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- 20 Abstract:
- 21

The dependence of hunter-gatherers on local net primary production (NPP) to provide food 22 played a major role in shaping long-term human population dynamics. Observations of 23 contemporary hunter-gatherers have shown an overall correlation between population density 24 and annual NPP, but with a thousand-fold variation in population density per unit NPP that 25 26 remains unexplained. Here we build a process-based hunter-gatherer population model embedded within a global terrestrial biosphere model, which explicitly addresses the extraction 27 of NPP through dynamically-allocated hunting and gathering activities. The emergent results 28 reveal a strong, previously unrecognized effect of seasonality on population density via diet 29 composition, whereby hunter-gatherers consume high fractions of meat in regions where 30 growing seasons are short, leading to greatly reduced population density due to trophic 31 inefficiency. This seasonal carnivory bottleneck largely explains the wide variation in population 32 density per unit NPP, and questions the prevailing usage of annual NPP as the proxy of carrying 33 capacity for ancient humans. Our process-based approach has the potential to greatly refine our 34 understanding of dynamical responses of ancient human populations to past environmental 35 36 changes.

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40 Introduction

Hunter-gatherer populations, that subsist on hunting, gathering and fishing, rely intimately on the 41 biotic fabrics of their local environments^{1–3}. Although only a handful of hunter-gatherer 42 populations remain, over 300 societies of contemporary hunter-gatherers have been documented 43 sporadically over the past two centuries¹. Due to the assumed similarities between their lifestyles 44 and those of our foraging ancestors, contemporary hunter-gatherers have provided many insights 45 on our species' past⁴⁻⁸, informing reconstructions of population changes on evolutionary 46 timescales^{5,6}, the timing and rates of global human dispersals^{4,7}, and the drivers behind the origin 47 of agriculture⁸. Yet, these contemporary societies do not provide direct analogues of ancient 48 foragers, as they had more complex technologies⁹ and had experienced interactions with and 49 pressures from neighbouring agricultural and industrial societies^{10,11}, such as acquiring 50 supplemental agricultural food^{2,12} or encountering novel pathogens near the time of 51 documentation, which may have modulated the population density-ecosystem relationships. 52 Thus, many of the observational data may provide distorted views on the pre-existing state, 53 casting doubt on statistical models and demographic parameters that are directly fitted to the 54 contemporary data⁵⁻⁸. Taking full advantage of the insights from contemporary hunter-gatherers 55 requires a mechanistic, process-oriented understanding of how environmental factors influence 56 the distribution and abundance of hunter-gatherer populations. 57

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

food storage-dependence¹⁴. It is however difficult to tease apart the causality among these inter 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 operates within the framework of an Earth system model (ESM) (Fig. 2). During the past 79 decades, the land components of ESMs have integrated vegetation modules to resolve key 80 processes of biogeochemical cycling of carbon, energy and water¹⁵, and have recently begun to 81 incorporate large mammalian herbivores based on metabolic and demographic equations^{16,17}. 82 Our model directly couples human population dynamics to such a land model¹⁷, simulating 83 human time allocation to hunting versus gathering in response to the interaction between humans 84 and food resources (see Methods). The model uses explicit formulations of daily carbon/energy 85 flows among vegetation, herbivores and humans, the outcome of which determines human 86 reproduction and mortality rates. These fluxes depend on a time allocation scheme with two 87 88 simple assumptions: first, total foraging time increases or decreases depending on the level of fullness of the previous day, and second, gathering vs. hunting time depends on the relative 89 abundance of plant vs. animal food and on an underlying a priori preference for meat. The model 90 is resolved on a daily time-step, thus capturing the seasonal cycle in high detail. 91
- 92

