals globally⁷⁴. Ungulates can take advantage of easily accessible food resources in croplands, thus increasing their densities near cropland⁷⁵. In addition, croplands are generally found in productive landscapes, so areas that are suitable for croplands may be also suitable for ungulates. Notably, our variable represents cropland proportion per area, indicating the likelihood of a positive effect stemming from high-density areas surrounding croplands rather than within croplands themselves. Indeed, comparisons between presence and abundance in croplands typically suggest negative effects³⁰.

Conversely, human population density was negatively associated with ungulate densities, possibly reflecting habitat degradation, direct disturbance, and hunting pressure. This finding aligns with previous studies indicating lower ungulate densities in more inhabited areas or near human settlements^{76,77}. However, variations among species have been noted sometimes^{5,78}, with some species exhibiting less sensitivity to human presence than others, such as wildebeest and impala compared to zebra, duikers and oribis.

Water sources play a crucial role in influencing savannah ungulate movements^{28,29}. Consistent with prior research^{5,27,78}, our results underscored water sources as among the most important drivers of ungulates abundance in savannah. Distance from permanent water bodies negatively impacted ungulate densities, explaining a considerable amount of variance in the model (~19%). Permanent water bodies can increase local carrying capacities, reduce daily animal movements, and buffer animals against climate fluctuations and extreme weather conditions like droughts⁷⁹. Conversely, distance from temporary water showed a mild positive relationship with ungulate densities and was the least important variable in the model (~2%). This is probably because ungulates cannot rely on temporary water bodies as a solid resource, especially during long dry periods.

Interestingly, the percentage of protected areas showed a modest negative effect on ungulate density, explaining very little to the overall variance (<1%). While protected areas may not always effectively safeguard savannah ungulates, especially if they do not encompass all seasonal resources⁸⁰, a moderate negative effect may also reflect higher predator densities within protected areas. Many large African predators are predominantly confined to protected areas nowadays, where fenced populations may reach considerable densities (e.g.,⁸¹). Thus, lower density of ungulates in protected areas may reflect top-down effects that are not captured by our predator variable, which only consider predator presence. Additionally, the resolution of our analysis may also influence these findings, as protected areas may occupy a substantial portion of a cell, but significant land areas within the cell may still face strong human pressures around the protected areas.

Biotic interactions

Our results highlight the significant impact of proxy variables of biotic interactions on ungulate densities. Predation exhibited the most pronounced effect among biotic interaction variables, with predators exerting a negative influence on ungulate density. This underscores the crucial role of predation in regulating herbivore populations^{16,35}, and highlights the importance of considering predator presence at broad geographic scales. Interestingly, the most noticeable difference was observed between areas with no predators and those with few predators (Fig. 2), while the distinction between different predator richness values was less marked. This highlights the limitations of our approach, as top-down regulation is mostly sensitive to predator numbers rather than richness. While ungulate predators differ in their ecology and may compete with each other, limiting their numbers (e.g., lions, cheetahs, leopards, hyenas;^{82–84}), higher predator richness does not necessarily indicate higher regulatory pressure exhibiting a non-linear pattern. Ideally, the effect of different predators may be weighed differently on prey depending on prey selection, however this presents several challenges. First, while the main predators for well-studied ungulate species are well known, this is less clear for less studied species (e.g., *Litocranius walleri* and *Capra walie*,⁵⁴). Second, prey selection depends on species relative abundance as well as environmental conditions^{85,86}, so may vary over environmental gradients. Finally, large predators (lions, hyenas, leopards) can predate a wider range of prey than smaller predators (cheetah, wild dogs), ultimately outcompeting or even displacing them. So, the effect of smaller predators ultimately depends on the presence of larger predators⁸⁷. For

