

1 Energy landscapes direct the movement preferences of 2 elephants

3 Keywords

4 elephant, *Loxodonta africana*, habitat preference, movement, energy landscape, step-selection function

5 Abstract

6 The movement of animals affects the biodiversity, ecological processes, and resilience of an ecosystem.
7 For the animals, moving has costs as well as benefits and the use of a given landscape provides insights
8 into animal decisions and behavioral ecology. Understanding how animals use the landscape can thus
9 clarify their effects on ecosystems and inform conservation measures aiming at preserving and restoring
10 the ecological functions of animal dispersal. Here, we investigated the habitat preferences of African
11 savanna elephants (*Loxodonta africana*) using GPS data from 155 individuals collected between 1998 and
12 2020 in Northern Kenya. In particular, we assessed how “energy landscapes”, i.e. the cost of locomotion,
13 together with elevation, vegetation productivity, water availability, and proximity to human settlements
14 influence the habitat preferences of elephants. We found that the energy landscape is the most consistent
15 predictor of elephants’ preferences, with individuals generally avoiding energetically costly areas and
16 preferring highly productive habitats. We also found that other predictors such as elevation, water
17 availability and human presence, are important in determining habitat usage, but varied greatly among
18 elephants, with some individuals preferring habitats avoided by others. Our analysis highlights the
19 importance of the energy landscape as a key driver of habitat preferences of elephants. Importantly, the
20 enerscape modeling environment allowed us to develop testable hypotheses from rather coarse-grained

data covering elephant movements and a few environmental parameters. Energy landscapes rely on fundamental biomechanical and physical principles and provide a mechanistic understanding of the observed preference patterns, allowing to disentangle key causal drivers of an animal's preferences from correlational effects. This, in turn, has important implications for assessing and planning conservation and restoration measures, such as dispersal corridors, by explicitly accounting for the energy costs of moving.

Introduction

Animal movement maintains important ecosystem functions, such as seed and nutrient dispersal (Doughty et al., 2013; Guimarães et al., 2008), promotes ecosystem stability (Gravel et al., 2016), and fosters biodiversity (Wilson, 1992). The most important players for these processes are megafauna, i.e. animals \geq 45 kg (Martin & Klein, 1989), which have large homeranges (Kelt & Van Vuren, 2001) and can thus disperse nutrients, seeds, and energy across large areas (Doughty et al., 2013; Guimarães et al., 2008; Malhi et al., 2016). Megafauna were once widespread globally before human pressure triggered their extinction and restricted their distribution (Sandom et al., 2014) and homeranges (Hirt et al., 2021), with severe effects on biotic connectivity (Berti & Svenning, 2020). In particular, of the 48 megaherbivores (\geq 1,000 kg) present at the beginning of the Late Pleistocene (starting around 120,000 years ago), only 8 have survived until today, almost all at risk of extinction and with decreasing distribution ranges (IUCN, 2022). In the light of a new ongoing mass extinction and pressing challenges due to climate change, it is imperative to conserve these remaining animals and their ecosystems.

The African savanna elephant (*Loxodonta africana*) is the largest megaherbivore alive today. Together with the slightly smaller African forest elephant (*Loxodonta cyclotis*) and the Asian elephant (*Elephas maximus*), *L. africana* is the only living species of the order *Proboscidea*, which included 16 more species that were present during the Late Pleistocene, but that went extinct due to climate and anthropogenic factors (Cantalapiedra et al., 2021). Proboscideans were once widespread, with fossils being found in

Africa, Eurasia, and the Americas (Shoshani, 1998), and had unique ecological roles, such as landscape engineering and seed dispersal (Guimarães et al., 2008; Malhi et al., 2016). The African elephant, once spread across all of Africa, has today a fragmented distribution, with wild populations often constrained to protected areas (Wall et al., 2021). Moreover, wild elephant populations show overall decreasing trends in numbers, mostly due to poaching and increased human land-use (Chase et al., 2016; Ripple et al., 2015; Veldhuis et al., 2019). Therefore, fully understanding the habitat requirements of elephants is key to optimize conservation and restoration efforts to protect currently threatened elephant populations as well as to better understand how extinct Proboscideans, and potentially megafauna in general, would have used and shaped their ecosystems.

Recent studies have begun to outline, define, and understand the habitat preferences of extant elephants and describe the drivers of their movement behavior patterns. Elevation is commonly used as a predictor for habitat preferences of both *L. africana* and *E. maximus* (Asner et al., 2016; Chibeya et al., 2021; Ngene et al., 2009; Talukdar et al., 2020), usually explaining a large proportion of the elephants' preferences. However, as other factors covary with elevation, it is not clear whether elevation itself influences elephants' movement rather than being a convenient proxy to capture other abiotic and biotic processes. For instance, vegetation structure and water availability as well as human presence and density all vary with elevation, which may thus shape movement behavior only indirectly, e.g. by affecting soil and water dynamics, vegetation structure, and anthropogenic pressure (Asner et al., 2016; Chibeya et al., 2021; Ngene et al., 2009; Taher et al., 2021; Talukdar et al., 2020). This confusion partly hinders efforts to fully comprehend the habitat preferences of elephants, e.g. by masking the real causal associations between the environment and habitat preferences with spurious correlations. Moreover, a number of observations suggest that elephants may not be as much limited by elevation as commonly thought, with some recorded cases of elephants climbing ~2,000 meters in elevation (Choudhury, 1999; Kuswanda et al., 2022).

