Inference of ecological and social drivers of human brain–size evolution

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The human brain is unusually large. It has tripled in size from Australopithecines to modern humans[1] and has become almost six times larger than expected for a placental mammal of human size[2]. Brains incur high metabolic costs[3] and accordingly a long-standing question is why the large human brain has evolved[4]. The leading hypotheses propose benefits of improved cognition for overcoming ecological[5–7], social[8–10] or cultural[11–14] challenges. However, these hypotheses are typically assessed using correlative analyses, and establishing causes for brain-size evolution remains difficult[15,16]. Here we introduce a metabolic approach that enables causal assessment of social hypotheses for brain-size evolution. Our approach yields quantitative predictions for brain and body size from formalized social hypotheses given empirical estimates of the metabolic costs of the brain. Our model predicts the evolution of adult *Homo sapiens*-sized brains and bodies when individuals face a combination of 60% ecological, 30% cooperative and 10% between-group competitive challenges, and suggests that between-individual competition has been unimportant for driving human brain-size evolution. Moreover, our model indicates that brain expansion in *Homo* was driven by ecological rather than social challenges, and was perhaps strongly promoted by culture. Our metabolic approach thus enables causal assessments that refine, refute and unify hypotheses of brain-size evolution.

The leading hypotheses for the evolution of brain size make different suggestions as to which cognitive challenges have been the most important in driving brain expansion. 'Ecological-intelligence' hypotheses emphasize challenges posed by the non-social environment, for example, finding, caching or processing food[5–7] (Fig. 1). By contrast, 'social-intelligence' hypotheses emphasize challenges posed by the social environment, for example, cooperating for resource extraction[10,15], manipulating others, avoiding manipulation or forming coalitions and alliances to outcompete others[8,9] (Fig. 1). Social challenges have

been suggested to constitute particularly powerful drivers of brain expansion, because they may have triggered evolutionary arms races in cognition[8–10]. Finally, 'cultural-intelligence' hypotheses emphasize challenges of learning from others, teaching and doing so when there is accumulated cultural knowledge[11–14]. Empirical tests of these hypotheses customarily investigate phylogenetically controlled correlations between brain size (or the size of brain components) and candidate selective factors (for example, diet type[5,17], tactical-deception rate[18], group size[10,19] and social-learning proclivity[20]). However, establishing causality has proven to be difficult. For example, given a positive correlation, it is unclear whether large group sizes favour bigger brains or big brains enable larger group sizes[16]. Moreover, there is the quantitative problem of explaining not only why bigger brains are favoured, but also why they are favoured to the particularly large size observed in humans (around 1.3 kg for a body size of approximately 50 kg in females[21,22]).

To address these problems, we merge elements of metabolic theory[23], life-history theory and differential games to obtain quantitative predictions for the evolution of brain and body size when individuals face ecological and social challenges given metabolic costs of the brain. Our approach incorporates social interactions into a previous non-social model[24] (Supplementary Information 1–3). As a first approximation, we consider a female population and partition the body mass of each individual into three tissues: 'brain', 'reproductive' and other 'somatic' tissue (Fig. 2a). Part of the energy consumption of reproductive tissue is for the production and maintenance of offspring, whereas part of energy consumption of the brain is for production (learning) and maintenance (memory) of energy-extraction skills. Accordingly, at each age the individual has a certain skill level measured in information units (that is, bytes). She extracts energy by using her skill level to overcome ecological or social energy-extraction challenges. Success in an ecological challenge depends on her own skill level, whereas success in a social challenge depends on her skill level and that of her social partners. We
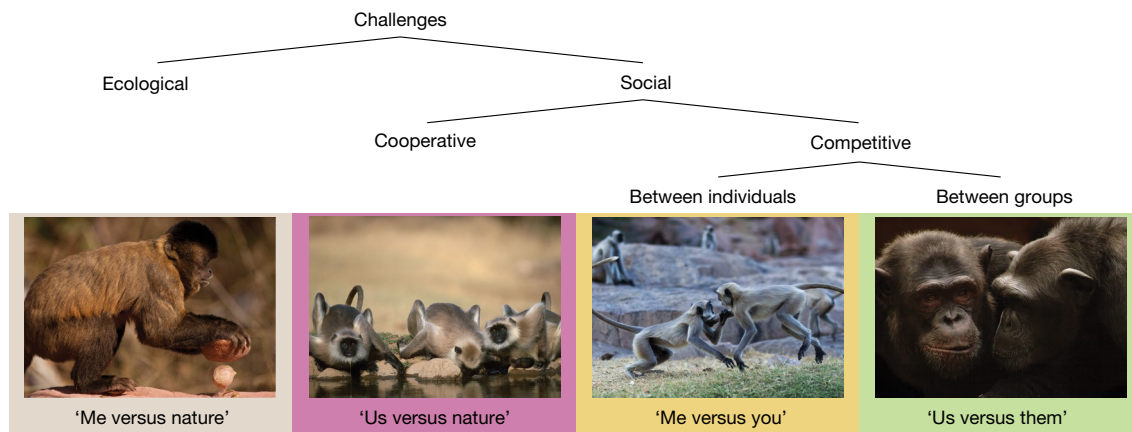

