

Energy landscapes direct the movement preferences of elephants

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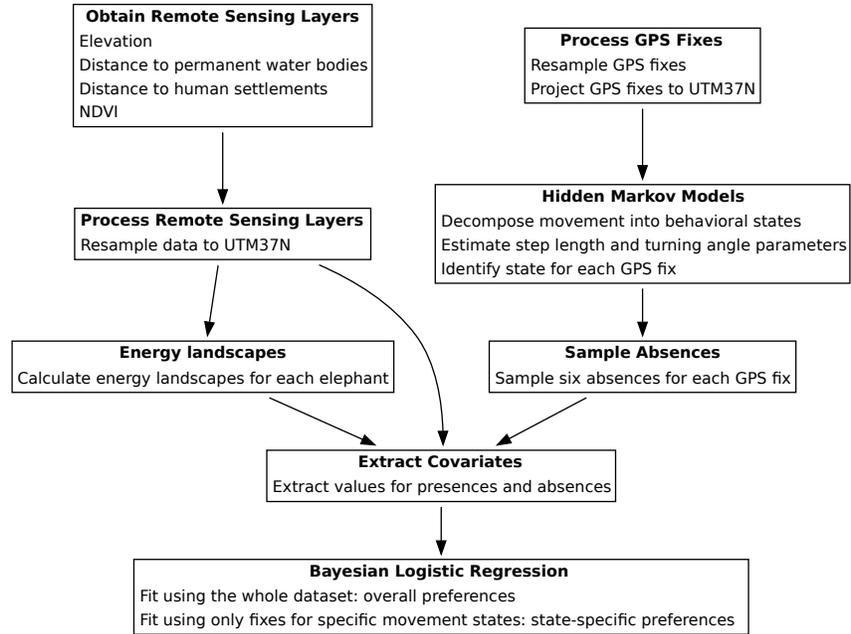
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