In this study, we used a recently published method, *enerscape* (Berti et al., 2022), in order to estimate the energetic costs that an animal has to sustain in order to travel across a topographically explicit landscape (Shepard et al., 2013; Wall et al., 2006). Specifically, we used *enerscape* to investigate how energy costs of travel influence the movement decisions and thus habitat preferences of 155 elephants in the Samburu area of Northern Kenya. This approach takes into account both the body mass of the animal and the slope of the terrain traversed (Berti et al., 2022; Pontzer, 2016) and thus captures the mechanistic cause of habitat preferences due to cost of locomotion better than simply using elevation (see also Wall et al., 2006). In particular, we tested the hypothesis that the energy landscape is a key driver, perhaps the most important direct cause, of habitat preferences for the elephants, with elevation only indirectly affecting animals' movement by influencing energy landscapes as well as other environmental factors, such as vegetation productivity and water availability. We achieved this by analyzing GPS telemetry data using a step-selection function in order to understand which environmental factors influenced the habitat preferences of elephants. By explicitly testing these causal relationships, our study aims to elucidate the direct drivers of elephants' preferences, providing a better understanding of the mechanisms determining habitat use. This, in turn, will help conservation efforts to plan more informed mitigation and restoration strategies.

Materials and Methods

Our main hypothesis is that the cost of locomotion has a causal effect on habitat preferences for elephants and that elevation only has an indirect effect by influencing the energy landscape and other environmental factors that determine elephant preferences. We tested this hypothesis by estimating the direct effects of energy landscapes and elevation for elephant preferences using a step-selection function approach. As vegetation productivity, human pressure, and water availability influence movement of elephants (Chibeya et al., 2021; Sach et al., 2019; Taher et al., 2021; Talukdar et al., 2020; Wall et al., 2013), we included also the Normalized Difference Vegetation Index (NDVI) and the distance to human settlements

and to permanent water bodies as explanatory variables for elephant preferences. Importantly, as these three predictors also covary with elevation (Chibeya et al., 2021; Ngene et al., 2009), by including them we further tell apart the direct effect of elevation after accounting for the other factors. Our workflow is summarized in Fig. 1.

GPS Collar Data

GPS data for 172 elephants spanning the period 1998-2020 was made available by Save The Elephant foundation (STE). STE is a non-profit organization that promotes protection of elephants and related ecological research with, among others, a multi-decades GPS radio tracking project in Kenya. Specifically, we obtained telemetry data for the Samburu region in Northern Kenya (36 - 39°E, -0.36 - 2.81°N; Fig. 2). This area has a large elevational gradient (from ~200 to ~5,000 meters a.s.l.), with rainfall mostly concentrated in two periods (April-June and October-December) and strongly influenced by the presence of mountain peaks. This variation in altitude and rainfall across the landscape is associated with changes in land-use: forested areas can be found at high elevations, whereas at lower elevations the landscape is dominated by savannah, with interspersed agricultural and farming areas. GPS data was already processed by STE to assure quality of the records, i.e. GPS fixes that had inaccurate longitude and latitude coordinates were already removed. To make sure that subsequent GPS fixes were separated by an analogous span of time, we resampled the original GPS data. Specifically, we derived the time interval between all consecutive fixes and calculated its 5% (Q_{low}) and 95% (Q_{high}) quantiles. Fixes that were sampled closer than $0.9 * Q_{low}$ from the previous one were removed. When a fix was separated by more than $1.1 * Q_{high}$ from the previous, we kept it, but considered it and subsequent fixes as part of another, separate track for the same animal. We derived these criteria by trying several thresholds and found that these values kept consecutive fixes within an acceptable accuracy of time intervals while minimizing the number of disconnected tracks. This step was necessary to make sure that the movement was modeled consistently across the whole time span of the recordings, e.g. the distance traveled between

fixes was comparable. As the original sampling frequency differed among individuals, with the majority of elephants having GPS position recorded every 30 or 60 minutes, resampling was done for each individual separately.

Remote Sensing Data and Energy Landscapes

We calculated the distance to human settlements using the World Settlement Footprint product (Marconcini et al., 2020) and the distance from permanent water bodies using the ESA WorldCover product (Zanaga et al., 2021). Both distances were calculated as the great-circle distances with a precision of one meter. A digital elevation model (DEM) for the region of interest was obtained from NASADEM (NASA JPL, 2020). Energy landscapes were computed using the R package *enerscape* (Berti et al., 2022), which calculates the energy cost of travel across the landscape using the body mass of the animal and the slope of the terrain traversed (Pontzer, 2016). Because the cost of locomotion depends on the body mass of animals, we calculated energy landscapes for females and males separately. As GPS collars were mounted only on adult individuals, we assumed a body mass of 2,744 kg for females and of 6,029 kg for males, which are typical values for adult individuals (Laws & Parker, 1968).

We calculated the Normalized Difference Vegetation Index (NDVI) from the Sentinel-2 Copernicus mission (Harmonized Sentinel-2 MSI, Level-2A; https://www.esa.int/Copernicus/Sentinel-2/Data_products). NDVI, which has values from -1 to 1, is a measure of the relative abundance of chlorophyll and was used here as a proxy for plant productivity. We calculated the median monthly NDVI using all images spanning the whole period of the Sentinel-2 mission (from June 2015 to February 2023). First, we removed pixels that were identified as clouds of cirrus formations as well as all images that had less than 20% of their area with clear sky conditions. Then, we split the dataset into calendar months and calculated the median reflectance of the near-infrared (*NIR*) and red (*RED*) bands, representing the monthly median values of the bands across the whole time

139 period 2015-2023. Finally, we calculated NDVI, for each month separately, as: $NDVI = \frac{NIR - RED}{NIR + RED}$. As
140 the satellite data does not span the whole temporal range of the GPS data, we assumed that the values
141 obtained for the period 2015-2023 were representative also of the previous years. In other words, we used
142 a monthly NDVI metric that reflects the overall value for the last eight years and assumed that the
143 previous years had similar overall monthly trends.