Fig. 1 | Ecological and social hypotheses for brain expansion. Ecological hypotheses emphasize challenges 'against nature', whereas social hypotheses emphasize challenges involving social partners. Here we

partition these hypotheses into four types of challenges that are expected to trigger different evolutionary processes.

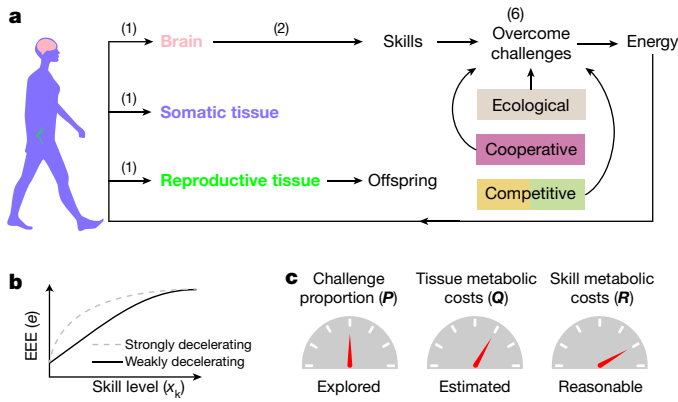[1]School of Biology, University of St Andrews, St Andrews, UK. *e-mail: mgf3@st-andrews.ac.uk

Fig. 2 | Model description. a, Schematic description of the model (see text for details). Numbers in parentheses indicate the corresponding equations in the Methods. **b**, **c**, The model depends on the shape of EEE with respect to skill (**b**) and three sets of parameters **P**, **Q** and **R** (**c**).

consider three types of social challenge: 'cooperative', in which the individual's skill level and that of a social partner of the same age (hereafter 'peer') interact to overcome a challenge; 'between-individual competitive', in which the individual uses her skill level against that of a peer to extract energy; and 'between-group competitive', in which the individual's skill level and that of a peer act together and against the skills of another two peers (that is, one coalition competing against another). We assume that during any small time-interval, the individual faces energy-extraction challenges, a proportion (P_j) of which are of type j (collectively denoted by **P**, with $j = 1, \ldots, 4$ indexing the four challenge

types and $\sum_{j=1}^{4} P_j = 1$). Given **P**, the growth strategy controls the amount of energy allocated to the production of each tissue throughout life, and we let the growth strategy evolve. The individual's energy-extraction efficiency (EEE) thus depends on her skill level, the skill levels of her social partners and the challenges faced, and we consider two shapes for EEE (Fig. 2b and Extended Data Fig. 1). We use previously published data, primarily from Kuzawa et al.[21], for parameter estimates, including metabolic costs of the brain (Fig. 2c, Methods and Extended Data Figs. 2, 3).