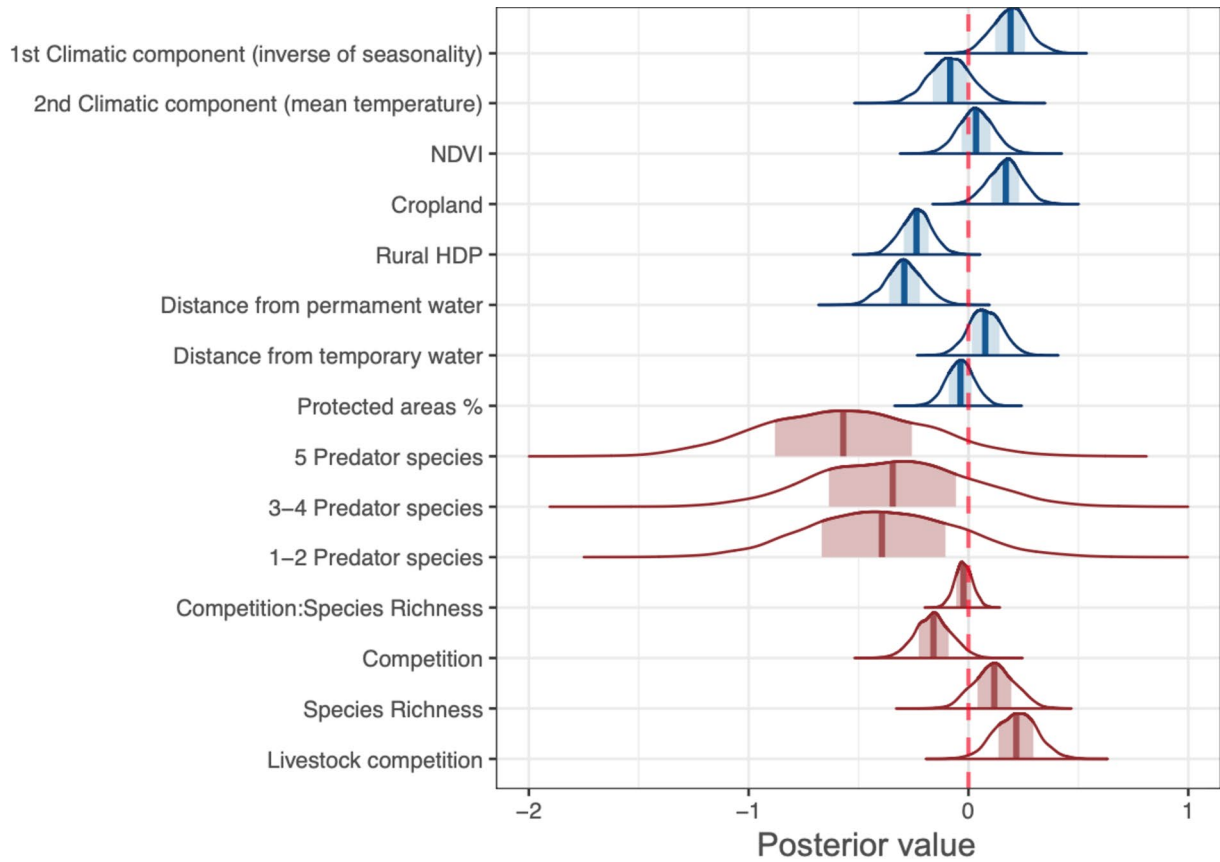


Fig. 2. Posterior estimate distributions for the model. Red dotted line corresponds to 0. For predator categorical variable, 0 species level was used as baseline (the estimate for this level is above 0). Species interactions posterior distributions are visualized in red, while environmental factors posterior distributions are visualized in blue.

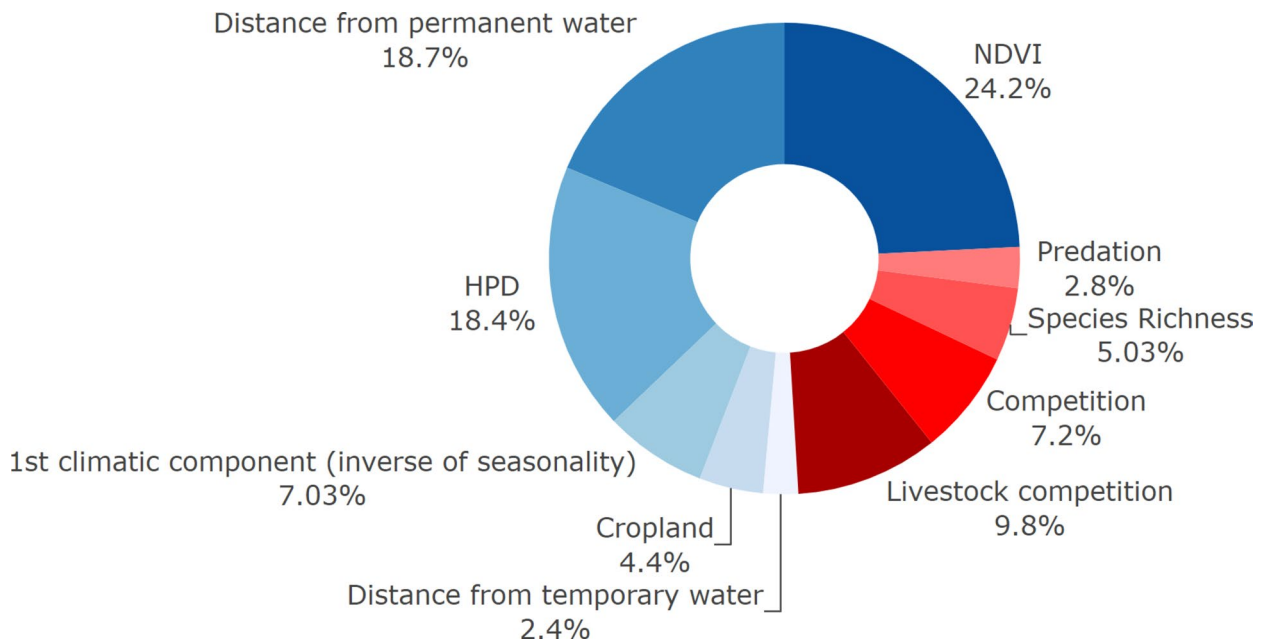


Fig. 3. Pie chart illustrating each variable's relative importance in explaining the model's total variance, expressed as percentage. Percentage of protected areas and the 2nd climatic component, whose importance was <1%, are not displayed for clarity. Environmental factors are represented in blue colours and biotic interactions in red colours.