144 Fitting Hidden Markov Models (HMMs)

145 We decomposed the movement process into distinct underlying states using a hidden Markov model
146 approach (HMM). HMMs are a class of state-space models that describe animal behavior as a set of states
147 defined by movement parameters and by the probabilities of transitions among states (Jonsen et al., 2005;
148 McClintock et al., 2020). Each state is characterized by its movement parameters, e.g. states associated
149 with long-distance dispersal have higher average step lengths. From the GPS fixes, we calculated the
150 relocation step length (meters) and the turning angle (radians). Step lengths were assumed to follow a
151 Gamma (Γ) distribution, characterized by two parameters: the mean and standard deviation. Turning
152 angles were assumed to follow a Von Mises (VM) distribution, characterized by two parameters: the
153 mean turning angle and the concentration of the distribution around it. If an individual had non-
154 contiguous fixes, as obtained from our resampling method, we fitted the whole GPS data together, but
155 specified different tracks to be considered as separate observations. In other words, we assumed that the
156 individual moved according to some general behavior that did not change across tracks, while making
157 sure that non-contiguous fixes did not introduce biases in the fitting procedure.

158 Fitting HMMs requires a pre-defined number of movement states and initial distribution parameters. This
159 may influence HMM results, as different numbers of states can lead to different parameter estimates and
160 changing the starting parameters can lead to different fitted estimates (Michelot et al., 2016). To explore
161 these potential issues, we fitted several HMMs per individual, changing the number of behavioral states

and the starting parameters, and assessed the consensus of different runs for the fitted parameters. Specifically, we fitted three sets of models, each set with one, two, or three movement states; notably, (Taylor et al., 2020) found that a three-state model was more accurate in explaining elephant movement patterns. For each set, we then fitted 10 model replicates that differed in their initial parameterization in order to assess the sensitivity of results to initial starting conditions. The starting parameters were randomly drawn from uniform distribution bound to the 10%-90% quantiles of the observed movement values from GPS recordings; for HMMs with more than one state, this range was additionally divided into corresponding intervals. For instance, the three starting parameters for the three states models were sampled from uniform distributions $U(q_{10\%}, q_{40\%})$, $U(q_{40\%}, q_{70\%})$, $U(q_{70\%}, q_{90\%})$, respectively.

We then compared HMMs within replicates using AIC and selected the most parsimonious model. We retained only the individuals for which all parsimonious models had the same number of movement states, indicating a fair amount of consensus among HMM runs; four individuals were thus removed from further analyses. We also removed individuals that had likely implausible high values of estimated average distance traveled and that had high variation in the fitted parameter values across different replicates, dropping six individuals from further analyses. We ended up with 155 total individuals that we could use to address our research question (Table S1). From the fitted HMMs, we also assigned to each GPS location the most likely movement state, obtained using the Viterbi algorithm (Zucchini & MacDonald, 2009). HMMs were fitted using the R package moveHMM (Michelot et al., 2016).

Step selection function

To assess the habitat preferences of elephants, we used a step-selection function approach (SSF). SSFs are particularly suited to analyze our dataset as they take into account the movement pattern of the individuals and the serial structure of GPS data (Thurfjell et al., 2014).

SSFs sample absences based on the previous location, the movement state of the animal, and the predictive distribution defined by the parameters of the movement state (Karels et al., 2019). First, a

186 movement state is assigned to each GPS location; then, step length and turning angle are sampled from
 187 their predictive distributions, fitted using the state-space HMM models; finally, an absence location for
 188 the next step is obtained by calculating the displacement from the observed GPS location. In particular, if
 189 $(x, y)_t^1$ is a GPS location of an individual at time t in movement state s , and $\alpha_t = \text{atan}\left(\frac{y_t - y_{t-1}}{x_t - x_{t-1}}\right)$ is the
 190 angle of the direction of the movement, we obtained an absence for the next step by sampling the step
 191 length (l) and turning angle (θ) from their respective distributions ($l_t \sim \Gamma_s$ and $\theta_t \sim VM_s$) and by adding
 192 this displacement to the GPS fix: $(x, y)_{t+1}^0 = (x_t^1 + l_t \cdot \cos(\alpha_t + \theta_t), y_t^1 + l_t \cdot \sin(\alpha_t + \theta_t))_t^1$. Following
 193 previous recommendations (Karels et al., 2019; Thurfjell et al., 2014), we sampled only six absences for
 194 each GPS observation as this number is likely enough to accurately fit SSFs, while reducing
 195 computational costs.

196 We estimated the habitat preferences of elephants by fitting a Bayesian logistic regression for each
 197 individual separately, contrasting the environmental factors of the GPS locations with those of the
 198 sampled absence locations. As covariates, we included elevation (m), energy landscapes (kcal), the
 199 distance (m) to the closest permanent water body and to the closest human settlement, and NDVI
 200 (adimensional). As previous studies suggested that elevation may indirectly affect preferences by
 201 influencing the other covariates (Asner et al., 2016; Berti et al., 2022; Chibeya et al., 2021; Ngene et al.,
 202 2009; Taher et al., 2021; Talukdar et al., 2020), we included elevation in our statistical model as a control
 203 in order to assure an unbiased estimate of the direct effects of the other covariates on preferences (Cinelli
 204 et al., 2020). Our causal model is depicted in Fig. 3. In addition to this analysis for the general preference
 205 of elephants, we also fitted logistic models for each movement state separately. This was achieved by
 206 filtering the data retaining only the steps specific to each state and fitting again the Bayesian model. This
 207 allowed us to assess whether habitat preferences of the elephants differed among movement behaviors.
 208 All predictors were centered to have zero mean and scaled to have unit variance before fitting the
 209 Bayesian models.

