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1 **Global hunter-gatherer population densities constrained by influence of**
2 **seasonality on diet composition**

3 **Authors:** Dan Zhu^{1,2*}, Eric D. Galbraith^{3,2,4}, Victoria Reyes-García^{2,4}, Philippe Ciais^{5,6}

4 **Affiliations:**

5 ¹ Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences,
6 Peking University, Beijing, China

7 ² Institut de Ciència i Tecnologia Ambientals (ICTA-UAB), Universitat Autònoma de Barcelona,
8 08193 Barcelona, Spain

9 ³ Department of Earth and Planetary Sciences, McGill University, Montreal, QC H3A 0G4,
10 Canada

11 ⁴ ICREA (Catalan Institution for Research and Advanced Studies), 08010 Barcelona, Spain

12 ⁵ Laboratoire des Sciences du Climat et de l'Environnement, IPSL-LSCE, CEA-CNRS-UVSQ-
13 UPSACLAY, 91191 Gif sur Yvette, France

14 ⁶ Climate and Atmosphere Research Center (CARE-C) The Cyprus Institute 20 Konstantinou
15 Kavafi Street, 2121, Nicosia, Cyprus

16
17 *Correspondence to: zhudan@pku.edu.cn

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Abstract:

The dependence of hunter-gatherers on local net primary production (NPP) to provide food played a major role in shaping long-term human population dynamics. Observations of contemporary hunter-gatherers have shown an overall correlation between population density and annual NPP, but with a thousand-fold variation in population density per unit NPP that remains unexplained. Here we build a process-based hunter-gatherer population model embedded within a global terrestrial biosphere model, which explicitly addresses the extraction of NPP through dynamically-allocated hunting and gathering activities. The emergent results reveal a strong, previously unrecognized effect of seasonality on population density via diet composition, whereby hunter-gatherers consume high fractions of meat in regions where growing seasons are short, leading to greatly reduced population density due to trophic inefficiency. This seasonal carnivory bottleneck largely explains the wide variation in population density per unit NPP, and questions the prevailing usage of annual NPP as the proxy of carrying capacity for ancient humans. Our process-based approach has the potential to greatly refine our understanding of dynamical responses of ancient human populations to past environmental changes.

40 Introduction

41 Hunter-gatherer populations, that subsist on hunting, gathering and fishing, rely intimately on the
42 biotic fabrics of their local environments¹⁻³. Although only a handful of hunter-gatherer
43 populations remain, over 300 societies of contemporary hunter-gatherers have been documented
44 sporadically over the past two centuries¹. Due to the assumed similarities between their lifestyles
45 and those of our foraging ancestors, contemporary hunter-gatherers have provided many insights
46 on our species' past⁴⁻⁸, informing reconstructions of population changes on evolutionary
47 timescales^{5,6}, the timing and rates of global human dispersals^{4,7}, and the drivers behind the origin
48 of agriculture⁸. Yet, these contemporary societies do not provide direct analogues of ancient
49 foragers, as they had more complex technologies⁹ and had experienced interactions with and
50 pressures from neighbouring agricultural and industrial societies^{10,11}, such as acquiring
51 supplemental agricultural food^{2,12} or encountering novel pathogens near the time of
52 documentation, which may have modulated the population density-ecosystem relationships.
53 Thus, many of the observational data may provide distorted views on the pre-existing state,
54 casting doubt on statistical models and demographic parameters that are directly fitted to the
55 contemporary data⁵⁻⁸. Taking full advantage of the insights from contemporary hunter-gatherers
56 requires a mechanistic, process-oriented understanding of how environmental factors influence
57 the distribution and abundance of hunter-gatherer populations.

58 Because hunter-gatherers acquire food directly from their surrounding environment, it has long
59 been thought that their population density should be closely linked to the productivity of their
60 local ecosystems^{1,2}, and numerous studies have used net primary production (NPP) as the main
61 predictor for ancient hunter-gatherer density changes^{4,7,13}. However, although contemporary
62 hunter-gatherer population density is positively correlated with NPP, NPP alone explains less
63 than 30% of the variability of population density (Fig. 1a). The fraction of NPP consumed by
64 hunter-gatherers (Φ_{NPP} , see Methods), which also indicates population density per unit NPP,
65 varies by three orders of magnitude across the recorded groups (Fig. 1b and Supplementary
66 Figure 1e). A portion of this scatter could reflect the confounding historical influences, but it has
67 also been assumed that the edible proportion of primary production differs among biomes².
68 However, our analysis does not show systematic differences in Φ_{NPP} between biome categories,
69 except for a lower Φ_{NPP} in boreal forest and a marginally significantly higher Φ_{NPP} in
70 Mediterranean forest (Fig. 1b and Supplementary Figure 2b). Nor does Φ_{NPP} show a consistent
71 change across the NPP gradient (Supplementary Figure 2c). The wide spread in Φ_{NPP} thus
72 remains unexplained. The weak statistical dependence of population density on NPP has
73 prompted a recourse to other explanatory variables, including biodiversity³, pathogen stress³,
74 precipitation seasonality⁸, climate variability¹⁴, and social complexity-related variables such as

75 food storage-dependence¹⁴. It is however difficult to tease apart the causality among these inter-
76 correlated variables using statistical methods alone.

77 Here we build a mechanistic understanding of hunter-gatherer populations with a global,
78 activity-based process model for which population density is an emergent feature. Our model
79 operates within the framework of an Earth system model (ESM) (Fig. 2). During the past
80 decades, the land components of ESMs have integrated vegetation modules to resolve key
81 processes of biogeochemical cycling of carbon, energy and water¹⁵, and have recently begun to
82 incorporate large mammalian herbivores based on metabolic and demographic equations^{16,17}.
83 Our model directly couples human population dynamics to such a land model¹⁷, simulating
84 human time allocation to hunting versus gathering in response to the interaction between humans
85 and food resources (see Methods). The model uses explicit formulations of daily carbon/energy
86 flows among vegetation, herbivores and humans, the outcome of which determines human
87 reproduction and mortality rates. These fluxes depend on a time allocation scheme with two
88 simple assumptions: first, total foraging time increases or decreases depending on the level of
89 fullness of the previous day, and second, gathering vs. hunting time depends on the relative
90 abundance of plant vs. animal food and on an underlying *a priori* preference for meat. The model
91 is resolved on a daily time-step, thus capturing the seasonal cycle in high detail.

92 93 **Results**

94 ***Modelled global distribution of hunter-gatherers***

95 Simulated steady-state global population density and foraging times under present-day climate
96 are shown in Fig. 3. The model simulates high densities in most regions with high NPP and
97 closely matches the observed relationship of density versus NPP derived from contemporary
98 hunter-gatherer data (Fig. 3b). Simulated foraging times are generally 3.5-5.5 hours per person
99 per day throughout the world, close to the average of available observations from a few hunter-
100 gatherer groups^{2,18,19} (ca. 4 hr. day⁻¹ ind.⁻¹). In the model, slightly more time is spent hunting than
101 gathering in the tropics, whereas most of the foraging time is devoted to hunting at high latitudes
102 (Fig. 3cde).