93 **Results**

94 Modelled global distribution of hunter-gatherers

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

- all plant or animal food equally, thus ignoring the wide variety such as the different energy 109 content, protein richness, and relative abundance of each food item within both broad 110 categories^{2,20–22}. Any bias in the vegetation and herbivore dynamics model¹⁷ could also 111 propagate to the human model, contributing to the model-data mismatch (note that the S2 112 113 experiment has corrected part of the biases in the vegetation inputs to the FORGE model, see Methods). Furthermore, discrepancies could arise from climate shifts and non-steady state 114 factors given that the model simulates equilibrium densities forced by present-day climate (while 115 the ethnographic records were collected during the past two hundred years¹) whereas some of the 116 populations were under positive growth rate when being studied²³. There are also significant 117 uncertainties in the diet composition data, as the estimation methods for the amounts of gathered, 118 hunted, and fished food are often inconsistent, sometimes measured in different units (weight or 119 calorie) and occasionally based on the ethnographers' impressions², which may further add to the 120 model-data scatter. 121
- The modelled global total hunter-gatherer population is 17 million, which is at the high end of 122 the estimates of prehistoric (pre-agriculture) population derived by extrapolating national 123 historical records, which range from 1-20 million²⁴. This can be partly explained by the fact that 124 our model was calibrated with data from contemporary hunter-gatherers, who presumably had 125 more advanced technologies and access to non-local foods than early-Holocene foragers²⁵ (see 126 Supplementary Discussion 2 for the test runs regarding the technology-dependent foraging 127 efficiency parameter). Geographical differences also contribute to our estimate being higher than 128 previous upscalings of contemporary hunter-gatherer populations, which include regression 129 models (10 \sim 12 million, refs.^{3,26}) and a proportional projection method (7 million, ref.¹). For the 130 former, the difference is primarily attributable to a higher density in Africa and southern Asia in 131 our model (Supplementary Figure 4), where the populations were suppressed in ref.³ due to a 132 high pathogen stress as a predictor in their regression (see Supplementary Discussion 1 for more 133 discussion about pathogen stress). For the latter, we find that the global estimate with the same 134 projection method but a different upscaling biome map ranges from 10 to 17 million, contingent 135 136 on how an average population density is calculated for each biome (see Supplementary Discussion 3). Therefore, we consider our result of 17 million, simulated by a process-based 137 model, to be a reasonable, independent estimate of potential global hunter-gatherer population 138 size under modern climate with advanced foraging technology, assuming foraging as the only 139 subsistence type. 140

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142 Linkage among seasonality, diet composition and population density

- As in the observations, simulated Φ_{NPP} (fraction of NPP consumed by hunter-gatherers) displays 143 144 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 145 negative correlation is clear in the scatter plot, both for grid cells where the observational data 146 are located (Fig. 4d) and for all populated grid cells in the model (Supplementary Figure 5), 147 showing a drop of Φ_{NPP} by almost an order of magnitude as meat fraction increases by 60%. 148 Remarkably, this emergent property of the model is corroborated by ethnographic data, which 149 falls over a comparable range (compare Figs. 4c and 4d). Indeed, in both the observations and 150 the model, a higher meat fraction of the diet is associated with a lower population density under 151 the same level of NPP (Supplementary Figure 6). It is possible that the use of aquatic resources, 152 which are not included explicitly in the model, could increase the density of some populations 153 relative to terrestrial NPP (and thus Φ_{NPP}) and thus confound the model-observation comparison. 154 However, we checked that the observed correlation between Φ_{NPP} and meat fraction holds when 155 the groups with fish-rich diets are excluded (Supplementary Figure 7). Therefore, although 156 aquatic resources are important for hunter-gatherers in some locations (Supplementary Figure 157 1d), the association between Φ_{NPP} and meat fraction appears to be a robust feature of the 158 159 observations. Notably, even the groups with intermediate ($30\% \le fishing \le 50\%$) or high ($\ge 50\%$) fishing percentages display significant negative correlations between Φ_{NPP} and meat fraction as 160 well (Supplementary Figure 7), lending confidence to this overall trend. 161
- 162 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 163 small seasonal variations in NPP, foragers can subsist mainly on gathering throughout the year 164 due to a substantially higher abundance of plant food than animal food at equilibrium (Fig. 5a). 165 By contrast, in regions with long non-growing seasons, edible plant biomass becomes depleted 166 and foragers depend on hunting to subsist through the season of scarcity. As a result, the 167 168 production rate of animals imposes a strong constraint on human population density in regions 169 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 170 trophic inefficiency (Fig. 5), the Φ_{NPP} is expected to be lower for humans subsisting more on 171 animals. Therefore, the apparent negative correlation between Φ_{NPP} and meat fraction (Fig. 4d 172 173 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 174 175 able to influence Φ_{NPP} through the limiting seasonal minima.