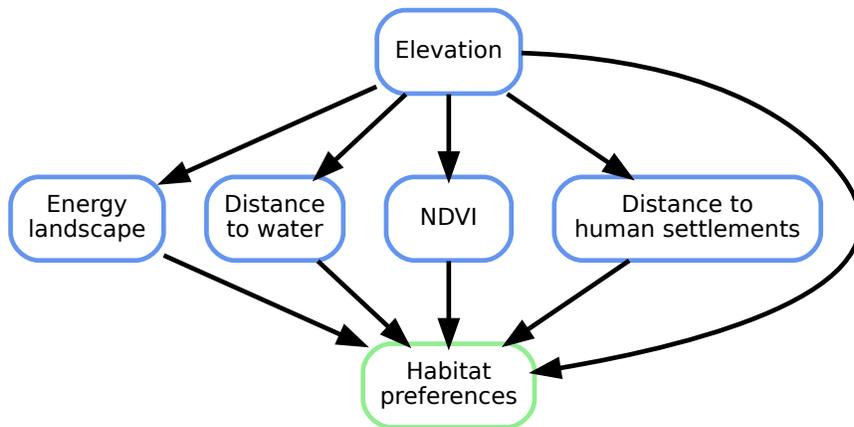
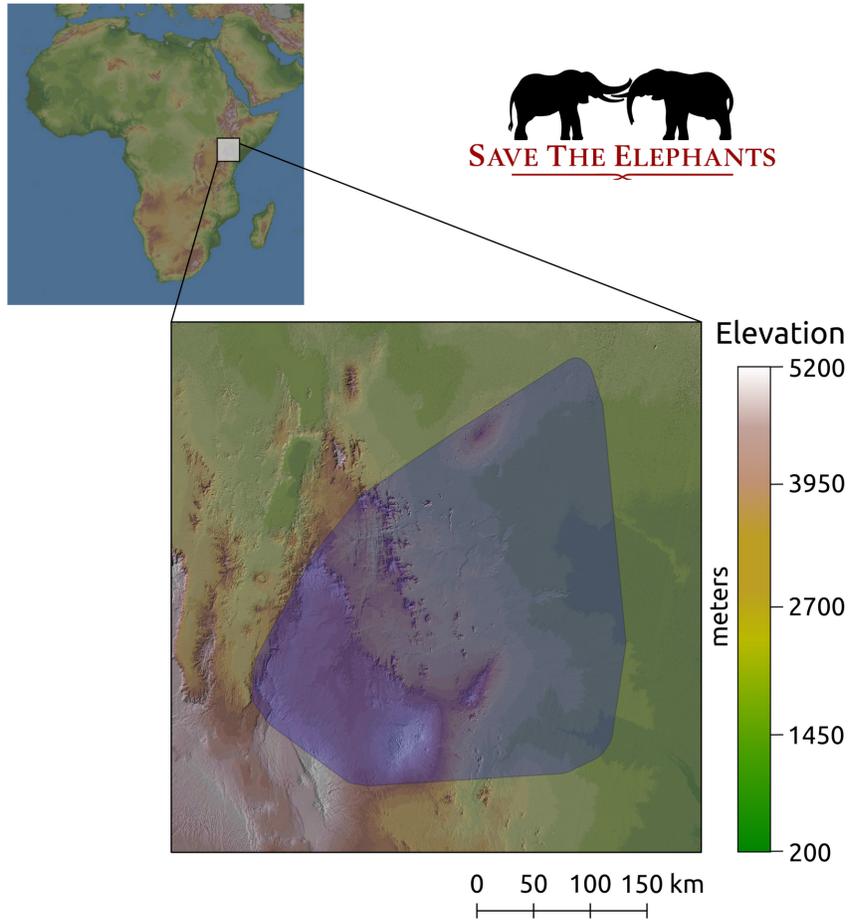
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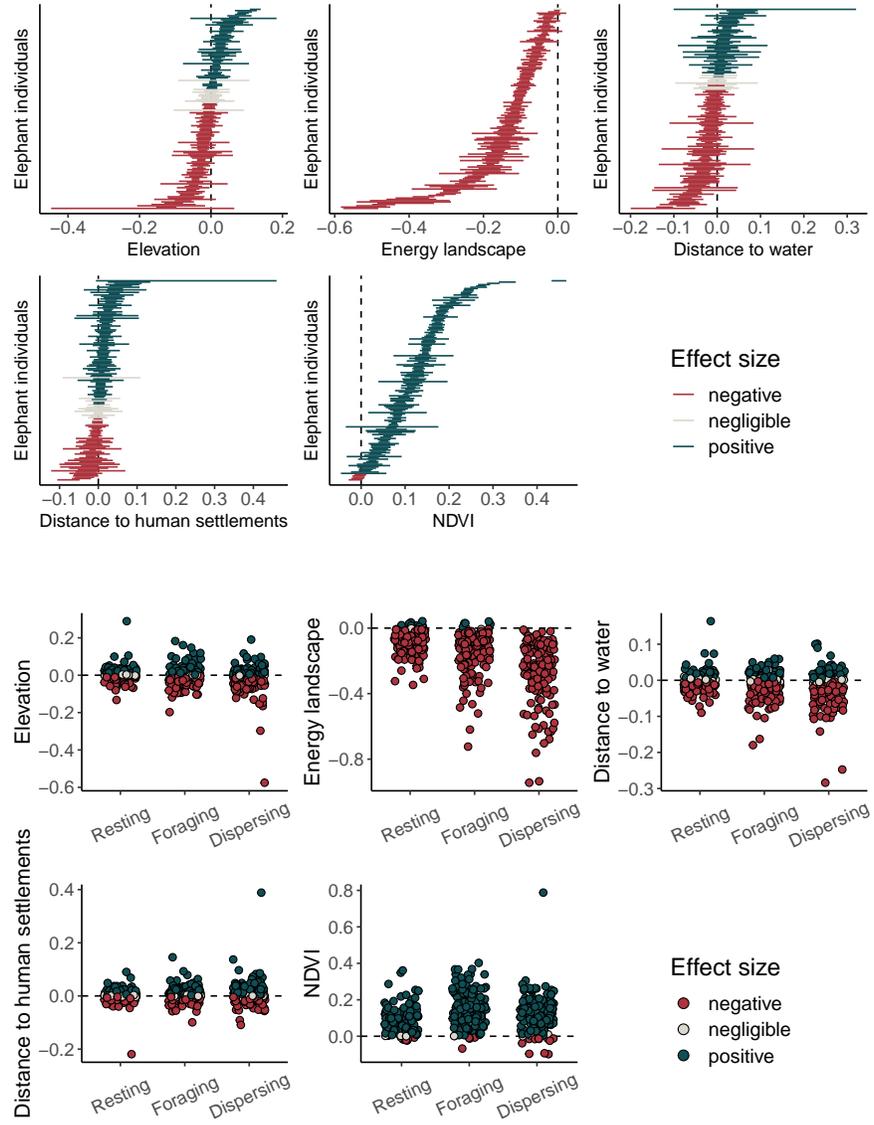
May 10, 2023