Analyses were performed using the R and python programming languages. State-space modeling (HMMs) and step-selection functions were performed in the UTM37N coordinate reference system (+proj=utm +zone=37 +a=6378249.145 +rf=293.465 +towgs84=-157,-2,-299,0,0,0,0 +units=m +no_defs) at a resolution of 30 x 30 meters. Bayesian logistic regressions were performed using the MCMC approach implemented in the Stan programming language and the R package *rstan* (Carpenter et al., 2017; Guo et al., 2020). Code and processed data to replicate our results and figures can be found at [removed for blind peer-review]. Due to the sensitive nature of the GPS data, we cannot share the original GPS data; queries to access it should be addressed directly to <https://www.savetheelephants.org/>.

Results

The best state-space models (HMMs), as assessed using AIC, always had three behavioral states (Table S2). The first state was characterized by a slow non-directed movement (average step length = 63 m; angle concentration = 0.22), which we interpreted as a *resting* state. The second state was faster and more directed movements (average step length = 283 m; angle concentration = 1.26), which we interpreted as a *foraging* state. The third state was the fastest and most-directed (average step length = 961 m; angle concentration = 2.26), which we interpreted as a *dispersing* state. The 10 replicates of HMM per individual had a high degree of consensus (Fig. S1), indicating that HMM replicates for the individuals converged to comparable, if not identical, values and that fitted parameters for the movement distributions were reliable.

From the meta-analysis of the coefficients fitted using the step-selection function, we found that 154 of the 155 elephants avoided high energy landscape values (Fig. 4), i.e. they preferred to move in areas associated with low cost of transport. Importantly, the effect size for 153 of these elephants was large (Cohen's $d > 0.80$), indicating that individuals showed a strong avoidance for high energy landscapes (Table S3). There was only one elephant that did not show avoidance or preference for energy landscapes

(Cohen's $d = 0.00$). Overall, these results confirmed our main hypothesis: elephants responded to energy landscapes very consistently, strongly avoiding areas with high cost of locomotion. We also found that elephants consistently preferred habitats with high NDVI values. In particular, 150 elephants preferred areas with high NDVI, with only 5 individuals showing avoidance for high NDVI values. Interestingly, the coefficient estimates had a large positive effect size for 147 individuals (Cohen's $d > 0.8$), indicating elephants strongly preferred high productive habitats in general.

We also found that elephants responded to elevation, but less consistently compared to energy landscapes and NDVI. In particular, 81 individuals avoided areas at high elevation, 13 individuals did not show any preference, and 61 elephants showed a preference for higher elevations. We found similar patterns for both distance to the closest water body (93 individuals with negative preferences, 10 with no preferences, and 52 with positive preferences) and for distance to the closest human settlement (46 individuals with negative preferences, 16 with no preferences, and 93 with positive preferences). Overall, we found a high heterogeneity among individual preferences when considering elevation, distance to water, and distance to human settlements as direct, causal predictors of elephant habitat preferences.

When analyzing the preferences for the three movement states separately, we found generally similar trends to the overall preferences (Fig. 5). In particular, individuals generally avoided high energy landscape values and preferred highly productive habitats, but showed contrasting trends among individuals when considering the preferences for elevation and distance to water and human settlements. Interestingly, individuals showed a stronger avoidance for high energy landscape values when they were moving faster: all elephants avoided energetically costly areas when considering only the dispersal movement state, whereas 6 individuals ignored or preferred costly energy landscapes when moving in the foraging state, a number that increased to 12 when considering only the resting state. These results suggest that elephants adjust their behavior depending on their movement state. In particular, elephants avoided costly areas when moving at fast speeds, but tended to show less strong preferences, or even

switch them, when moving slowly. Despite this, the large majority of the individuals still avoided such costly areas in all movement states.

Discussion

We assessed the habitat preferences for 155 elephants from GPS recordings spanning around 21 years in the Samburu region in Kenya. Our analysis revealed that almost all elephants strongly avoided areas characterized by high movement costs, as assessed by energy landscapes, strongly supporting and further generalizing the conclusions of (Wall et al., 2006). Conversely, elephants exhibited a preference for areas of high productivity, which is in line with previous results (e.g. Chibeya et al., 2021; Wall et al., 2013). However, the individual preferences for the other predictors, namely elevation and distances to water and human settlements, varied greatly among elephants. Importantly, our analysis does not negate the significance of predictors beyond the energy landscape and habitat productivity in influencing the habitat usage of elephants. Rather, it highlights that the responses of individual elephants to these predictors are contingent upon the prevailing environmental conditions, such as seasonal variations, as well as their personal preferences. Nevertheless, energy landscapes, which are based on fundamental biomechanical and physical principles, almost unequivocally explained preferences of elephants. Overall, our results highlight that the energy landscape, together with habitat productivity, are key drivers of habitat preferences for elephants and that they affect habitat usage consistently across individuals.

Contrary to previous studies that used elevation, but not energy landscapes, our approach permits to model explicitly a plausible causal relationship between terrain and movement preferences. Indeed, species do not respond directly to elevation, but rather to other environmental factors regulated by elevation, most notably temperature and precipitation (Austin, 2002; Hof et al., 2012). This was the rationale commonly used in previous studies that used elevation as a proxy for unobserved environmental factors. The concept of energy landscapes is not new (Shepard et al., 2013), not even for elephants (Wall

et al., 2006). However, software to calculate them for terrestrial animals was not available until recently (Berti et al., 2022), which limited the application of energy landscapes as a defining factor in studies of behavioral ecology in complex ecosystem landscapes.