103 The simulated population density agrees reasonably well with the ethnographic data (Pearson
104 correlation coefficient $r=0.58$, Supplementary Figure 3ab), and there is also a strong correlation
105 between simulated and ethnographically recorded diet compositions, though less of the observed
106 variance is explained ($r=0.40$ for the meat fraction of the diet, Supplementary Figure 3cd).
107 Model-data discrepancies may be partly due to the lack of fishing in the model, which is a major
108 source of food in many coastal societies (Supplementary Figure 1d). In addition, the model treats

109 all plant or animal food equally, thus ignoring the wide variety such as the different energy
110 content, protein richness, and relative abundance of each food item within both broad
111 categories^{2,20-22}. Any bias in the vegetation and herbivore dynamics model¹⁷ could also
112 propagate to the human model, contributing to the model-data mismatch (note that the S2
113 experiment has corrected part of the biases in the vegetation inputs to the FORGE model, see
114 Methods). Furthermore, discrepancies could arise from climate shifts and non-steady state
115 factors given that the model simulates equilibrium densities forced by present-day climate (while
116 the ethnographic records were collected during the past two hundred years¹) whereas some of the
117 populations were under positive growth rate when being studied²³. There are also significant
118 uncertainties in the diet composition data, as the estimation methods for the amounts of gathered,
119 hunted, and fished food are often inconsistent, sometimes measured in different units (weight or
120 calorie) and occasionally based on the ethnographers' impressions², which may further add to the
121 model-data scatter.

122 The modelled global total hunter-gatherer population is 17 million, which is at the high end of
123 the estimates of prehistoric (pre-agriculture) population derived by extrapolating national
124 historical records, which range from 1-20 million²⁴. This can be partly explained by the fact that
125 our model was calibrated with data from contemporary hunter-gatherers, who presumably had
126 more advanced technologies and access to non-local foods than early-Holocene foragers²⁵ (see
127 Supplementary Discussion 2 for the test runs regarding the technology-dependent foraging
128 efficiency parameter). Geographical differences also contribute to our estimate being higher than
129 previous upscalings of contemporary hunter-gatherer populations, which include regression
130 models (10~12 million, refs.^{3,26}) and a proportional projection method (7 million, ref.¹). For the
131 former, the difference is primarily attributable to a higher density in Africa and southern Asia in
132 our model (Supplementary Figure 4), where the populations were suppressed in ref.³ due to a
133 high pathogen stress as a predictor in their regression (see Supplementary Discussion 1 for more
134 discussion about pathogen stress). For the latter, we find that the global estimate with the same
135 projection method but a different upscaling biome map ranges from 10 to 17 million, contingent
136 on how an average population density is calculated for each biome (see Supplementary
137 Discussion 3). Therefore, we consider our result of 17 million, simulated by a process-based
138 model, to be a reasonable, independent estimate of potential global hunter-gatherer population
139 size under modern climate with advanced foraging technology, assuming foraging as the only
140 subsistence type.

Linkage among seasonality, diet composition and population density

As in the observations, simulated Φ_{NPP} (fraction of NPP consumed by hunter-gatherers) displays a huge spatial variation with a thousand-fold range (Fig. 4b). The spatial distribution of Φ_{NPP} follows an inverse relationship with the meat fraction of the diet (compare Figs. 4a and 4b). The negative correlation is clear in the scatter plot, both for grid cells where the observational data are located (Fig. 4d) and for all populated grid cells in the model (Supplementary Figure 5), showing a drop of Φ_{NPP} by almost an order of magnitude as meat fraction increases by 60%. Remarkably, this emergent property of the model is corroborated by ethnographic data, which falls over a comparable range (compare Figs. 4c and 4d). Indeed, in both the observations and the model, a higher meat fraction of the diet is associated with a lower population density under the same level of NPP (Supplementary Figure 6). It is possible that the use of aquatic resources, which are not included explicitly in the model, could increase the density of some populations relative to terrestrial NPP (and thus Φ_{NPP}) and thus confound the model-observation comparison. However, we checked that the observed correlation between Φ_{NPP} and meat fraction holds when the groups with fish-rich diets are excluded (Supplementary Figure 7). Therefore, although aquatic resources are important for hunter-gatherers in some locations (Supplementary Figure 1d), the association between Φ_{NPP} and meat fraction appears to be a robust feature of the observations. Notably, even the groups with intermediate ($30\% \leq \text{fishing} < 50\%$) or high ($\geq 50\%$) fishing percentages display significant negative correlations between Φ_{NPP} and meat fraction as well (Supplementary Figure 7), lending confidence to this overall trend.

The meat fraction of the modelled hunter-gatherer diet is mainly driven by a scarcity of vegetation edible by humans during winter or dry seasons in the model. In regions with relatively small seasonal variations in NPP, foragers can subsist mainly on gathering throughout the year due to a substantially higher abundance of plant food than animal food at equilibrium (Fig. 5a). By contrast, in regions with long non-growing seasons, edible plant biomass becomes depleted and foragers depend on hunting to subsist through the season of scarcity. As a result, the production rate of animals imposes a strong constraint on human population density in regions with short growing seasons, regardless of how abundant plant food may be during the growing season (Fig. 5b). Since relatively little energy flows from primary to secondary production due to trophic inefficiency (Fig. 5), the Φ_{NPP} is expected to be lower for humans subsisting more on animals. Therefore, the apparent negative correlation between Φ_{NPP} and meat fraction (Fig. 4d and Supplementary Figure 5) is caused both directly by the effect of shifts in humans' trophic position, and indirectly by the covariation between meat fraction and seasonality, the latter being able to influence Φ_{NPP} through the limiting seasonal minima.

176 With the process-based model, we quantify the contribution of the two effects, by conducting
177 two experiments in which humans only subsist on either plants or animals (via allocating all
178 foraging time in either gathering or hunting, hereafter “onlyGather” and “onlyHunt”). The
179 difference in the resulted Φ_{NPP} between the two runs could be regarded as the direct impact of the
180 trophic position. In the results of onlyGather, humans only persist in regions with long growing
181 seasons ($> \text{ca.} 180$ days), but the total population size in these populated areas is 9.5 times higher
182 than that in the onlyHunt experiment for the same area (Supplementary Figure 8).
183 Correspondingly, Φ_{NPP} is mostly higher in onlyGather than in onlyHunt (albeit the opposite
184 occurs in a few grid cells with relatively shorter growing seasons where a full reliance on hunting
185 slightly increases population density), and $\log_{10}(\Phi_{\text{NPP}})$ increases by 0.85 (or, Φ_{NPP} increases by
186 seven times) on average in onlyGather compared to onlyHunt (Supplementary Figure 8e).
187 Therefore, the direct effect of diet composition via trophic energetics contributes about half to
188 the apparent slope of Φ_{NPP} versus meat fraction.