We find that increasing the proportion of cooperative challenges decreases both adult absolute brain size (hereafter 'brain size') and adult relative brain size (hereafter 'encephalization quotient', which is the adult brain size divided by expected brain size for a given body size[2]; Fig. 3a–c and Extended Data Fig. 4). By contrast, increasing the proportion of between-individual competitive challenges increases brain size when EEE is weakly decelerating with skill (Fig. 3a), but decreases brain size when EEE is strongly decelerating (Fig. 3b and Extended Data Fig. 4). However, although between-individual competition increases brain size with weakly decelerating EEE, the result is larger brains and smaller bodies than those of modern humans (Fig. 3a and Extended Data Fig. 4). Between-individual competition also decreases body mass as it increases the difficulty of energy extraction and thus limits the energy available for body growth; consequently, between-individual competition increases the encephalization quotient, either because brain size increases and body size decreases or because brain size decreases and body size decreases more strongly than brain size. Increasing the proportion of between-group competition generally decreases brain size, but increases the encephalization quotient, because body size decreases more strongly than brain size (Fig. 3a, b). However,
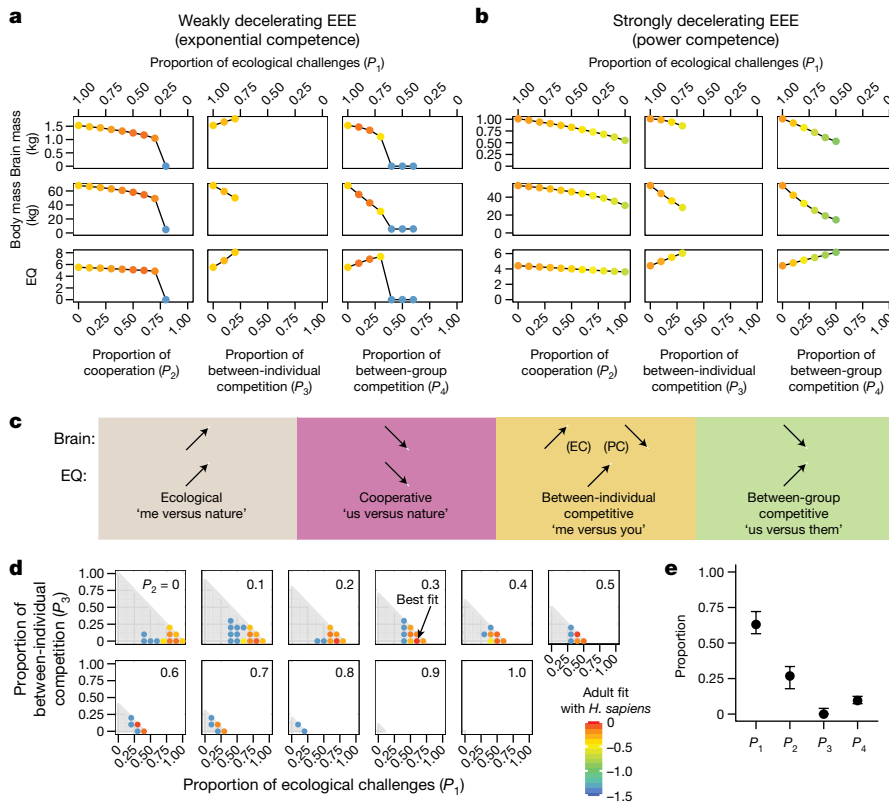

Fig. 3 | Effects of challenge types on brain size and best-fitting scenario for adult *H. sapiens*. a, **b**, Effects of increasing the proportion of a challenge type while decreasing the proportion of ecological challenges. EQ, encephalization quotient. **a**, Weakly decelerating EEE (exponential competence). **b**, Strongly decelerating EEE (power competence). Dot colour indicates the adult fit with brain and body mass of *H. sapiens* (that is, $-D(\tau_a)$; Supplementary Information 6). Zero adult fit means