Inclusion of elevation as a predictor variable may also serve as a proxy, in addition to energy costs, to other physical attributes of the terrain, such as slope or terrain ruggedness. This is because areas at higher elevations may possess steeper slopes and uneven terrains, which can significantly influence the habitat selection of elephants. However, this is not always the case and we suggest that using energy landscapes, which joins biomechanical models with the physical aspect of the terrain, is a better approach due to the clear ecological assumptions and direct causal relationship that can be drawn between landscape and preferences. Our results showing that elephants consistently respond to energy landscapes, but not elevation, seem to confirm this assumption, i.e. that energy costs of transport are not always directly correlated with elevation. Importantly, we could not completely remove elevation from our statistical model, as other covariates that were not included in our models and that covary with elevation may also drive elephant preferences, most notably temperature and precipitation. If other environmental factors that covary with elevation and that have an effect on preferences of elephants are not considered, then the coefficient estimates of the statistical model would be biased due to the hidden confounding effect of elevation (Cinelli et al., 2020). Future studies should therefore ideally measure and include all potential covariates that are correlated and regulated by elevation, e.g. temperature and precipitation, and that may influence animal habitat preferences before omitting elevation from statistical models.

It was rather surprising to find that elephants consistently avoided high energy landscapes and preferred highly productive areas, but did not show such clear patterns for the distance to water and human settlements. Previous studies that analyzed shorter time spans and that included seasonal variations found that precipitation patterns, and thus water availability, is an important driver of elephant preferences (Chibeya et al., 2021; Sach et al., 2019; Taher et al., 2021; Talukdar et al., 2020; Wall et al., 2013). We acknowledge that discrepancies between these observations and our results may be due to the large spatial

and temporal scale of our analysis, which focused on an area of around 40,000 km² for a 21 years timespan, omitting fine-scale temporal variability such as seasonality in precipitation. For example, (Bastille-Rousseau et al., 2020) found that elephants prefer to stay close to permanent water bodies and human settlements during the dry season, but not in the wet season, when water can be found also in temporary basins. In addition, our analysis included distance to the closest human settlement as a proxy for human disturbance, but did not consider other societal aspects that may play an important role in determining the behavior of elephants. For instance, local communities show a large variability in the degree they are willing to accept wild elephants (Vogel et al., 2023), which can influence the risk perceived by the elephants and their movement behavior (Vogel et al., 2020). Moreover, habitat preferences can be heterogeneous among elephant individuals (Bastille-Rousseau et al., 2020; Bastille-Rousseau & Wittemyer, 2022), which may further explain potential discrepancies between our results and previous studies. For instance, during the reproductive period bulls behave quite differently from their normal behavior (Taylor et al., 2020), while females with offspring may choose different habitats depending on the needs of the whole herd, rather than individual preferences. All together, these considerations suggest future avenues of research to better comprehend the observed variability in preference among individuals and to disentangle further the causal relationships between environmental factors and the utilization of the landscape by elephants. Enerscape modeling allowed us to formulate hypotheses of elephant movement decisions and habitat use in a given landscape, in this case Samburu, at a given time. Taken forward, these hypotheses can be tested, using more fine grained data, e.g. higher resolution GPS fixes coupled with better resolved terrain slopes and environmental predictors measured concurrently to the telemetry data.

A particularly promising future direction is to join the energy cost of transport with resource availability, which would allow modeling a more holistic energy landscape (Shepard et al., 2013). Here, we model energy landscapes simply as the energetic cost of transport, as software to achieve this was readily available (Berti et al., 2022). However, as we found that elephants strongly prefer highly productive

habitats, it seems natural to include resource availability in future energy landscape models. This requires a model tailored specifically to elephants and that could clarify important details of habitat use and preferences of elephants. Notably, such implementation could account for seasonality in resource availability and define variable energy landscapes that change through time (Masello et al., 2017), improving the realism of our approach and its applicability to specific conservation issues (Bastille-Rousseau & Wittemyer, 2021). In addition, as the travel speed of elephants is limited by high temperatures (Dyer et al., 2023), this approach could also explicitly model how habitat usage of elephants may change under climate change, with potentially unique insights for conservation.

We highlighted the importance of energy landscapes to explain the habitat preferences of elephants. We expect this to be particularly relevant also to predict how elephants use the landscape both within their current distribution as well as for planning dispersal corridors for conservation and restoration planning. As the current distribution of both the African elephants (*Loxodonta africana* and *L. cyclotis*) and the smaller Asian elephant (*Elephas maximus*) is fragmented (IUCN, 2022), we expect that in many ecosystems movement across isolated patches will be strongly influenced by energy landscapes. For example, corridors have been proposed to restore the fragmented distribution of elephants in Sumatra (Kuswanda et al., 2022); our study, and energy landscapes in general, could help planning such corridors in areas that experience a significant energy landscape gradient. In addition to practical applications, our findings are also relevant for theoretical studies: as the energy landscape increases disproportionately with body mass (Pontzer, 2016), larger animals should be particularly affected by energy landscapes. This has implications for dispersal of large animals and megafauna, which disproportionately enhance biotic connectivity and biodiversity (Berti & Svenning, 2020; Malhi et al., 2016), that should be further explored. In this context, our results can also help paleoecological studies to better understand biodiversity patterns of living and extinct elephants, e.g. by delineating with higher accuracy their potential past distributions.

In conclusion, our findings emphasize the importance of including energy landscapes as a key driver of habitat preferences for elephants and, potentially, all terrestrial animals, especially megafauna. Using energy landscapes, instead of elevation, is theoretically supported by physical and biomechanical principles and has clearer ecological assumptions. This, we believe, is a strong argument for drawing a direct causal association between energy landscapes and preferences, as supported by our results. Our study should not be considered as a definitive answer to explain animal preferences, but as a path towards a more mechanistic understanding of why animals prefer certain habitats. With changing climate most ecological parameters will change and for large animals even the metabolic costs of movement can change because of overheating (Dyer et al., 2023). As we get better at collecting more fine-grained data on ecological parameters, we need to develop more sophisticated models for their analysis, as we have shown here. Hopefully, this can provide a better understanding on how animals use the landscape and help conservation and restoration efforts in planning dispersal corridors to enhance recovery of isolated populations.