- With the process-based model, we quantify the contribution of the two effects, by conducting 176 two experiments in which humans only subsist on either plants or animals (via allocating all 177 foraging time in either gathering or hunting, hereafter "onlyGather" and "onlyHunt"). The 178 difference in the resulted Φ_{NPP} between the two runs could be regarded as the direct impact of the 179 180 trophic position. In the results of onlyGather, humans only persist in regions with long growing seasons (> ca.180 days), but the total population size in these populated areas is 9.5 times higher 181 than that in the onlyHunt experiment for the same area (Supplementary Figure 8). 182 183 Correspondingly, Φ_{NPP} is mostly higher in onlyGather than in onlyHunt (albeit the opposite occurs in a few grid cells with relatively shorter growing seasons where a full reliance on hunting 184 slightly increases population density), and $\log_{10}(\Phi_{\text{NPP}})$ increases by 0.85 (or, Φ_{NPP} increases by 185 seven times) on average in onlyGather compared to onlyHunt (Supplementary Figure 8e). 186 Therefore, the direct effect of diet composition via trophic energetics contributes about half to 187 the apparent slope of Φ_{NPP} versus meat fraction. 188
- 189 The modelled contrast of seasonal cycles in diet composition between long versus short growing season regions (Fig. 5) is qualitatively supported by observations in the Ache (in tropical 190 $(in \text{ Kalahari desert})^{20}$, and in the Hiwi (in savanna)²⁷ and Bushmen groups (in Kalahari desert)²⁸. The former, 191 living in places with relatively high NPP all year round, exhibits little seasonal variance in both 192 193 meat and plant intake, whereas the latter two, living in highly seasonal environments, exhibit a highly varied share of plant food across seasons. An in-depth quantitative evaluation is however 194 difficult due to the limited number of hunter-gatherer groups with detailed, seasonally based diet 195 records, and because the model cannot capture the highly diverse phenology of various plant and 196 animal species at the local ecosystems. 197
- Given the strong role of meat fraction in controlling population density predicted by the process-198 based model, we carried out a statistical analysis of contemporary hunter-gatherer data in order 199 to test if meat fraction emerges as a significant predictor (see Supplementary Discussion 1). Our 200 201 analysis shows that, indeed, a multivariable stepwise linear regression with nine empirical predictors (NPP, tree and grass coverage, biodiversity, growing season length, percentages of 202 food derived from hunting, gathering and fishing, and absolute latitude) identifies the hunting 203 percentage as the strongest explanatory variable for population density, followed by NPP and 204 grass cover, while the other variables are non-significant. Hunting percentage itself can be 205 explained by growing season length, followed by grass coverage (see Supplementary Discussion 206 1). Whereas it has been previously noted that the fraction of animal food tends to increase at 207 higher latitudes^{25,29}, our result suggests that it is mainly the short growing season that explains 208 this gradient, as the effect of latitude itself is non-significant when growing season length is 209 considered. A structural equation model, which considers both direct and indirect effects of the 210

- 211 predictors, also confirms the dominant effect of hunting percentage on population density in the
- observational dataset, and supports the link that seasonality influences population density via the
- hunting percentage (Supplementary Figure 9 and Supplementary Table 1). Relationships
- 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
- season length (r=0.37, p<0.001), which however becomes non-significant after controlling for
- 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 biosphere model, to explore the influence of environmental factors on hunter-gatherer population 220 density. The model explicitly simulates micro-scale processes including daily carbon/energy 221 flows among plants, animals and humans, combined with a dynamic time allocation for hunting 222 and gathering activities with simple assumptions. The emergent macroscopic relationships from 223 224 the model are well supported by ethnographic observations of contemporary hunter-gatherers, revealing a causal mechanism whereby short growing seasons drive high fractions of meat in the 225 diet, leading to greatly reduced population density per unit NPP largely as a result of trophic 226 inefficiency. 227

- The empirical negative association between hunting fraction and population density has been 228 reported or implied in previous studies^{14,30}, but it was assumed that population density was the 229 causal factor, rather than vice versa: a higher population density was suggested to lead to less 230 frequent residential moves, more food storage, and thus greater dependence on the stationary and 231 higher productive food of plants and coastal resources¹⁴. Our process-based coupled human-232 ecosystem model suggests a more parsimonious explanation, given that it reproduces the 233 observed relationships as a straightforward consequence of bioenergetics. Reinforcing 234 mechanisms between demography and diet via cultural factors may still be relevant, as suggested 235 by ref.¹⁴ and by anthropological studies on diet from both ecological/biological and sociocultural 236 perspectives³¹. In particular, food storage and sharing have received much attention, due to their 237 close association with societal characteristics and ability to mitigate food scarcity at daily to 238 seasonal timescales 3^{2-34} . It may be interesting to include food storage and sharing in our model 239 framework in the future to quantitatively explore the interplay between environment, 240 241 demography, diet, and sociocultural aspects.
- The integral links between seasonality, diet composition and population density have strong implications for studies that explore ancient human populations. Although seasonal cycles in the availability of different types of food have left traces in fossil teeth of extinct hominins³⁵ and