a perfect fit. **c**, Qualitative effects of challenge types on brain mass and encephalization quotient. **d**, Best fitting scenario for *H. sapiens*. Dots indicate the adult fit for every challenge combination that was solvable. Shaded regions indicate the simplex in which P_j can vary. The best fit occurs in $\boldsymbol{P^*} = (0.6, 0.3, 0, 0.1)$ (adult fit: -0.03). **e**, 'High fit' intervals around $\boldsymbol{P^*}$ where adult fit is greater than -0.05 and dots are interpolated points with the best fit.
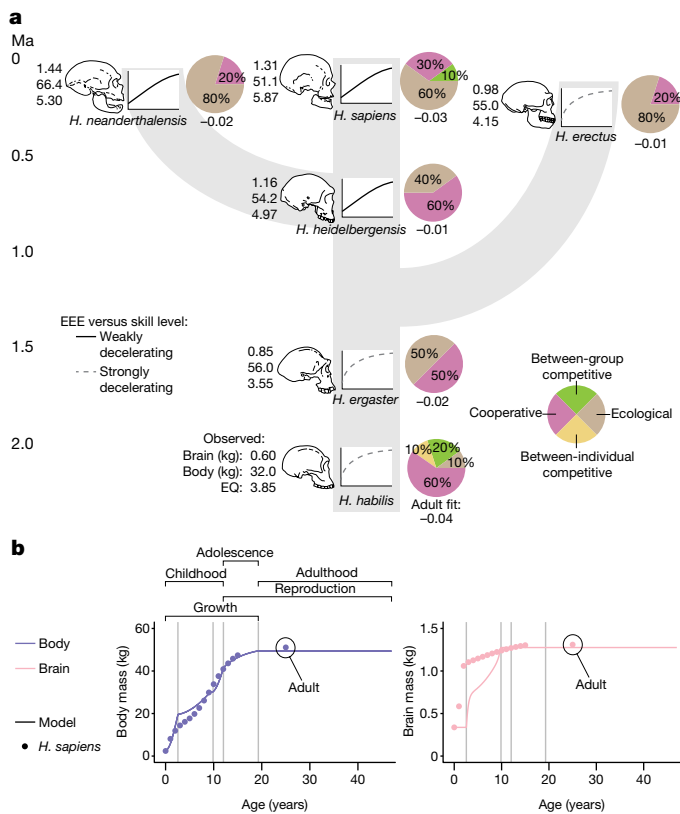
a

b

Fig. 4 | Best-fitting scenarios across adult *Homo*, and resulting predicted life history for *H. sapiens*. a, Best adult fitting scenarios across *Homo* (figure modified with permission from figure 8.1 of ref. [1]). Pie charts and plots respectively show the challenge combination and shape of EEE versus skill that yielded the best adult fit using the same Q and R parameters (Extended Data Figs. 6, 7). **b**, Life history with the challenge combination yielding the best adult fit for *H. sapiens*. Resulting life periods are indicated above the body mass plot. Vertical lines are ages at which the growth strategy changes suddenly; within childhood, they occur when brain growth begins and terminates.

with weakly decelerating EEE and additive cooperation, between-group competition increases both brain size and the encephalization quotient (Extended Data Fig. 4). Moderately frequent between-individual or between-group competition can lead to no allocation to brain and body growth (blue dots in Fig. 3a and Extended Data Fig. 4; see also Extended Data Fig. 5a, d); additionally, moderately frequent between-group competition in the presence of substantial cooperation can lead to arms races in brain size, which fail to yield stable, large brains (for example, because of cycling in brain size or eventual collapse to no allocation into brain growth (Extended Data Fig. 5)). This is because energy extraction becomes exceedingly difficult in the presence of large-brained competitors such that investments in brain or body growth do not pay off and the individual instead invests in early reproduction.