References

- Asner, G. P., Vaughn, N., Smit, I. P. J., & Levick, S. (2016). Ecosystem-scale effects of megafauna in African savannas. *Ecography*, 39(2), 240–252. <https://doi.org/10.1111/ecog.01640>
- Austin, M. P. (2002). Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. *Ecological Modelling*, 157(2), 101–118. [https://doi.org/10.1016/S0304-3800\(02\)00205-3](https://doi.org/10.1016/S0304-3800(02)00205-3)
- Bastille-Rousseau, G., Wall, J., Douglas-Hamilton, I., Lesowapir, B., Loloju, B., Mwangi, N., & Wittemyer, G. (2020). Landscape-scale habitat response of African elephants shows strong selection for foraging opportunities in a human dominated ecosystem. *Ecography*, 43(1), 149–160. <https://doi.org/10.1111/ecog.04240>
- Bastille-Rousseau, G., & Wittemyer, G. (2021). Characterizing the landscape of movement to identify

- critical wildlife habitat and corridors. *Conservation Biology*, 35(1), 346–359.
<https://doi.org/10.1111/cobi.13519>
- Bastille-Rousseau, G., & Wittemyer, G. (2022). Simple metrics to characterize inter-individual and temporal variation in habitat selection behaviour. *Journal of Animal Ecology*, 91(8), 1693–1706.
<https://doi.org/10.1111/1365-2656.13738>
- Berti, E., Davoli, M., Buitenwerf, R., Dyer, A., Hansen, O. L. P., Hirt, M., Svenning, J.-C., Terlau, J. F., Brose, U., & Vollrath, F. (2022). The r package enerscape: A general energy landscape framework for terrestrial movement ecology. *Methods in Ecology and Evolution*, 13(1), 60–67.
<https://doi.org/10.1111/2041-210X.13734>
- Berti, E., & Svenning, J.-C. (2020). Megafauna extinctions have reduced biotic connectivity worldwide. *Global Ecology and Biogeography*, 29(12), 2131–2142. <https://doi.org/10.1111/geb.13182>
- Cantalapiedra, J. L., Sanisidro, Ó., Zhang, H., Alberdi, M. T., Prado, J. L., Blanco, F., & Saarinen, J. (2021). The rise and fall of proboscidean ecological diversity. *Nature Ecology & Evolution*, 5(9), Article 9. <https://doi.org/10.1038/s41559-021-01498-w>
- Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A Probabilistic Programming Language. *Journal of Statistical Software*, 76(1). <https://doi.org/10.18637/jss.v076.i01>
- Chase, M. J., Schlossberg, S., Griffin, C. R., Bouché, P. J. C., Djene, S. W., Elkan, P. W., Ferreira, S., Grossman, F., Kohi, E. M., Landen, K., Omondi, P., Peltier, A., Selier, S. A. J., & Sutcliffe, R. (2016). Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ*, 4, e2354. <https://doi.org/10.7717/peerj.2354>
- Chibeya, D., Wood, H., Cousins, S., Carter, K., Nyirenda, M. A., & Maseka, H. (2021). How do African elephants utilize the landscape during wet season? A habitat connectivity analysis for Sioma Ngwezi landscape in Zambia. *Ecology and Evolution*, 11(21), 14916–14931.
<https://doi.org/10.1002/ece3.8177>
- Choudhury, A. (1999). Status and conservation of the Asian Elephant *Elephas maximus* in north-eastern

India. *Mammal Review*, 29(3), 141–174. <https://doi.org/10.1046/j.1365-2907.1999.00045.x>

Cinelli, C., Forney, A., & Pearl, J. (2020). A Crash Course in Good and Bad Controls. *SSRN Electronic Journal*. <https://doi.org/10.2139/ssrn.3689437>

Cohen, J. (2013). *Statistical Power Analysis for the Behavioral Sciences*. Routledge.

Doughty, C. E., Wolf, A., & Malhi, Y. (2013). The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. *Nature Geoscience*, 6(9), Article 9. <https://doi.org/10.1038/ngeo1895>

Dyer, A., Brose, U., Berti, E., Rosenbaum, B., & Hirt, M. R. (2023). The travel speeds of large animals are limited by their heat-dissipation capacities. *PLOS Biology*, 21(4), e3001820. <https://doi.org/10.1371/journal.pbio.3001820>

Gravel, D., Massol, F., & Leibold, M. A. (2016). Stability and complexity in model meta-ecosystems. *Nature Communications*, 7(1), Article 1. <https://doi.org/10.1038/ncomms12457>

Guimarães, P. R., Galetti, M., & Jordano, P. (2008). Seed Dispersal Anachronisms: Rethinking the Fruits Extinct Megafauna Ate. *PLOS ONE*, 3(3), e1745. <https://doi.org/10.1371/journal.pone.0001745>

Guo, J., Gabry, J., Goodrich, B., Weber, S., Lee, D., Sakrejda, K., Martin, M., University, T. of C., Sklyar (R/cxxfunplus.R), O., Team (R/pairs.R, T. R. C., R/dynGet.R), Oehlschlaegel-Akiyoshi (R/pairs.R), J., Maddock (gamma.hpp), J., Bristow (gamma.hpp), P., Agrawal (gamma.hpp), N., Kormanyos (gamma.hpp), C., & Steve, B. (2020). *rstan: R Interface to Stan* (2.21.2). <https://CRAN.R-project.org/package=rstan>

Hirt, M. R., Barnes, A. D., Gentile, A., Pollock, L. J., Rosenbaum, B., Thuiller, W., Tucker, M. A., & Brose, U. (2021). Environmental and anthropogenic constraints on animal space use drive extinction risk worldwide. *Ecology Letters*, 24(12), 2576–2585. <https://doi.org/10.1111/ele.13872>

Hof, A. R., Jansson, R., & Nilsson, C. (2012). The usefulness of elevation as a predictor variable in species distribution modelling. *Ecological Modelling*, 246, 86–90. <https://doi.org/10.1016/j.ecolmodel.2012.07.028>

IUCN. (2022). *The IUCN Red List of Threatened Species*. Version 2022-2. <https://www.iucnredlist.org>.