Abstract

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







1 Energy landscapes direct the movement preferences of 2 elephants

3 Keywords

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

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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

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

26 Introduction

27 Animal movement maintains important ecosystem functions, such as seed and nutrient dispersal (Doughty
28 et al., 2013; Guimarães et al., 2008), promotes ecosystem stability (Gravel et al., 2016), and fosters
29 biodiversity (Wilson, 1992). The most important players for these processes are megafauna, i.e. animals \geq
30 45 kg (Martin & Klein, 1989), which have large homeranges (Kelt & Van Vuren, 2001) and can thus
31 disperse nutrients, seeds, and energy across large areas (Doughty et al., 2013; Guimarães et al., 2008;
32 Malhi et al., 2016). Megafauna were once widespread globally before human pressure triggered their
33 extinction and restricted their distribution (Sandom et al., 2014) and homeranges (Hirt et al., 2021), with
34 severe effects on biotic connectivity (Berti & Svenning, 2020). In particular, of the 48 megaherbivores (\geq
35 1,000 kg) present at the beginning of the Late Pleistocene (starting around 120,000 years ago), only 8
36 have survived until today, almost all at risk of extinction and with decreasing distribution ranges (IUCN,
37 2022). In the light of a new ongoing mass extinction and pressing challenges due to climate change, it is
38 imperative to conserve these remaining animals and their ecosystems.

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

44 Africa, Eurasia, and the Americas (Shoshani, 1998), and had unique ecological roles, such as landscape
45 engineering and seed dispersal (Guimarães et al., 2008; Malhi et al., 2016). The African elephant, once
46 spread across all of Africa, has today a fragmented distribution, with wild populations often constrained
47 to protected areas (Wall et al., 2021). Moreover, wild elephant populations show overall decreasing trends
48 in numbers, mostly due to poaching and increased human land-use (Chase et al., 2016; Ripple et al.,
49 2015; Veldhuis et al., 2019). Therefore, fully understanding the habitat requirements of elephants is key
50 to optimize conservation and restoration efforts to protect currently threatened elephant populations as
51 well as to better understand how extinct Proboscideans, and potentially megafauna in general, would have
52 used and shaped their ecosystems.