To determine if any combination of social-challenge parameters P yields an accurate prediction of adult brain and body sizes of *H. sapiens* and closely related species, we obtained solutions exhaustively across the P parameter space while holding the other parameters (Q and R) fixed (Fig. 3d, e; Supplementary Information 5). We find near-perfect adult fits across *Homo* species (Fig. 4a and Extended Data Figs. 6–8). A near-perfect adult fit for *H. sapiens* occurs with a large proportion of ecological challenges (approximately 60%), a moderate proportion of cooperative challenges (around 30%), a small proportion of between-group competitive challenges (around 10%), and an approximately complete absence of between-individual competitive challenges (around 0%) (Figs. 3e, 4a and Extended Data Figs. 6, 9). In the resulting reconstruction for *Homo*, ecological challenges increase brain size

whereas social challenges decrease it (Extended Data Fig. 4), the proportion of ecological challenges tends to increase from early to late *Homo* species, and a steep increase in encephalization quotient from *Homo ergaster* to *Homo heidelbergensis* is due to a transition from strongly to weakly decelerating EEE (Fig. 4a). The adult best-fit eco-social scenario for *H. sapiens* also yields a predicted life history that closely matches the species' life-history timing (Fig. 4b and Extended Data Fig. 10). The resulting ontogenetic fit is high for body size, but lower for brain size early in ontogeny (Fig. 4b), perhaps caused in part by our use of a power-law relationship between resting metabolic rate and body mass that underestimates resting metabolic rate early in the ontogeny[24]. With the adult brain size resulting from the best-fitting scenario for *H. sapiens* ($x_b^*(t_a) = 1.276$ kg) , the predicted adult skill level for energy extraction is 3.92 terabytes (TB), which can be calculated with an equation transforming brain mass to skill level[24] ($\hat{x}_k = s_k B_b x_b^*(t_a)/B_k$ where $\hat{x}_k$ is the asymptotic skill level in adulthood; equation (5) in the Methods). By comparison, current rough estimates[25] suggest a human-neocortex storage capacity of approximately 600 TB (Supplementary Information 4.3).

Using previously published data[21] for parameter estimates, our results suggest that adult human-sized brains and bodies may result from ecological challenges as drivers of brain expansion, with cooperation and between-group competition decreasing brain and body size and between-group competition increasing the encephalization quotient by decreasing body size more strongly than brain size (Fig. 3a and Extended Data Fig. 4b). In this eco-social scenario, between-individual competition is unimportant, as it does not lead to human-sized brains and bodies. Cooperation decreases brain size, because it allows individuals to rely on their partners' skills and thus decrease their own investment into costly brains (cooperation invites cheating), which is consistent with diminished brain sizes in cooperatively breeding birds[26] and mammals[27], including primates[28]. For instance, among mole rats, naked mole rats are the most specialized in cooperative breeding and have the smallest relative brain size[29] (however, allomaternal care and brain size are positively associated in mammals[30], but allomaternal care constitutes cooperation targeted at young, which vanishes in adulthood as opposed to the peer-cooperation studied here). Similarly, between-group competition can decrease brain size probably because between-group competition involves cooperation between group members, allowing individuals to rely on their partners' skill. The result that exceedingly frequent competition decreases absolute and relative brain size may be relevant to the observed decreased brain size in cetaceans with the largest group sizes[19]. Cooperation can also decrease body size in our model, because when brain size is disfavoured so too can be body size. This is because a consequence of our model is that a key reason to grow somatic tissue is to make energy available for brain growth: increasing the mass of inexpensive somatic tissue can increase the energy available for tissue (and brain) growth due to the physical constraint imposed by the power-law relationship between resting metabolic rate and body mass[24].

Overall, our assessment fails to support social hypotheses as explanations for the evolution of human brain size, and is more consistent with ecological hypotheses. Our results suggest causal interpretations that differ from some current thinking on the evolution of human cognition. Specifically, we obtained an eco-social scenario that involves a substantial proportion of cooperation (30% against nature and 10% against others), which could shape cognition towards cooperation. This would help to explain aspects of human cognition that facilitate cooperation[11], even if cooperation has not been a driver of human brain expansion. Additionally, because our analysis suggests that brain expansion in *Homo* has not been driven by peer cooperation or competition, our results indicate that social complexity may have had a more limited role in human brain size expansion than is commonly thought—although we emphasize that our analysis is an illustrative starting point and future extensions are encouraged (see Supplementary Information 9). Therefore, our results highlight the fundamental question of why ecological challenges would have favoured substantial brain