Accessed on 28/02/2023.

- Jonsen, I. D., Flemming, J. M., & Myers, R. A. (2005). Robust State–Space Modeling of Animal Movement Data. *Ecology*, 86(11), 2874–2880. <https://doi.org/10.1890/04-1852>
- Karels, D. L., McCown, J. W., Scheick, B. K., Kerk, M. van de, Bolker, B. M., Oli, M. K., Karels, D. L., McCown, J. W., Scheick, B. K., Kerk, M. van de, Bolker, B. M., & Oli, M. K. (2019). Incorporating movement patterns to discern habitat selection: Black bears as a case study. *Wildlife Research*, 46(1), 76–88. <https://doi.org/10.1071/WR17151>
- Kelt, D. A., & Van Vuren, D. H. (2001). The Ecology and Macroecology of Mammalian Home Range Area. *The American Naturalist*, 157(6), 637–645. <https://doi.org/10.1086/320621>
- Kuswanda, W., Garsetiasih, R., Gunawan, H., Situmorang, R. O. P., Hutapea, F. J., Kwatrina, R. T., Karlina, E., Atmoko, T., Zahrah, M., Takandjandji, M., & Gunaryadi, D. (2022). Can Humans and Elephants Coexist? A Review of the Conflict on Sumatra Island, Indonesia. *Diversity*, 14(6), Article 6. <https://doi.org/10.3390/d14060420>
- Laws, R. M., & Parker, I. S. C. (1968). Recent studies on elephant populations in East Africa. *Symp. Zool. Soc. Lond.*, 21, 319–359.
- Malhi, Y., Doughty, C. E., Galetti, M., Smith, F. A., Svenning, J.-C., & Terborgh, J. W. (2016). Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences*, 113(4), 838–846. <https://doi.org/10.1073/pnas.1502540113>
- Marconcini, M., Metz-Marconcini, A., Üreyen, S., Palacios-Lopez, D., Hanke, W., Bachofer, F., Zeidler, J., Esch, T., Gorelick, N., Kakarla, A., Paganini, M., & Strano, E. (2020). Outlining where humans live, the World Settlement Footprint 2015. *Scientific Data*, 7(1), Article 1. <https://doi.org/10.1038/s41597-020-00580-5>
- Martin, P. S., & Klein, R. G. (1989). *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press.
- Masello, J. F., Kato, A., Sommerfeld, J., Mattern, T., & Quillfeldt, P. (2017). How animals distribute themselves in space: Variable energy landscapes. *Frontiers in Zoology*, 14(1), 33.

<https://doi.org/10.1186/s12983-017-0219-8>

McClintock, B. T., Langrock, R., Gimenez, O., Cam, E., Borchers, D. L., Glennie, R., & Patterson, T. A.

(2020). Uncovering ecological state dynamics with hidden Markov models. *Ecology Letters*,

23(12), 1878–1903. <https://doi.org/10.1111/ele.13610>

Michelot, T., Langrock, R., & Patterson, T. A. (2016). moveHMM: An R package for the statistical

modelling of animal movement data using hidden Markov models. *Methods in Ecology and*

Evolution, 7(11), 1308–1315. <https://doi.org/10.1111/2041-210X.12578>

NASA JPL. (2020). *NASADEM Merged DEM Global 1 arc second V001* [Data set]. NASA EOSDIS

Land Processes DAAC.

https://doi.org/10.5067/MEASURES/NASADEM/NASADEM_HGT.001

Ngene, S. M., Skidmore, A. K., Van Gils, H., Douglas-Hamilton, I., & Omondi, P. (2009). Elephant

distribution around a volcanic shield dominated by a mosaic of forest and savanna (Marsabit,

Kenya). *African Journal of Ecology*, 47(2), 234–245. <https://doi.org/10.1111/j.1365->

2028.2008.01018.x

Pontzer, H. (2016). A unified theory for the energy cost of legged locomotion. *Biology Letters*, 12(2),

20150935. <https://doi.org/10.1098/rsbl.2015.0935>

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley,

G. I. H., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter, L. E., Sandom, C. J.,

Terborgh, J., & Valkenburgh, B. V. (2015). Collapse of the world's largest herbivores. *Science*

Advances, 1(4), e1400103. <https://doi.org/10.1126/sciadv.1400103>

Sach, F., Dierenfeld, E. S., Langley-Evans, S. C., Watts, M. J., & Yon, L. (2019). African savanna

elephants (*Loxodonta africana*) as an example of a herbivore making movement choices based on

nutritional needs. *PeerJ*, 7, e6260. <https://doi.org/10.7717/peerj.6260>

Sandom, C., Faurby, S., Sandel, B., & Svenning, J.-C. (2014). Global late Quaternary megafauna

extinctions linked to humans, not climate change. *Proceedings of the Royal Society B: Biological*

Sciences, 281(1787), 20133254. <https://doi.org/10.1098/rspb.2013.3254>

482 Shepard, E. L. C., Wilson, R. P., Rees, W. G., Grundy, E., Lambertucci, S. A., & Vosper, S. B. (2013).
 483 Energy Landscapes Shape Animal Movement Ecology. *The American Naturalist*, 182(3), 298–
 484 312. <https://doi.org/10.1086/671257>

485 Shoshani, J. (1998). Understanding proboscidean evolution: A formidable task. *Trends in Ecology &*
 486 *Evolution*, 13(12), 480–487. [https://doi.org/10.1016/S0169-5347\(98\)01491-8](https://doi.org/10.1016/S0169-5347(98)01491-8)