- been detected in the gut microbiome composition of the Hadza foragers in East Africa³⁶, 245 seasonality has not been included in prior modelling studies^{4,6,7,13} that used only annual NPP 246 and/or mean paleoclimate variables, which would have biased expectations for the spatio-247 temporal pattern of early human distribution and migration. Furthermore, the lengthening of 248 growing seasons following the last deglaciation, combined with the end-Pleistocene megafaunal 249 extinctions that occurred in different regions at different timing and rates³⁷, might have driven 250 long-term changes in diet composition towards less meat-dependence. Our results suggest that a 251 shift from meat-dominated to plant-dominated diet could have boosted population much more 252 than implied by NPP changes alone. Given that demography might be at the core of cultural 253 evolution³⁸, which further shaped human societies^{8,39}, it is crucial to study the trajectory of past 254 population growth and its drivers, under the changing paleoclimate, vegetation and animal 255 distributions. 256
- The model developed here represents a new type of computational modeling for ancient human-257 ecology studies, breaking from a tradition⁴⁰ that has mainly included niche (species distribution) 258 models based on statistical methods and without human feedbacks on the environment, and 259 agent-based models which resolve individual behaviors and interactions but require very detailed 260 local information that is challenging to assess and have only been applied at a local/community 261 scale^{41,42}. By incorporating hunter-gatherers in a realistic, interactive and dynamical global 262 environment, the ESM framework helps to clarify how short growing seasons force humans to 263 rely on meat-rich diets, reducing Φ_{NPP} and thus the population density per unit NPP. Additional 264 factors beyond those resolved in our current model, such as technological transitions^{25,43} and 265 long-range migrations, are sure to have played important roles in determining changes in hunter-266 gatherer population abundance and diet through time. With further development, the approach 267 has the potential to provide more highly resolved pictures of the complex, multifaceted 268 interactions between our ancestors and the Earth system. 269

- 270 Methods
- 271

272 Contemporary hunter-gatherer data

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

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

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

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

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

- recorded hunting percentage is about 30% while the true meat fractions are up to 80% when 314 women's contribution to hunting is included⁵¹. The bias appears to be lower for groups in the tropics like Amazon Basin and Congo Basin⁵³, where recent field observations show less than 315 316 10% of total hunted food from women⁵³. Unfortunately, revisiting and verifying the secondary 317 data on diet composition is difficult due to the disappearance of the foraging lifestyles for most 318 of the recorded hunter-gatherer groups. We therefore conducted a sensitivity test to see how the 319 observed negative relationship between Φ_{NPP} and hunting fraction (Fig. 4c) might be influenced 320 by expected uncertainties and biases in the ethnographic dietary records. As detailed in 321 Supplementary Discussion 1, we found that the relationship between Φ_{NPP} and hunting fraction is 322 robust to the expected biases, with only a minor impact on the slope of the correlation over the 323 most probable range of bias. 324
- 325

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

327 <u>Model overview</u>

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

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

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

367 <u>Daily intake</u>

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

$$I_V = B_V t_g e_g a$$

$$I_A = B_A t_h e_h a$$
(1)

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

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

(2)

387
$$e_g = e_{max} \frac{B_V}{B_V + c B_H}$$
388
$$e_h = e_{max} \frac{B_A}{B_A + c B_H}$$

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

397

Energy expenditure and energetic reserve

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

399 $E = E_c + E_g t_g + E_h t_h$ (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.

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

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

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

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

417 There is an upper limit of $F(F_{\text{max}})$, 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 <u>*Time allocation*</u>

In the current model, we only simulate the time spent in foraging, and leave all other activities such as childcare, domestic maintenance and socializing to an aggregate 'other' category. The hunting, gathering and total foraging time $(t_f=t_h+t_g)$ are updated every day in the following two steps. First, t_f increases or decreases by 1 hr day⁻¹ depending on the changes in the 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
$$t_f \in [t_{f,min}, t_{f,max}]$$

428 $t_{\rm h}$ and $t_{\rm g}$ 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^{-12,18,19}. We therefore set $t_{\rm f,min}$ =0.5 and $t_{\rm f,max}$ =8 hr day⁻¹.