expansion in humans but less so in other taxa[10,15]. One clue is suggested by our finding that *H. sapiens*-sized brains and bodies can be obtained only under weakly decelerating EEE (Figs. 3, 4 and Extended Data Fig. 6a): in other words, only when young individuals can maintain a substantial rate of increase in their efficiency of energy extraction as they acquire skills. One possibility is that culture (or cumulative culture) facilitates weakly decelerating EEE if learning from the pool of skills in the population allows individuals to maintain a relatively high rate of increase in EEE as their skill level increases when young. More specifically, the evolution of progressively elaborated social learning, teaching and language[11–14] may have enabled young individuals to continue gaining skills with age, possibly promoting less strongly decelerating EEE. In this respect, our results are consistent with aspects of various cultural hypotheses for brain evolution[13,14] and an explicit account of the effect of culture on EEE could help to address whether culture (or cumulative culture) has enabled ecological challenges to drive brain expansion in humans in ways that have not occurred in other taxa.

Online content

Any Methods, including any statements of data availability and Nature Research reporting summaries, along with any additional references and Source Data files, are available in the online version of the paper at https://doi.org/10.1038/s41586-018-0127-x.

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METHODS

Here we summarize our model; see Supplementary Information for a detailed description of the methods. No experiments were performed in this study and no empirical data were collected.

Model description. We consider a female population with overlapping generations and partition the body mass of each individual into three tissues: brain, reproductive and other somatic tissues. Each individual extracts energy from the environment at each time point to grow and maintain her tissues. We assume that some of the energy consumed by reproductive tissue is for production and maintenance of offspring, while some of that consumed by brain tissue is for production (learning) and maintenance (memory) of domain-general, energy-extraction skills. Accordingly, at each age the individual has a certain skill level measured in information units (that is, bytes). She extracts energy by using her skill level to overcome energy-extraction challenges that can be ecological or social. Success in an ecological challenge depends on her skill level and on the challenge difficulty, which is determined by the (non-evolving) environment. By contrast, success in a social challenge depends on her skill level and that of her social partners. We consider three different types of social challenge: cooperative challenges, in which the individual's skill level and that of a social partner of the same age (peer) interact to overcome a challenge that has a difficulty that is determined by the environment; between-individual competitive challenges, in which the individual uses her skill level against that of a peer to extract energy, such that the difficulty of energy extraction is determined by her competitor's skill level; and between-group competitive challenges, in which the individual's skill level and that of a peer act together and against the skills of another two peers (that is, one coalition competing against another), which determines the challenge difficulty. During any small time-interval, the individual faces challenges, a proportion P_j of which are of type j (with $j = 1, …, 4$ indexing the four challenge types and $\sum_{j=1}^{4} P_j = 1$). For instance, $P_1 = 1$ denotes that individuals face only ecological challenges, whereas $P_1 = P_2 = 0.5$ denotes that individuals only face ecological and cooperative challenges and with equal proportions. We define the growth-metabolic rate as the rate of heat release by a resting individual due to tissue production. Moreover, we define the growth strategy as the fraction of the growth-metabolic rate due to the production of each tissue throughout life. Thus, the growth strategy generates an ontogenetic profile of brain and body size. We consider that the growth strategy evolves by natural selection, and study its evolution using standard evolutionary-invasion analysis; that is, we consider the increase in frequency by selection of rare genetic mutations that control the growth strategy. There is a stable monomorphic female brain size in the population when rare mutants of the growth strategy cannot invade the population; that is, such resident growth strategy is 'uninvadable'[31,32]. We obtain an uninvadable growth strategy using evolutionary-invasion analysis for function-valued traits, since the growth strategy is a function of time (age). Because skill level depends (though not exclusively) on brain size due to energy conservation principles[24], the evolution of brain size causes the evolution of skill level. Accordingly, a cooperating partner's skill level and the difficulty of competitive challenges are evolving environments, which constitute the ultimate distinction between ecological and social challenges in our analysis. This evolving environment implements the notion that sociality can yield evolutionary arms races in cognition as proposed by social hypotheses[8–10].