53 Recent studies have begun to outline, define, and understand the habitat preferences of extant elephants
54 and describe the drivers of their movement behavior patterns. Elevation is commonly used as a predictor
55 for habitat preferences of both *L. africana* and *E. maximus* (Asner et al., 2016; Chibeya et al., 2021;
56 Ngene et al., 2009; Talukdar et al., 2020), usually explaining a large proportion of the elephants'
57 preferences. However, as other factors covary with elevation, it is not clear whether elevation itself
58 influences elephants' movement rather than being a convenient proxy to capture other abiotic and biotic
59 processes. For instance, vegetation structure and water availability as well as human presence and density
60 all vary with elevation, which may thus shape movement behavior only indirectly, e.g. by affecting soil
61 and water dynamics, vegetation structure, and anthropogenic pressure (Asner et al., 2016; Chibeya et al.,
62 2021; Ngene et al., 2009; Taher et al., 2021; Talukdar et al., 2020). This confusion partly hinders efforts
63 to fully comprehend the habitat preferences of elephants, e.g. by masking the real causal associations
64 between the environment and habitat preferences with spurious correlations. Moreover, a number of
65 observations suggest that elephants may not be as much limited by elevation as commonly thought, with
66 some recorded cases of elephants climbing ~2,000 meters in elevation (Choudhury, 1999; Kuswanda et
67 al., 2022).

68 In this study, we used a recently published method, *enerscape* (Berti et al., 2022), in order to estimate the
69 energetic costs that an animal has to sustain in order to travel across a topographically explicit landscape
70 (Shepard et al., 2013; Wall et al., 2006). Specifically, we used *enerscape* to investigate how energy costs
71 of travel influence the movement decisions and thus habitat preferences of 155 elephants in the Samburu
72 area of Northern Kenya. This approach takes into account both the body mass of the animal and the slope
73 of the terrain traversed (Berti et al., 2022; Pontzer, 2016) and thus captures the mechanistic cause of
74 habitat preferences due to cost of locomotion better than simply using elevation (see also Wall et al.,
75 2006). In particular, we tested the hypothesis that the energy landscape is a key driver, perhaps the most
76 important direct cause, of habitat preferences for the elephants, with elevation only indirectly affecting
77 animals' movement by influencing energy landscapes as well as other environmental factors, such as
78 vegetation productivity and water availability. We achieved this by analyzing GPS telemetry data using a
79 step-selection function in order to understand which environmental factors influenced the habitat
80 preferences of elephants. By explicitly testing these causal relationships, our study aims to elucidate the
81 direct drivers of elephants' preferences, providing a better understanding of the mechanisms determining
82 habitat use. This, in turn, will help conservation efforts to plan more informed mitigation and restoration
83 strategies.

84 Materials and Methods

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

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

96 GPS Collar Data

97 GPS data for 172 elephants spanning the period 1998-2020 was made available by Save The Elephant
98 foundation (STE). STE is a non-profit organization that promotes protection of elephants and related
99 ecological research with, among others, a multi-decades GPS radio tracking project in Kenya.
100 Specifically, we obtained telemetry data for the Samburu region in Northern Kenya (36 - 39°E, -0.36 -
101 2.81°N; Fig. 2). This area has a large elevational gradient (from ~200 to ~5,000 meters a.s.l.), with
102 rainfall mostly concentrated in two periods (April-June and October-December) and strongly influenced
103 by the presence of mountain peaks. This variation in altitude and rainfall across the landscape is
104 associated with changes in land-use: forested areas can be found at high elevations, whereas at lower
105 elevations the landscape is dominated by savannah, with interspersed agricultural and farming areas. GPS
106 data was already processed by STE to assure quality of the records, i.e. GPS fixes that had inaccurate
107 longitude and latitude coordinates were already removed. To make sure that subsequent GPS fixes were
108 separated by an analogous span of time, we resampled the original GPS data. Specifically, we derived the
109 time interval between all consecutive fixes and calculated its 5% (Q_{low}) and 95% (Q_{high}) quantiles. Fixes
110 that were sampled closer than $0.9 * Q_{low}$ from the previous one were removed. When a fix was separated
111 by more than $1.1 * Q_{high}$ from the previous, we kept it, but considered it and subsequent fixes as part of
112 another, separate track for the same animal. We derived these criteria by trying several thresholds and
113 found that these values kept consecutive fixes within an acceptable accuracy of time intervals while
114 minimizing the number of disconnected tracks. This step was necessary to make sure that the movement
115 was modeled consistently across the whole time span of the recordings, e.g. the distance traveled between