189 The modelled contrast of seasonal cycles in diet composition between long versus short growing
190 season regions (Fig. 5) is qualitatively supported by observations in the Ache (in tropical
191 forest)²⁰, and in the Hiwi (in savanna)²⁷ and Bushmen groups (in Kalahari desert)²⁸. The former,
192 living in places with relatively high NPP all year round, exhibits little seasonal variance in both
193 meat and plant intake, whereas the latter two, living in highly seasonal environments, exhibit a
194 highly varied share of plant food across seasons. An in-depth quantitative evaluation is however
195 difficult due to the limited number of hunter-gatherer groups with detailed, seasonally based diet
196 records, and because the model cannot capture the highly diverse phenology of various plant and
197 animal species at the local ecosystems.

198 Given the strong role of meat fraction in controlling population density predicted by the process-
199 based model, we carried out a statistical analysis of contemporary hunter-gatherer data in order
200 to test if meat fraction emerges as a significant predictor (see Supplementary Discussion 1). Our
201 analysis shows that, indeed, a multivariable stepwise linear regression with nine empirical
202 predictors (NPP, tree and grass coverage, biodiversity, growing season length, percentages of
203 food derived from hunting, gathering and fishing, and absolute latitude) identifies the hunting
204 percentage as the strongest explanatory variable for population density, followed by NPP and
205 grass cover, while the other variables are non-significant. Hunting percentage itself can be
206 explained by growing season length, followed by grass coverage (see Supplementary Discussion
207 1). Whereas it has been previously noted that the fraction of animal food tends to increase at
208 higher latitudes^{25,29}, our result suggests that it is mainly the short growing season that explains
209 this gradient, as the effect of latitude itself is non-significant when growing season length is
210 considered. A structural equation model, which considers both direct and indirect effects of the

211 predictors, also confirms the dominant effect of hunting percentage on population density in the
212 observational dataset, and supports the link that seasonality influences population density via the
213 hunting percentage (Supplementary Figure 9 and Supplementary Table 1). Relationships
214 between Φ_{NPP} and other variables, apart from hunting percentage (Fig. 4c), were also examined
215 (Supplementary Figure 10), showing a significant positive correlation between Φ_{NPP} and growing
216 season length ($r=0.37, p<0.001$), which however becomes non-significant after controlling for
217 hunting percentage in the partial correlation analysis (Supplementary Table 2).

218 **Discussion**

219 This study built a process-based hunter-gatherer dynamics model, coupled to a global terrestrial
220 biosphere model, to explore the influence of environmental factors on hunter-gatherer population
221 density. The model explicitly simulates micro-scale processes including daily carbon/energy
222 flows among plants, animals and humans, combined with a dynamic time allocation for hunting
223 and gathering activities with simple assumptions. The emergent macroscopic relationships from
224 the model are well supported by ethnographic observations of contemporary hunter-gatherers,
225 revealing a causal mechanism whereby short growing seasons drive high fractions of meat in the
226 diet, leading to greatly reduced population density per unit NPP largely as a result of trophic
227 inefficiency.

228 The empirical negative association between hunting fraction and population density has been
229 reported or implied in previous studies^{14,30}, but it was assumed that population density was the
230 causal factor, rather than vice versa: a higher population density was suggested to lead to less
231 frequent residential moves, more food storage, and thus greater dependence on the stationary and
232 higher productive food of plants and coastal resources¹⁴. Our process-based coupled human-
233 ecosystem model suggests a more parsimonious explanation, given that it reproduces the
234 observed relationships as a straightforward consequence of bioenergetics. Reinforcing
235 mechanisms between demography and diet via cultural factors may still be relevant, as suggested
236 by ref.¹⁴ and by anthropological studies on diet from both ecological/biological and sociocultural
237 perspectives³¹. In particular, food storage and sharing have received much attention, due to their
238 close association with societal characteristics and ability to mitigate food scarcity at daily to
239 seasonal timescales³²⁻³⁴. It may be interesting to include food storage and sharing in our model
240 framework in the future to quantitatively explore the interplay between environment,
241 demography, diet, and sociocultural aspects.

242 The integral links between seasonality, diet composition and population density have strong
243 implications for studies that explore ancient human populations. Although seasonal cycles in the
244 availability of different types of food have left traces in fossil teeth of extinct hominins³⁵ and

245 been detected in the gut microbiome composition of the Hadza foragers in East Africa³⁶,
246 seasonality has not been included in prior modelling studies^{4,6,7,13} that used only annual NPP
247 and/or mean paleoclimate variables, which would have biased expectations for the spatio-
248 temporal pattern of early human distribution and migration. Furthermore, the lengthening of
249 growing seasons following the last deglaciation, combined with the end-Pleistocene megafaunal
250 extinctions that occurred in different regions at different timing and rates³⁷, might have driven
251 long-term changes in diet composition towards less meat-dependence. Our results suggest that a
252 shift from meat-dominated to plant-dominated diet could have boosted population much more
253 than implied by NPP changes alone. Given that demography might be at the core of cultural
254 evolution³⁸, which further shaped human societies^{8,39}, it is crucial to study the trajectory of past
255 population growth and its drivers, under the changing paleoclimate, vegetation and animal
256 distributions.

257 The model developed here represents a new type of computational modeling for ancient human-
258 ecology studies, breaking from a tradition⁴⁰ that has mainly included niche (species distribution)
259 models based on statistical methods and without human feedbacks on the environment, and
260 agent-based models which resolve individual behaviors and interactions but require very detailed
261 local information that is challenging to assess and have only been applied at a local/community
262 scale^{41,42}. By incorporating hunter-gatherers in a realistic, interactive and dynamical global
263 environment, the ESM framework helps to clarify how short growing seasons force humans to
264 rely on meat-rich diets, reducing Φ_{NPP} and thus the population density per unit NPP. Additional
265 factors beyond those resolved in our current model, such as technological transitions^{25,43} and
266 long-range migrations, are sure to have played important roles in determining changes in hunter-
267 gatherer population abundance and diet through time. With further development, the approach
268 has the potential to provide more highly resolved pictures of the complex, multifaceted
269 interactions between our ancestors and the Earth system.

270 **Methods**

272 **Contemporary hunter-gatherer data**

273 The hunter-gatherer population density and coordinates were acquired from ref.³, which
274 combined the ethnographic datasets from refs.^{1,2,44} (357 data points in total). For the diet
275 composition (percentages of hunting, gathering, and fishing), we combined the two datasets of
276 subsistence from Kelly² and Binford^{1,45} (340 data points in total), which indicate proportions of
277 food derived from terrestrial animals, terrestrial plants, and aquatic resources¹, in terms of weight
278 or calorie². Average of the two datasets were used if a population is present in both sources.