Energy-extraction efficiency. An important quantity in the model is the individual's EEE, defined as the rate of energy extraction divided by the rate of energy extraction if the individual is maximally successful at energy extraction. We model the individual's EEE as a function of her skill level and that of cooperating or competing peers. To do this, we consider two mathematical functions commonly used in contest models: a 'power competence' function that allows for strongly decelerating EEE as the individual gains skills when she is young, and an 'exponential competence' function that allows for weaker deceleration (Fig. 2b and Extended Data Fig. 1c). We also let the skills of cooperating partners interact in an additive, multiplicative or submultiplicative (geometric mean) way (the geometric mean is a good descriptor of the average skill in the pair if peers have disparate skill levels). Additionally, we assume that if a sufficiently young individual fails to overcome a challenge, then she can extract energy from an environment facilitated by her mother.

Parameters. The model has 4 basic parameters, collectively denoted by P, that specify the proportion of each social challenge, and the effects of which we study here; 13 further parameters, collectively denoted by Q, that measure the metabolic costs of the brain and other tissues, the size of the brain and other tissues at birth and the demography of the population, for which empirical estimates are available; and a final 9 parameters, collectively denoted by R, that measure skill metabolic costs, maternal provisioning, mutation size and how skill level affects energy extraction, for which we use reasonable values given the available data (Fig. 2c; Supplementary Information 4). For example, R parameters include the metabolic cost of memory and the values we use for

this (in megajoules per year per terabyte) fall within an empirically estimated range for resting energy consumption for stored motor patterns in cerebellum Purkinje cells in rats[33]. The exact values used for R are chosen within such reasonable ranges as they yield a high ontogenetic fit between predicted and observed body and brain mass in *H. sapiens* when there are only ecological challenges (that is, $P_1 = 1$; Extended Data Fig. 3g, h). This approach is a reasonable starting point given that the fundamental constraint for a large brain is thought to be the metabolic costs of brain, which are incorporated in the estimated Q parameters. The values chosen for the R parameters mean that the difficulty of ecological challenges is high but not exceedingly so, memory is metabolically expensive (although in the low end of the empirically estimated range), and skills are moderately effective at overcoming the challenges. Using these Q and R parameter values, it was previously shown that ecological challenges alone can generate adult brain and body sizes of ancient human scale: of late *H. erectus* scale with strongly decelerating EEE and of Neanderthal scale with weakly decelerating EEE[24]. Here we use the same Q and R parameter values to study the effects of the social-challenge parameters P.

Key equations. We assume that the population is large and mostly constituted by individuals with a resident growth strategy and by vanishingly rare individuals with a mutant growth strategy. At age t, a focal mutant individual has a mass of tissue i (for $i \in \{b, r, s\}$ for brain, reproductive and somatic) of $x_i(t)$ (in kilograms) and a skill level of $x_k(t)$ (in terabytes). The growth rate of tissue $i \in \{b, r, s\}$ is

$$\dot{x}_i(t) = \frac{1}{E_i} u_i(t) \left[B_{\text{rest}}(t) - \sum_{i \in \{b,r,s\}} B_i x_i(t) \right] \quad (1)$$

where $\dot{x}_i(t)$ denotes the derivative of $x_i(t)$ with respect to t. The term in square brackets is the growth-metabolic rate ($B_{\text{syn}}(t)$), which equals the resting metabolic rate, $B_{\text{rest}}(t)$, minus the maintenance metabolic rate, $\sum_{i \in \{b,r,s\}} B_i x_i(t)$. The metabolic cost of producing (respectively, maintaining) a mass of tissue i is E_i (respectively, B_i). The growth strategy is the fraction of the growth-metabolic rate due to the production of each tissue throughout life, and for the mutant it is denoted by $u_i(t)$ for all t and all $i \in \{b, r, s\}$ (or u for short). We let the growth strategy be the evolving trait. In turn, the mutant skill growth rate is

$$\dot{x}_k(t) = \frac{1}{E_k} [s_k B_{\text{rest,b}}(t) - B_k x_k(t)] \quad (2)$$