(5)

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

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

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

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

 $Benif_h = B_A e_h$ 440

 $Benif_a = B_V e_a$ 441

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

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

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

Updating food resources 456

468

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

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

469
$$\frac{dB_V}{dt} = \Phi_V \left(f_{fruit} NPP + f_{below} NPP_{grass} \right) - \lambda B_V - I_V P_H$$
470
$$f_{below} = \frac{88.3 - 0.0534 MAP}{100}$$
(7)

100

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

The herbivore dynamics module is coupled once per year with the human dynamics module. Detailed descriptions of the herbivore module can be found in ref.¹⁷. In summary, herbivore population density ($P_{A,tot}$, ind. km⁻²) is updated on a yearly time-step using a logistic equation (Eq. 8 in ref.¹⁷). The herbivore birth and mortality rates depend on an animal fat reserve pool (kg 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:
- $\frac{dB_A}{dt} = -I_A P_H \tag{8}$

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 $P_{A,tot}$. The decreased $P_{A,tot}$ is passed to the herbivore 488 module to calculate a new $P_{A,tot}$ for the next year. B_A is then updated and used in the human 489 module for the new year:

 $B_A = \Phi_A P_{A,tot} W_A \times 0.28 \tag{9}$

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.

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

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

509 <u>Human population dynamics</u>

510 The population birth rate $(r_{\text{birth}}, \text{yr}^{-1})$ 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
$$r_{birth} = \frac{r_a}{1 + e^{-r_b(\frac{F}{F_{max}} - r_c)}}$$
 (10)

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

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

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

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

527 where $P_{\rm H}$ (ind. km⁻²) is the human population density for each grid cell. The $P_{\rm H}$ 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 $P_{\rm H}$ falls below P_0 , $P_{\rm H}$ 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:

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

534 <u>Model setup</u>

525

533

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

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

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

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:

S0: inputs to FORGE are directly from ORCHIDEE outputs;

565

579

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;

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

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

- ecosystems in state-of-the-art terrestrial biosphere models (Supplementary Figure 15), our results
 highlight the need for a more realistic simulation of plant phenology in order to improve the
 simulation of contemporary and ancient hunter-gatherers. Unless otherwise specified, the model
 results shown are from the S2 experiment.
- 597

599

598 Sensitivity tests of parameters

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

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

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

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

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

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

640 Data availability

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

643 **Code availability**

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

648

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655 **Author contributions**

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

- 660 **Competing interests**
- 661 Authors declare no competing interests.
- 662

663 Figure legends

Fig. 1 | Contemporary hunter-gatherer population density vs. net primary production. (a)

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 ($y = 9.6 \times$

 $10^{-4}x - 1.53$) with 95% confidence intervals shown in grey. (b) Violin plot for Φ_{NPP} (fraction

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)
- black bars the inter-quantile (or 5^{th} –95th) ranges. Except for a lower Φ_{NPP} in boreal forest and a
- slightly higher Φ_{NPP} in Mediterranean forest, Φ_{NPP} does not differ significantly among the other five higher times (ANOVA test n > 0.05)

five biome types (ANOVA test p > 0.05).

675

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

683

Fig. 3 | Modelled population density and time allocation. (a) Map of hunter-gatherer 684 population density equilibrated under present-day climate (results in the S2 experiment, see 685 Methods). (b) Relationship between population density and NPP at the grid cells where the 686 observational data are located. The red solid line indicates linear regression of log₁₀(pop. density) 687 vs. NPP ($y = 11.7 \times 10^{-4}x - 1.78$, N=334, r=0.72), with 95% confidence intervals shown in 688 red shading. For comparison, regression of the observations is shown in grey (same as those in 689 Fig. 1a). (c-e) Modelled time spent in foraging (c), separated into gathering (d) and hunting (e). 690 The grid cells where modelled population density is less than $0.2 \text{ ind.}/100 \text{km}^2$ are shown in white 691 in the maps, and excluded in (b). 692

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

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693

703Fig. 5 | Seasonality, diet composition and carbon flows. Model results were averaged over all704grid cells of either gathering-dominated (modelled annual mean hunted food <40%, see Fig. 4a)</td>705or hunting-dominated (hunted food \geq 40%) regions, at dynamic equilibrium. Mean population706density of the two regions is 0.19 and 0.04 ind./km², and mean meat fraction of the diet is 22%707and 55%, respectively. To synchronize the seasonal cycles between the two hemispheres, outputs708of the southern hemisphere were shifted by 6 months. The numbers on the links indicate709percentages of annual NPP that flow to herbivores, humans, and litter (dead plants) and soil

- 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.
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