279 To explore the potential impact of environmental variables on population density and diets,
280 we extracted the values of the following variables from their global maps: annual NPP from the
281 satellite-derived MOD17A3 product⁴⁶ (averaged over 2001-2010); fractional coverage of trees
282 and grasses from a satellite-derived vegetation cover product⁴⁷; biodiversity index from ref.³,
283 which was the average of scaled richness of animals (mammals + birds) and vascular plants;
284 growing season length (GSL) calculated as the days in a year when daily gross primary
285 production (GPP) exceeds 20% of the maximum daily GPP for each grid cell, wherein the daily
286 GPP was from an upscaled global map based on FLUXNET tower sites⁴⁸ (different thresholds
287 were tested but made little difference, e.g. GSL defined by a threshold of 10% and 20% are
288 highly correlated, $r=0.93$). Due to slight differences of the land-sea mask of these global land-
289 only products, a few coastal populations were located in grid cells with a non-valid value; in
290 such case, the value of the nearest land pixel was used. These potential environmental predictors
291 are used in statistical analyses of the ethnographic data as detailed in Supplementary Discussion
292 1.

293 Unlike Tallavaara et al.³, we did not use the climate-based Miami model to calculate NPP
294 but instead used MODIS NPP, because the Miami model was shown to overestimate NPP in the
295 tropics since it only considers annual mean temperature and precipitation and misses important
296 factors like nutrient limitation in tropical forests⁴⁹. It was argued in ref.³ that the satellite-based
297 NPP was unfavourable because of the recent human appropriation of NPP. However, we
298 consider it a minor problem here because the majority of the sites have very small coverages of
299 cropland, according to a satellite product⁵⁰ (242 out of the 357 sites have <5% cropland cover,
300 305 sites <20%).

301 We calculated the fraction of NPP consumed by hunter-gatherers (Φ_{NPP}), which represents
302 the proportion of total energy available to heterotrophs that flows into hunter-gatherers, as
303 follows: per capita daily energy consumption, averaged over eight different groups², is 2480 kcal
304 ind.⁻¹ day⁻¹, which equals to 174 kgC ind.⁻¹ yr⁻¹, using the conversion coefficients of 9.8 MJ
305 kgDM⁻¹ (see the text below Eq. 4) and 0.45 gC gDM⁻¹. This same value is multiplied by
306 population density and divided by NPP to derive Φ_{NPP} for each site.

307 A potential systematic bias in the ethnographic diet composition data is worth attention. In
308 this study we regard the recorded hunting fractions as representing meat fractions of the diet.
309 However, the hunting fractions are likely to underestimate the true consumption of animals due
310 to the fact that early observers had devalued women's contribution in meat provision, including
311 small animals, eggs and insects. Such contributions had been often categorized as "gathering", or
312 simply ignored, as the focus of "hunting" had been on relatively large, mobile prey. This bias
313 could be large for groups in arid regions, e.g., the Western Desert in Australia^{51,52}, for which the

314 recorded hunting percentage is about 30% while the true meat fractions are up to 80% when
315 women's contribution to hunting is included⁵¹. The bias appears to be lower for groups in the
316 tropics like Amazon Basin and Congo Basin⁵³, where recent field observations show less than
317 10% of total hunted food from women⁵³. Unfortunately, revisiting and verifying the secondary
318 data on diet composition is difficult due to the disappearance of the foraging lifestyles for most
319 of the recorded hunter-gatherer groups. We therefore conducted a sensitivity test to see how the
320 observed negative relationship between Φ_{NPP} and hunting fraction (Fig. 4c) might be influenced
321 by expected uncertainties and biases in the ethnographic dietary records. As detailed in
322 Supplementary Discussion 1, we found that the relationship between Φ_{NPP} and hunting fraction is
323 robust to the expected biases, with only a minor impact on the slope of the correlation over the
324 most probable range of bias.

325 **Description of the process-based hunter-gatherer dynamics model**

326 *Model overview*

327
328 We designed the hunter-gatherer dynamics model, FORGE (FORager dynamics in Global
329 Ecosystem model), in the framework of Earth system models. It is coupled to the ORCHIDEE
330 (Organising Carbon and Hydrology In Dynamic Ecosystems) terrestrial biosphere model⁵⁴,
331 which is the land component of the IPSL (Institut Pierre Simon Laplace) ESM. ORCHIDEE
332 simulates the energy and water balance, vegetation dynamics, and carbon cycle of land
333 ecosystems. Inputs for ORCHIDEE include meteorological variables (air temperature,
334 precipitation, incoming short and long wave radiation, wind speed, air humidity, and air
335 pressure), atmospheric CO₂ concentration, land cover, topography and soil texture maps. Spatial
336 resolution and domain of each simulation are customized depending on the inputted climate
337 forcing. In the model, each grid cell is occupied by a suite of plant functional types (PFTs), with
338 their fractional covers adding up to one. ORCHIDEE has recently incorporated a module of large
339 mammalian herbivores that simulates animal population density driven by vegetation and
340 climate¹⁷. The main revision of the herbivore module compared to ref.¹⁷ is the inclusion of
341 browsers (herbivores that eat woody plants) whereas the previous version only calculated
342 grazers. The same parameterizations are used for browsers as grazers except that browsers feed
343 on the leaf and fruit compartments of tree PFTs, assuming 10% of these biomass is reachable to
344 browsers. The summation of grazer and browser density in each grid cell provides the potential
345 animal food density for humans.

346 The new FORGE model (Fig. 2) couples hunter-gatherers with vegetation and herbivores in
347 each grid cell via daily foraging activities and resultant carbon/energy flows, which then updates
348 an energetic reserve (body fat) that determines birth rate and mortality rate of human
349 populations. The human foraging activities are formulated based on a time allocation scheme.
350 The feedback of human hunting on herbivore dynamics is taken into account, while the impact of
351 humans on vegetation growth is neglected in the current model, but the model infrastructure
352 leaves room for future developments regarding human-induced environmental changes (e.g.
353 changes in land cover, fire regimes, etc.) and subsequent impacts on the ecosystems. Major
354 simplifications of FORGE include that i) only an average human (body weight = 50 kg ind⁻¹) is
355 represented; ii) fishing is not implemented in the current land-only model, leading to a potential
356 underestimation in population density of the groups for which marine resources provide much
357 food, mostly in coastal regions (Supplementary Figure 1); iii) human migration⁵⁵ across grid

358 cells is not accounted for, although the fact that the ethnographically recorded average migration
 359 distance per move and the total distance moved between camps in a year are ca. 27 km and 280
 360 km, respectively¹, means that most hunter-gatherers would not move over more than the
 361 dimensions of one grid cell (on the order of 10^4 km² each) in an annual cycle; and (iv) the lack of
 362 representation of small animals in the model, including birds, reptiles, insects, and small
 363 mammals (<5~10 kg ind.⁻¹), could lead to underestimations in available animal food and meat
 364 fraction of the diet, which coincides with the potential systematic underestimations in the
 365 ethnographic hunting fraction data mentioned above. Detailed formulations of FORGE are
 366 described below.