487 Taher, T. M., Lihan, T., Arifin, N. A. T., Khodri, N. F., Mustapha, M. A., Patah, P. A., Razali, S. H. A., &
 488 Nor, S. M. (2021). Characteristic of habitat suitability for the Asian elephant in the fragmented
 489 Ulu Jelai Forest Reserve, Peninsular Malaysia. *Tropical Ecology*, 62(3), 347–358.
 490 <https://doi.org/10.1007/s42965-021-00154-5>

491 Talukdar, N. R., Choudhury, P., Ahmad, F., Ahmed, R., Ahmad, F., & Al-Razi, H. (2020). Habitat
 492 suitability of the Asiatic elephant in the trans-boundary Patharia Hills Reserve Forest, northeast
 493 India. *Modeling Earth Systems and Environment*, 6(3), 1951–1961.
 494 <https://doi.org/10.1007/s40808-020-00805-x>

495 Taylor, L. A., Vollrath, F., Lambert, B., Lunn, D., Douglas-Hamilton, I., & Wittemyer, G. (2020).
 496 Movement reveals reproductive tactics in male elephants. *Journal of Animal Ecology*, 89(1), 57–
 497 67. <https://doi.org/10.1111/1365-2656.13035>

498 Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and
 499 conservation. *Movement Ecology*, 2(1), 4. <https://doi.org/10.1186/2051-3933-2-4>

500 Veldhuis, M. P., Ritchie, M. E., Ogutu, J. O., Morrison, T. A., Beale, C. M., Estes, A. B., Mwakilema,
 501 W., Ojwang, G. O., Parr, C. L., Probert, J., Wargute, P. W., Hopcraft, J. G. C., & Olff, H. (2019).
 502 Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. *Science*, 363(6434),
 503 1424–1428. <https://doi.org/10.1126/science.aav0564>

504 Vogel, S. M., Lambert, B., Songhurst, A. C., McCulloch, G. P., Stronza, A. L., & Coulson, T. (2020).
 505 Exploring movement decisions: Can Bayesian movement-state models explain crop consumption
 506 behaviour in elephants (*Loxodonta africana*)? *Journal of Animal Ecology*, 89(4), 1055–1068.
 507 <https://doi.org/10.1111/1365-2656.13177>

508 Vogel, S. M., Vasudev, D., Ogutu, J. O., Taek, P., Berti, E., Goswami, V. R., Kaelo, M., Buitenwerf, R.,
 509 Munk, M., Li, W., Wall, J., Chala, D., Amoke, I., Odingo, A., & Svenning, J.-C. (2023).
 510 Identifying sustainable coexistence potential by integrating willingness-to-coexist with habitat
 511 suitability assessments. *Biological Conservation*, 279, 109935.
 512 <https://doi.org/10.1016/j.biocon.2023.109935>
 513 Wall, J., Douglas-Hamilton, I., & Vollrath, F. (2006). Elephants avoid costly mountaineering. *Current*
 514 *Biology*, 16(14), R527–R529. <https://doi.org/10.1016/j.cub.2006.06.049>
 515 Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., Blake, S., Strindberg, S., Henley, M., Vollrath, F.,
 516 Maisels, F., Ferwerda, J., & Douglas-Hamilton, I. (2021). Human footprint and protected areas
 517 shape elephant range across Africa. *Current Biology*, 31(11), 2437-2445.e4.
 518 <https://doi.org/10.1016/j.cub.2021.03.042>
 519 Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., & Douglas-Hamilton, I. (2013). Characterizing
 520 properties and drivers of long distance movements by elephants (*Loxodonta africana*) in the
 521 Gourma, Mali. *Biological Conservation*, 157, 60–68.
 522 <https://doi.org/10.1016/j.biocon.2012.07.019>
 523 Wilson, D. S. (1992). Complex Interactions in Metacommunities, with Implications for Biodiversity and
 524 Higher Levels of Selection. *Ecology*, 73(6), 1984–2000. <https://doi.org/10.2307/1941449>
 525 Zanaga, D., Van De Kerchove, R., De Keersmaecker, W., Souverijns, N., Brockmann, C., Quast, R.,
 526 Wevers, J., Grosu, A., Paccini, A., Vergnaud, S., Cartus, O., Santoro, M., Fritz, S., Georgieva, I.,
 527 Lesiv, M., Carter, S., Herold, M., Li, L., Tsendbazar, N.-E., ... Arino, O. (2021). *ESA*
 528 *WorldCover 10 m 2020 v100* [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.5571936>
 529 Zucchini, W., & MacDonald, I. L. (2009). *Hidden Markov Models for Time Series: An Introduction*
 530 *Using R*. Chapman and Hall/CRC. <https://doi.org/10.1201/9781420010893>

Figure captions

Figure 1. The workflow used in this study to assess the habitat preferences of elephants. GPS fixes were obtained from Save The Elephant foundation (<https://www.savetheelephants.org/>). Remote sensing layers were obtained using Google Earth Engine (<https://earthengine.google.com/>).

Figure 2. The study region in Northern Kenya (Isiolo, Laikipia, Marsabit, Meru, and Samburu counties). Terrain colors show the elevation of the terrain. The blue shade is the minimum convex polygon containing all GPS records for the elephants. GPS data was made available by Save The Elephants foundation.

Figure 3. The directed acyclic graph depicting the causal relationships between covariates (blue rectangles) and the response (green rectangle). Arrows show the hypothesized causal relationship.

Figure 4. Coefficient estimates from step-selection function. Horizontal bars show the 95% credible interval of elephant preferences. Each bar represents one elephant individual. Colors show the effect size of the estimate (Cohen's d). Interpretation of effect size follows Cohen (2013).

Figure 5. Coefficient estimates for the predictors included in the Bayesian logistic regression for the three movement states: resting, foraging, and dispersing. Colors show the effect size, obtained as Cohen's d; interpretation of effect size follows Cohen (2013).