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

119 Remote Sensing Data and Energy Landscapes

120 We calculated the distance to human settlements using the World Settlement Footprint product
121 (Marconcini et al., 2020) and the distance from permanent water bodies using the ESA WorldCover
122 product (Zanaga et al., 2021). Both distances were calculated as the great-circle distances with a precision
123 of one meter. A digital elevation model (DEM) for the region of interest was obtained from NASADEM
124 (NASA JPL, 2020). Energy landscapes were computed using the R package *enerscape* (Berti et al.,
125 2022), which calculates the energy cost of travel across the landscape using the body mass of the animal
126 and the slope of the terrain traversed (Pontzer, 2016). Because the cost of locomotion depends on the
127 body mass of animals, we calculated energy landscapes for females and males separately. As GPS collars
128 were mounted only on adult individuals, we assumed a body mass of 2,744 kg for females and of 6,029
129 kg for males, which are typical values for adult individuals (Laws & Parker, 1968).

130 We calculated the Normalized Difference Vegetation Index (NDVI) from the Sentinel-2 Copernicus
131 mission (Harmonized Sentinel-2 MSI, Level-2A;
132 https://www.esa.int/Copernicus/Sentinel-2/Data_products). NDVI, which has values from -1 to 1, is a
133 measure of the relative abundance of chlorophyll and was used here as a proxy for plant productivity. We
134 calculated the median monthly NDVI using all images spanning the whole period of the Sentinel-2
135 mission (from June 2015 to February 2023). First, we removed pixels that were identified as clouds of
136 cirrus formations as well as all images that had less than 20% of their area with clear sky conditions.
137 Then, we split the dataset into calendar months and calculated the median reflectance of the near-infrared
138 (*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

162 and the starting parameters, and assessed the consensus of different runs for the fitted parameters.
163 Specifically, we fitted three sets of models, each set with one, two, or three movement states; notably,
164 (Taylor et al., 2020) found that a three-state model was more accurate in explaining elephant movement
165 patterns. For each set, we then fitted 10 model replicates that differed in their initial parameterization in
166 order to assess the sensitivity of results to initial starting conditions. The starting parameters were
167 randomly drawn from uniform distribution bound to the 10%-90% quantiles of the observed movement
168 values from GPS recordings; for HMMs with more than one state, this range was additionally divided into
169 corresponding intervals. For instance, the three starting parameters for the three states models were
170 sampled from uniform distributions $U(q_{10\%}, q_{40\%})$, $U(q_{40\%}, q_{70\%})$, $U(q_{70\%}, q_{90\%})$, respectively.
171 We then compared HMMs within replicates using AIC and selected the most parsimonious model. We
172 retained only the individuals for which all parsimonious models had the same number of movement
173 states, indicating a fair amount of consensus among HMM runs; four individuals were thus removed from
174 further analyses. We also removed individuals that had likely implausible high values of estimated
175 average distance traveled and that had high variation in the fitted parameter values across different
176 replicates, dropping six individuals from further analyses. We ended up with 155 total individuals that we
177 could use to address our research question (Table S1). From the fitted HMMs, we also assigned to each
178 GPS location the most likely movement state, obtained using the Viterbi algorithm (Zucchini &
179 MacDonald, 2009). HMMs were fitted using the R package moveHMM (Michelot et al., 2016).

180 Step selection function

181 To assess the habitat preferences of elephants, we used a step-selection function approach (SSF). SSFs are
182 particularly suited to analyze our dataset as they take into account the movement pattern of the
183 individuals and the serial structure of GPS data (Thurfjell et al., 2014).
184 SSFs sample absences based on the previous location, the movement state of the animal, and the
185 predictive distribution defined by the parameters of the movement state (Karelus 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 (Karelus 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.

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

218 Results

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

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

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

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

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

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

259 Discussion

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

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

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

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

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

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

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

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

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

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

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531 Figure captions

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

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

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

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

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