367 Daily intake

368 The model considers two types of subsistence activity, hunting and gathering. The
 369 contribution of each activity to the diet depends on the abundance of animal biomass and edible
 370 vegetation biomass, the time spent in hunting and gathering, as well as the technology-dependent
 371 efficiency of both activities:

$$372 \quad I_V = B_V t_g e_g a$$

$$373 \quad I_A = B_A t_h e_h a \quad (1)$$

374 where I_V and I_A are daily dry matter intake of vegetation and meat (kgDM day⁻¹ ind.⁻¹); B_V
 375 and B_A are biomass density of edible vegetation and animals (kgDM m⁻²); t_g and t_h are the time
 376 allocated to gathering and hunting (hr day⁻¹); a is the searching area per person hour, fixed at
 377 4000 m² hr⁻¹ ind.⁻¹; e_g and e_h are the efficiencies of gathering and hunting, representing the
 378 fraction of the corresponding biomass that is acquired when hunter-gatherers pass the searched
 379 area.

380 In a linear form this equation would imply that the food resources and foragers are both
 381 uniformly distributed within each grid cell and foragers encounter them randomly. In reality,
 382 excursions are undertaken from localized camps, different food items are distributed in patches,
 383 and foragers know how to target the higher energy-return items first². To partly account for these
 384 aspects of sub-grid heterogeneity, we assume e_g and e_h to decrease as B_V and B_A decrease relative
 385 to human density, capturing the increasing difficulty of foraging as the best resources are
 386 sequentially depleted. We model this with an asymptotic function:

$$387 \quad e_g = e_{max} \frac{B_V}{B_V + c B_H}$$

$$388 \quad e_h = e_{max} \frac{B_A}{B_A + c B_H} \quad (2)$$

389 where B_H is human biomass density (kg m⁻²), equal to P_H (population density which is
 390 prognostically simulated in the model, see Eq. 11) multiplied by mean body weight (W_H , 50 kg
 391 ind.⁻¹); e_{max} is the maximum fraction of the edible plant/animal biomass that can be acquired
 392 when hunter-gatherers pass the searched area, fixed at 1 and tested in a sensitivity analysis (see
 393 below); c determines the patch depletion rate; the value of c is fixed at 100, and is tested in the
 394 sensitivity analysis. Notably, the inclusion of Eq. 2 produces a dynamic similar to that found in
 395 ecological studies of per capita prey consumption by wild predators, which often decreases with
 396 predator density for a given prey density⁵⁶.

397 Energy expenditure and energetic reserve

398 The per capita daily energy expenditure E (MJ day⁻¹ ind.⁻¹) is calculated as:

399
$$E = E_c + E_g t_g + E_h t_h \quad (3)$$

400 where E_c is the energy expenditure excluding those spent during foraging, fixed as 8.37 MJ
401 day⁻¹ ind.⁻¹ (i.e. 2000 kcal day⁻¹ ind.⁻¹); E_g and E_h are the energy spent per hour gathering or
402 hunting, fixed as 1.25 MJ hr⁻¹ ind.⁻¹ (according to ref.⁵⁷) for both parameters in the model.

403 Based on daily food intake and energy expenditure, per capita energetic reserve (mainly in
404 fat cells) is updated daily as below. This is the key variable that indicates health condition and is
405 used to calculate birth rate and mortality rate (see below).

406
$$\frac{dF}{dt} = \frac{I-E}{m}$$

407
$$I = m_V I_V + m_A I_A \quad (4)$$

408 where F (kg ind.⁻¹) is per capita energetic reserve; m (MJ kg⁻¹) is the conversion coefficient
409 between energy and fat mass, set to 39.3 if $I < E$ (catabolism) or 54.6 if $I > E$ (anabolism) (ref.⁵⁸).
410 The gross energy value of plants and animals is around 3800-4800 for different plants (ca. 5000
411 for seeds) and 4400-5600 for different animal taxa (ref.⁵⁹, in the unit kcal kgDM⁻¹). We thus
412 assume the same value for both food types for simplicity. Further considering the ca. 30% energy
413 loss in excreta, and that the metabolisable energy content is less than the gross energy value of
414 food, we finally set m_V and m_A to 9.8 MJ kgDM⁻¹. It should be noted that the energy density of a
415 mammal's carcass depends on its fat content²², thus a fixed m_A value in the current model is a
416 simplification and does not account for variations across species and over time.

417 There is an upper limit of F (F_{max}), assumed to be 30% of body weight, i.e. 15 kg ind.⁻¹ in
418 the model. Accordingly, whenever F is about to exceed F_{max} , daily intake will be reduced so that
419 F stays at F_{max} .

420 Time allocation

421 In the current model, we only simulate the time spent in foraging, and leave all other
422 activities such as childcare, domestic maintenance and socializing to an aggregate 'other'
423 category. The hunting, gathering and total foraging time ($t_f = t_h + t_g$) are updated every day in the
424 following two steps. First, t_f increases or decreases by 1 hr day⁻¹ depending on the changes in the
425 energetic reserve F during the previous day:

426
$$t_f(t) = \begin{cases} t_f(t-1) - 1, & \text{if } \Delta F > 0 \text{ and } F(t) > 0.5 F_{max} \\ t_f(t-1) + 1, & \text{else} \end{cases}$$

427
$$t_f \in [t_{f,min}, t_{f,max}] \quad (5)$$

428 t_h and t_g are then changed proportionately. Such reduction of foraging time when humans
429 have eaten plenty of food in the previous day could represent idle relaxation, a phenomenon
430 widely observed in many animals⁶⁰ as well as hunter-gatherers⁶¹. An upper limit on foraging
431 time would also be driven by the need to do the other essential activities not modelled here.
432 Foraging time reported for dozens of hunter-gatherer groups, averaged between males and
433 females, range between 0.8-6.8 hr day⁻¹^{12,18,19}. We therefore set $t_{f,min}=0.5$ and $t_{f,max}=8$ hr day⁻¹.

434 Second, the allocation between hunting and gathering depends on the relative energy benefit
 435 of the two activities, as well as a craving for meat, parameterized as an exponential decay
 436 function of meat proportion in the diet of the previous day:

$$437 \quad th_{frac} = \frac{Benif_h}{Benif_h + Benif_g} C_{meat}$$

$$438 \quad f_{meat} = \frac{I_A}{I_A + I_V}$$

$$439 \quad C_{meat} = e^{-q (f_{meat} - 1)}$$

$$440 \quad Benif_h = B_A e_h$$

$$441 \quad Benif_g = B_V e_g$$

$$442 \quad th_{frac} \in [0.05, 0.95] \quad (6)$$

443 where th_{frac} is the fraction of t_f allocated to hunting. The additional meat-craving term, C_{meat} ,
 444 is introduced to represent that hunter-gatherers generally have a preference for meat, which may
 445 reflect nutritional needs (e.g. fat and essential amino acids)⁶² as well as cultural importance². The
 446 parameter q is fixed at 2.5 but also tested (see Supplementary Table 3). In cases when f_{meat} falls
 447 below 10% (the minimum observed hunting+fishing fraction), th_{frac} is set to 0.95. t_h and t_g are
 448 then calculated as $t_f \times th_{frac}$ and $t_f \times (1 - th_{frac})$ respectively.