all these reasons, we preferred to use a simple measure of predator presence. Certainly, accounting for predators as presence-absence and total number of species is far from ideal, and yet the effect of predator presence is noticeable at this geographic scale contributing to improve model performance. Interestingly, despite the strong effect, the variance explained by this variable is relatively minor, suggesting that gradients of predator richness, especially total absence of predators, is limited within the study area. A more nuanced representation of predators' presence and abundance might certainly contribute to explain additional variance in the data (Fig. 3).

The functional similarity among ungulate species exhibited a negative effect on their density, suggesting that interspecific competition may have an important influence on herbivore³³. In areas with limited predator numbers and high ungulate densities, functionally similar species may experience scramble competition with other ungulates, thereby constraining carrying capacity. Surprisingly, we found no interaction effect between functional similarity and species richness. This may be because competition intensity is ultimately dependent on the abundance of competitors, rather than their presence. While facilitation effects among ungulates have been widely studied (e.g.,^{88,89}), its effect might be potentially less important than competition or may depend on seasonality^{90,91}. Facilitation effects may be captured by the species richness (number of ungulates irrespective of their similarity) variable that had a positive correlation with ungulate density. Accounting for potential competition at this scale necessarily requires simplifications, for example, ungulate trophic requirements change between the dry and the wet season^{92,93}, and even competition or facilitation dynamics with livestock are season dependent⁵⁸. We could not account for seasonality in the model because very few estimates were associated with a specific sampling season, thus substantially reducing the dataset and its representativeness. Recently, however, Bierhoff et al.⁵ highlighted how spatial factors influenced ungulate densities more than temporal (seasonal and annual) factors within the Tarangire Ecosystem of northern Tanzania, due to their ability to move across space when needed. Given the large extent and coarse resolution of our analysis, seasonality is only expected to introduce noise but not altering the observed geographic pattern.

The biotic interaction variable that most contributed to the variance was livestock density, showing positive effect. Livestock is expected to yield a negative effect on wild species⁹⁴, both because of competition for resources, and possible disease spread⁹⁵. However, a positive association of wild ungulate density with livestock density is not unexpected. In fact, both groups benefit from similar conditions (productive landscapes, water availability), and absence of livestock may indicate a low suitability for wild ungulates too. Such positive association has already been shown in previous studies^{30,79}, with responses varying by species diet habits. Browsers and mixed feeders seem to suffer more from the competition with domestic animals, while grazers tend to show a positive response. It has been speculated this may also indicate a potential facilitation effect, with cattle benefitting grazers, especially ruminants, by removing old, tall, poor-quality grass while stimulating the growth of early successional plants⁹⁴. Competition with livestock is also season dependent⁵⁸, so the patterns observed here must be intended as averages despite seasonal fluctuations.

Despite the limitations discussed, biotic variables seem to perform well, suggesting simplifications are acceptable at this scale of the analysis and enhance interpretation. Our results indicate that the geographic pattern of abundance of African ungulates in savannah is shaped by multiple environmental and anthropogenic factors, but it is also very dependent on the several biotic interactions that occur between the various species involved (as shown also in⁷⁹). While abiotic factors are the main drivers of abundance patterns at this scale, accounting for species interactions brought a substantial contribution to the variance explained in our model (25%), enhancing our comprehension of geographic abundance patterns. Considering their relative importance at the continental scale, we can speculate that the relative importance of biotic interactions increases at more regional scales. Our findings align with the existing literature suggesting a relevant role of biotic factors in shaping large-scale patterns of biodiversity^{10,13,15–17}. More specifically, it supports the search for proxies of biotic interactions at the geographic scale to further enhance population density predictions (e.g.,¹⁸).

Conclusion

Our study provides a comprehensive assessment of the factors influencing ungulate density in the African savannah biome, highlighting a concomitant effect of environmental variables, human pressure variables, and biotic interactions. While not always possible, proxies of biotic interactions should be considered in large-scale studies of species abundance. This will require simplifications which are inadequate for local-scale studies but can reveal new predictors and enhance the understanding of the drivers of geographic patterns and predictive power at large-scale.

Data availability

Many of the data used are openly accessible at the cited sources, some others were collected for this study. All population density data collected and related sources, as well as the final dataset, are accessible through figshare at <https://doi.org/10.6084/m9.figshare.25703217.v1>.

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Author contributions

LS conceived the idea with contributions from LM and WT; LS and LM designed methodology with contributions from WT; NP, LS and FC collected the data; NP analysed the data; NP and LS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

The authors declare no competing interests.

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