449 This time allocation scheme is highly simplified. It does not consider, for example, seasonal
 450 variations of other necessary activities such as providing shelter, extreme weather that makes
 451 foraging activities risky or unworthy (e.g. the Hiwi in tropical savannah don't forage during the
 452 middle of the day to avoid heat²⁷), and additional social/cultural factors. Further improvements
 453 and tests of the scheme are possible in the future, given more observational data on human time
 454 allocation dynamics. Yet, it provides an unprecedented approach to include the fundamental limit
 455 of time on the ability to capture existing biomass.

456 Updating food resources

457 Not all vegetation and herbivore biomass are edible or accessible to humans. We denote the
 458 edible and/or accessible fraction of vegetation and herbivores as Φ_V and Φ_A , respectively, which
 459 are assumed to be fixed parameters in the current model over the globe ($\Phi_V=0.015$, $\Phi_V=0.1$, see
 460 sensitivity tests below). This is a simplification; for example, many fruits in tropical forests grow
 461 high in the canopy, making them harder to reach than the case in short-vegetation biomes².
 462 Unfortunately, robust estimates of the edible/accessible fraction for major biomes worldwide are
 463 unavailable, and therefore we do not vary Φ_V and Φ_A between grid cells in the current model, in
 464 order to avoid arbitrarily introducing spatial relationships of human density versus NPP. Apart
 465 from fruits, hunter-gatherers can also eat roots and tuber, which are from the belowground
 466 primary production of some herbaceous plants. We thus also include part of the belowground
 467 grass NPP as potential food sources.

468 The B_V (biomass density of edible vegetation) is updated on a daily time-step:

$$469 \quad \frac{dB_V}{dt} = \Phi_V (f_{fruit} NPP + f_{below} NPP_{grass}) - \lambda B_V - I_V P_H$$

$$470 \quad f_{below} = \frac{88.3 - 0.0534 MAP}{100} \quad (7)$$

471 Where λ (day^{-1}) is the daily turnover rate of the edible vegetation biomass; f_{fruit} is the
 472 fraction of NPP (including both tree and grass) allocated to fruits, set to 6.5% in the current
 473 model according to a synthesis⁶³ of fruit fall observations across tropical and temperate forests;
 474 f_{below} is the fraction of grass NPP allocated belowground, calculated as a function of mean annual
 475 precipitation (MAP, mm yr^{-1}) following the empirical equation from ref.⁶⁴, which captures the
 476 higher belowground allocations in dryer ecosystems. The lower limit of f_{below} is set to 20%. The
 477 inputted NPP and λ are either from ORCHIDEE outputs or from observation-derived values (see
 478 “Model setup” section for the different runs).

479 The herbivore dynamics module is coupled once per year with the human dynamics module.
 480 Detailed descriptions of the herbivore module can be found in ref.¹⁷. In summary, herbivore
 481 population density ($P_{A,\text{tot}}$, ind. km^{-2}) is updated on a yearly time-step using a logistic equation
 482 (Eq. 8 in ref.¹⁷). The herbivore birth and mortality rates depend on an animal fat reserve pool (kg
 483 ind.^{-1}) that is updated daily according to their energy intake through grazing or browsing.

484 Within the human module, B_A is updated on a daily time-step:

$$485 \quad \frac{dB_A}{dt} = -I_A P_H \quad (8)$$

486 At the end of each year, the accumulated number of hunted animals ($\frac{\sum I_A P_H}{W_A \times 0.28}$) is subtracted
 487 from the herbivore population density $P_{A,\text{tot}}$. The decreased $P_{A,\text{tot}}$ is passed to the herbivore
 488 module to calculate a new $P_{A,\text{tot}}$ for the next year. B_A is then updated and used in the human
 489 module for the new year:

$$490 \quad B_A = \Phi_A P_{A,\text{tot}} W_A \times 0.28 \quad (9)$$

491 where W_A is the mean body weight of herbivores, set to 180 kg ind.^{-1} in the current model;
 492 0.28 is the conversion between live weight and dry mass after excluding water and bones.

493 Note that the herbivore population dynamics is also affected by seasonality, with relatively
 494 higher animal starvation mortalities in regions with longer winters/dry seasons¹⁷. However,
 495 temporally, simulated meat density is relatively stable throughout the year in the model (see Fig.
 496 5), because the animal population density is updated only once per year. The annual update is
 497 justified by the fact that the animals represented have lifespans of ~ 25 years¹⁷, so that seasonal
 498 fluctuations in population numbers are strongly damped. Unlike humans, herbivores can feed on
 499 plant litter (dead grasses and fallen leaves/fruits in the model) to live through non-growing
 500 seasons, providing vital food for hunter-gatherers to survive the long winters/dry seasons in the
 501 model.

502 It should be emphasized that the modelled feedbacks of human foraging are very different
 503 for vegetation and animal density. Gathering is assumed to have negligible impacts on primary
 504 productivity, since the B_v that is harvested represents the edible part of plants, which generally
 505 do not contribute to plant growth, and for which harvesting can even aid in reproduction (e.g.
 506 through the spreading of seeds⁶⁵). In contrast, hunting can directly reduce the annual production
 507 of herbivores by reducing $P_{A,\text{tot}}$. However this effect would be small at low rates of hunting, for
 508 which competition among herbivores places the limit on $P_{A,\text{tot}}$.

509 Human population dynamics

510 The population birth rate (r_{birth} , yr^{-1}) is assumed to depend on the average body condition,
511 represented by the daily-varying energetic reserve F . Thus, r_{birth} is calculated every day and
512 averaged over the year to be used in Eq. (11),

513
$$r_{birth} = \frac{r_a}{1 + e^{-r_b(\frac{F}{F_{max}} - r_c)}} \quad (10)$$

514 where $r_a = 0.1$, $r_b = 15$, $r_c = 0.5$. This sigmoidal function is similar to the equation used to
515 calculate herbivore birth rate¹⁷, with the parameters modified so as to give a maximum birth rate
516 of 10%, close to the recorded highest crude birth rate during the past two centuries (ca. 6%, ref⁶⁶)
517 (see sensitivity tests of the three parameters below).

518 For mortality, we consider two processes. First, a background mortality rate (M_b) which is
519 the inverse of lifespan, fixed as $\frac{1}{80} = 0.0125 yr^{-1}$. Second, starvation-induced mortality (M_s , yr^{-1}),
520 caused by the exhaustion of body energy storage as represented by the complete depletion of fat
521 reserves. The M_s is calculated using a similar method as in the herbivore module¹⁷. Namely, we
522 assume a normal distribution of body fat within the population, with a mean $\mu = F$ and a standard
523 deviation $\sigma = 0.125 F_{max}$; the probability that fat mass falls below 0 is taken as the value of M_s .
524 Similar to r_{birth} , M_s is also calculated every day and averaged over the year.

525 Finally, the annual dynamics of the human population density are calculated as:

526
$$\frac{dP_H}{dt} = r_{birth} P_H - (M_s + M_b) P_H \quad (11)$$

527 where P_H (ind. km^{-2}) is the human population density for each grid cell. The P_H is initialized
528 as $P_0 = 10^{-3}$ ind. km^{-2} , a lower value than the minimum density ever recorded (0.002 ind. km^{-2} ,
529 ref.^{1,2}). Whenever P_H falls below P_0 , P_H is reset to P_0 .

530 Once each year, the reproduction energy cost (313 kcal day^{-1} , or 478 MJ for a year,
531 according to ref.⁶⁷) is subtracted from the energetic reserve F in order to account for the energy
532 input to birth:

533
$$\Delta F = -\frac{478 r_{birth}}{m} \quad (12)$$

534 Model setup

535 To derive the input variables for FORGE, we firstly ran ORCHIDEE for the globe at 2°
536 spatial resolution and for 200 years as a spin-up to reach the equilibrium of vegetation
537 production and biomass under present-day climate conditions. The climate forcing was the CRU-
538 NCEP reanalysis dataset⁶⁸, repeating the years 2001-2010. The atmospheric CO₂ concentration
539 was fixed at 380 ppm (the average level during 2001-2010). For the land cover, although
540 ORCHIDEE can simulate vegetation distributions equilibrated under the given climate
541 conditions, we instead prescribed an observation-based PFT map in order to reduce the bias of
542 ORCHIDEE outputs that would propagate to the FORGE model. This PFT map was based on
543 ESA CCI Land Cover map v2.0.7b for 2010, which was further merged with the LUH2 dataset
544 to generate a pre-industrial PFT map (year 850) with minimal crop coverages. See detailed
545 descriptions of the PFT map at <https://orchidas.lsce.ipsl.fr/dev/lccci/>.

546 The last 10 years' outputs from ORCHIDEE are used to provide the inputs to FORGE.
547 These include the inputs required by the herbivore module: fractional cover of PFTs (aggregated

548 into three types: grass, tree, bare ground), carbon influx rates (i.e. NPP allocated to the edible
549 plant tissues, and influx to the edible litter pool) and decay rates of the edible pools, and annual
550 mean temperature; as well as inputs required by the human module: NPP, decay rate of the fruit
551 compartment, and annual precipitation (used in Eq. 7). The input variables are at a daily time
552 step. FORGE was then run for 300 years to reach the equilibrium of population density of both
553 herbivores and hunter-gatherers. The last 50 years were averaged and presented as the results.

554 Supplementary Figure 11 shows the ORCHIDEE-simulated NPP, in comparison with
555 MODIS NPP. ORCHIDEE can reproduce the overall pattern of the satellite-derived NPP, with a
556 reasonable agreement with MODIS NPP at the sites (Pearson correlation coefficient $r=0.67$).
557 However, ORCHIDEE underestimated NPP in tropical forests and arid ecosystems including
558 some classical hunter-gatherer areas like the Great Basin in North America, Kalahari in southern
559 Africa, and interior Australia (Supplementary Figure 11). The underestimation of annual NPP in
560 the dry regions is partly due to an underestimation of growing season length by ORCHIDEE
561 (Supplementary Figure 12).

562 In order to test the impact of the bias of ORCHIDEE-simulated NPP, and to minimize this
563 bias that would propagate to the FORGE-simulated hunter-gatherer densities, we conducted three
564 sets of simulations, with different input files while identical FORGE model:

565 S0: inputs to FORGE are directly from ORCHIDEE outputs;

566 S1: compared to S0, the daily NPP is multiplied by a scaling factor so that the annual NPP
567 (average for 2001-2010) equals to MODIS NPP for each grid cell;

568 S2: compared to S0, the daily NPP is replaced by the observation-based values, that is,
569 annual MODIS NPP interpolated into daily values according to an observation-derived daily
570 GPP product⁴⁸. Note that the herbivore module in FORGE separates grazers feeding on grass
571 NPP and browsers feeding on tree NPP, and here we assume the same NPP values (per unit PFT
572 area) for tree and grass PFTs in the same grid cell. Besides, the ORCHIDEE-simulated daily
573 decay rates of edible plant tissues (λ) are replaced by a constant of 0.01 day^{-1} during growing
574 season (when $\text{NPP}_{\text{daily}} > \text{NPP}_{\text{daily,max}}$) and 0.05 day^{-1} during non-growing season (when
575 $\text{NPP}_{\text{daily}} \leq \text{NPP}_{\text{daily,max}}$), in order to avoid an inconsistent timing of senescence (a period of high
576 decay rates of leaves and fruits) with the observed seasonality in NPP. The λ values are chosen
577 so that the integrated annual decay rates are generally comparable to those simulated by
578 ORCHIDEE (used in S0 and S1).

579

580 Modelled population densities and their relationships between NPP and meat fraction of the
581 diet from the S0 and S1 runs are shown in Supplementary Figures 13 and 14. Among S0, S1, and
582 S2, the emergent relationships between population density and NPP, and Φ_{NPP} and meat fraction,
583 are similar (Supplementary Figure 14), except for a steeper slope of log-population density
584 versus NPP in S0 due to the lack of data points under the high end of NPP (as ORCHIDEE
585 underestimates NPP in tropical forests, see Supplementary Figure 11). Regarding the global
586 patterns of population density (Supplementary Figure 13), however, both S0 and S1 predict an
587 unrealistic absence of hunter-gatherers in many arid ecosystems including those in western
588 Plains in North America, Kalahari, and interior Australia, the classical hunter-gatherer territories.
589 These regions are populated in the S2 results (Fig. 3a). The difference between S1 and S2 (for
590 which the annual total NPP in the inputs are identical) therefore indicates the critical role of a
591 substantially long growing season length in sustaining hunter-gatherers in the less productive
592 ecosystems. Considering a prevailing underestimation in growing season length for the arid

593 ecosystems in state-of-the-art terrestrial biosphere models (Supplementary Figure 15), our results
594 highlight the need for a more realistic simulation of plant phenology in order to improve the
595 simulation of contemporary and ancient hunter-gatherers. Unless otherwise specified, the model
596 results shown are from the S2 experiment.

597

598 **Sensitivity tests of parameters**

599

600 We consider several parameters in FORGE, listed in Supplementary Table 3, to be highly
601 uncertain. We therefore conducted sensitivity tests using Sobol’s method⁶⁹ (a variance-based
602 sensitivity analysis), which decomposes the variance of model output into fractions that can be
603 attributed to different inputs. Sobol’s method has the advantage of measuring sensitivity across
604 the whole input space, as well as accounting for nonlinearity and parameter interactions, so that
605 the total-order index (S_T) indicates the importance of each parameter considering both its main
606 effect (first-order sensitivity index, S_1) and the contribution of its interaction with other
607 parameters.

608 Sobol’s method requires thousands of runs, which is computationally expensive for global
609 experiments. We thus carried out the tests at two sites with contrasting characteristics. First, a
610 temperate forest with a long growing season and a low hunting fraction in the diet at 42N, 123W
611 in. Second, a boreal forest with a short growing season and a high hunting fraction at 56N, 69W
612 (Supplementary Figure 16). For each site, we conducted 9000 runs in which the parameters were
613 sampled within their ranges listed in Supplementary Table 3, using Saltelli’s sampling scheme
614 which is more efficient than random sampling. Supplementary Figure 17 shows how the varied
615 parameter values affect the corresponding equations. All the sensitivity tests were done using the
616 Python package “SALib” (<https://salib.readthedocs.io/en/latest/index.html>).

617 The resulting S_T and S_1 (Supplementary Figure 18) indicate different sensitivities to the
618 parameters between the two sites. For the hunting-dominated site, population density is most
619 sensitive to Φ_A , followed by e_{\max} and c , whereas for the gathering-dominated site, population
620 density is sensitive to the four parameters Φ_V , Φ_A , e_{\max} , and c . The three parameters used to
621 calculate birth rate make negligible contributions to the variance in modelled population. Indeed,
622 birth rate impacts the time it takes to reach equilibrium population under a given set of
623 environmental conditions, but has a negligible effect on the equilibrium value itself. Nor is the
624 population density sensitive to the parameter q , which determines the meat craving response.

625 Supplementary Figure 19 further shows the quantitative response of model results to the
626 parameters. As expected, a higher Φ_V (or Φ_A) value increases population density at the
627 gathering-dominated (or hunting-dominated) site, while a higher c value decreases the population
628 at both sites. A higher e_{\max} value increases population density at both sites, but the beneficial
629 effect diminishes at high population densities for the hunting-dominated site, probably a result of
630 overhunting. Meat fraction in the diet is mainly determined by the relative values of Φ_V and Φ_A
631 (Supplementary Figure 18). Compared to population density and meat fraction, foraging time is
632 relatively more equally sensitive to all the tested parameters (Supplementary Figure 18), but its
633 results in the 9000 runs are relatively centralized across the tested parameter space for both sites
634 (Supplementary Figure 19).

635 For the standard configuration, we set $\Phi_V=0.015$, $\Phi_A=0.1$, $e_{\max}=1$, and $c=200$ so as to match
636 the average value of population density and meat fraction across the sites. Note that changing

637 these globally-constant parameter values increases or decreases population everywhere, but has
638 minor impacts on the modelled relationships with environmental variables (Supplementary
639 Figure 20).

640 **Data availability**

641 The contemporary hunter-gatherer data and environmental variables used in the analysis are
642 available in the supplementary materials.

643 **Code availability**

644 Source code (in Python) of the FORGE model and its output files (in NetCDF format) for this
645 study, including the three sets of global simulations (S0, S1, S2), are provided in a
646 Supplementary zipped file. The corresponding input files for the FORGE model are available at
647 <https://doi.org/10.6084/m9.figshare.14995320.v2>.

648

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655 **Author contributions**

656 D.Z. and E.D.G. conceived the study and model design. D.Z. built the model, performed the
657 analyses, and wrote the first draft. E.D.G. provided discussion and suggestions throughout the
658 process. V.R-G. and P.C. contributed to the interpretation of the results and writing of the
659 manuscript.

660 **Competing interests**

661 Authors declare no competing interests.

662

663 **Figure legends**

664 **Fig. 1 | Contemporary hunter-gatherer population density vs. net primary production. (a)**
665 Relationship between population density, from ethnographic records at 357 locations
666 (Supplementary Figure 1), and NPP, according to the MODIS satellite-derived product (see
667 Methods). The solid line gives the linear regression of $\log_{10}(\text{pop. density})$ vs. NPP ($y = 9.6 \times$
668 $10^{-4}x - 1.53$) with 95% confidence intervals shown in grey. **(b)** Violin plot for Φ_{NPP} (fraction
669 of NPP consumed by hunter-gatherers, calculated as population density multiplied by a constant
670 intake rate and divided by NPP, see Methods) of populations located in different biomes
671 (Supplementary Figure 2). The white circles represent median values and the thick (or thin)
672 black bars the inter-quantile (or 5th–95th) ranges. Except for a lower Φ_{NPP} in boreal forest and a
673 slightly higher Φ_{NPP} in Mediterranean forest, Φ_{NPP} does not differ significantly among the other
674 five biome types (ANOVA test $p > 0.05$).

675

676 **Fig. 2 | Schematic of FORGE (FORager dynamics in Global Ecosystem model), coupled to**
677 **the ORCHIDEE global terrestrial biosphere model.** FORGE simulates daily energy (carbon)
678 intake from plants and animals and energy expenditure (black arrows); these energy in/out-fluxes
679 update an energetic reserve pool (body fat) every day, which indicates the average health state
680 and then impacts birth rate and mortality rate, determining changes in hunter-gatherer population
681 density every year. The daily intake rate depends on food abundance and on the time spent in
682 hunting and gathering, calculated with time allocation algorithms (see Methods for details).

683

684 **Fig. 3 | Modelled population density and time allocation. (a)** Map of hunter-gatherer
685 population density equilibrated under present-day climate (results in the S2 experiment, see
686 Methods). **(b)** Relationship between population density and NPP at the grid cells where the
687 observational data are located. The red solid line indicates linear regression of $\log_{10}(\text{pop. density})$
688 vs. NPP ($y = 11.7 \times 10^{-4}x - 1.78$, $N=334$, $r=0.72$), with 95% confidence intervals shown in
689 red shading. For comparison, regression of the observations is shown in grey (same as those in
690 Fig. 1a). **(c-e)** Modelled time spent in foraging (c), separated into gathering (d) and hunting (e).
691 The grid cells where modelled population density is less than $0.2 \text{ ind./}100\text{km}^2$ are shown in white
692 in the maps, and excluded in (b).

693

694 **Fig. 4 | Meat fraction of the diet controls Φ_{NPP} . (a,b)** Modelled fraction of hunted food in the
695 diet (a) and Φ_{NPP} (fraction of NPP consumed by hunter-gatherers) (b). **(c,d)** Relationship
696 between Φ_{NPP} and meat fraction of the diet according to ethnographic records (c) and model
697 results (d). The black and red solid lines give the linear regressions of $\log_{10}(\Phi_{\text{NPP}})$ vs. meat
698 fraction from observations (c) ($y = -1.93x - 3.68$) and the model (c) ($y = -1.78x - 3.68$,
699 $N=334$, $r= -0.73$), with 95% confidence intervals shown in shading. The grid cells where
700 modelled population density is less than $0.2 \text{ ind./}100\text{km}^2$ are shown in white in the maps, and
701 excluded in (d).

702

703 **Fig. 5 | Seasonality, diet composition and carbon flows.** Model results were averaged over all
704 grid cells of either gathering-dominated (modelled annual mean hunted food $<40\%$, see Fig. 4a)
705 or hunting-dominated (hunted food $\geq 40\%$) regions, at dynamic equilibrium. Mean population
706 density of the two regions is 0.19 and 0.04 ind./km^2 , and mean meat fraction of the diet is 22%
707 and 55% , respectively. To synchronize the seasonal cycles between the two hemispheres, outputs
708 of the southern hemisphere were shifted by 6 months. The numbers on the links indicate
709 percentages of annual NPP that flow to herbivores, humans, and litter (dead plants) and soil

710 pools. Note that for legibility, the link widths are not strictly proportional to the magnitude of
711 flows. Spring: MAM; Summer: JJA; Autumn: SON; Winter: DJF.

712

713

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