The brain metabolic rate is $B_{\text{rest,b}}(t)$, and the metabolic cost of gaining (respectively, maintaining) a skill unit is E_k (respectively, B_k). The fraction of brain metabolic rate allocated to energy-extraction skills is s_k. Resting metabolic rate is a power function of body mass, $x_B(t)$, and a function of EEE, which we denote by $e(x_k(t), y_k(t))$:

$$B_{\text{rest}}(t) = K e(x_k(t), y_k(t)) x_B^{\beta}(t) \quad (3)$$

where $y_k(t)$ is the skill level at age t of a resident individual. The brain metabolic rate is the sum of brain's maintenance and growth metabolic rates:

$$B_{\text{rest,b}}(t) = B_b x_b(t) + E_b \dot{x}_b(t) \quad (4)$$

An uninvadable growth strategy $u_i^*(t)$ for all t and all $i \in \{b, r, s\}$ (or u^*) is a best response to itself (similar to a Nash equilibrium) regarding the lifetime number of offspring it yields[31,32] (see 'Evolutionary differential game'). We denote the tissue mass and skill level resulting from an uninvadable growth strategy as $x_i^*(t)$ for all t and all $i \in \{b, r, s, k\}$ (or x^* for short).

Switching times. With the parameter values that we use, the uninvadable growth strategies typically produce a life history with four critical ages at which the growth strategy changes suddenly (called switching times in optimal control terminology): the age of brain growth onset t_{b0}, which is when allocation to brain growth starts; the age of brain growth arrest t_b, when allocation to brain growth stops; the age at maturity t_m, when allocation to growth of reproductive tissue starts; and the age at adulthood t_a, when allocation to growth of non-reproductive tissues stops. These four ages are an output, not parameters, of the model.

Asymptotic skill level. In adulthood (that is, after t_a), brain growth is absent and when memory is expensive enough skill growth asymptotically ceases[24]. Specifically, $\dot{x}_b^*(t) = 0$ for $t \geq t_a$ and $\dot{x}_k^*(t)$ tends to 0 as t tends to T, where T is the age of menopause. Substituting this and equation (4) into equation (2) yields the asymptotic skill level

$$\hat{x}_k = s_k \frac{B_b}{B_k} x_b^*(t_a) \quad (5)$$

Equations for EEE. In Supplementary Information 2.1, we show that EEE can be written as

$$e(x_k(t), y_k(t)) = \sum_{j=1}^{4} P_j \left[\frac{c_j}{c_j + d_j} + \frac{d_j}{c_j + d_j} \varphi \right] \quad (6)$$

The term in square brackets (denoted by e_j) gives the EEE when facing a challenge of type j and is composed of two terms. The first term is the proportion of time that the individual succeeds at the challenge, and the second term is the proportion of time that the individual fails at the challenge but extracts energy from maternal provisioning. The individual's competence at a type-j challenge is c_j and in general depends on her own and on her social partners' skill level. The difficulty of a type-j challenge is d_j and in general depends on the social and non-social environment (that is, on the social partners' skill level and the constant environment). Because the mutant is rare, her social partners are residents. The EEE from maternal provisioning is φ, which decreases with age.

Using our assumption of domain-general skills, we let the competence function be independent of the challenge type, $c_j(G_j(x_k, y_k)) = c(G_j(x_k, y_k))$, where $G_j(x_k, y_k)$ is a production function describing how the skills of the cooperating partners interact (that is, in an additive, multiplicative or submultiplicative way). We consider two forms for the competence function:

$$c(G_j(x_k, y_k)) = \begin{cases} G_j^\gamma(x_k, y_k) & \text{with power competence} \\ \exp(G_j(x_k, y_k))^\gamma & \text{with exponential competence} \end{cases} \quad (7)$$

where γ measures the effectiveness (decidability) of skills at the challenge. The production function $G_j(x_k, y_k)$ is

$$G_j(x_k, y_k)$$
$$= \begin{cases} x_k & \text{for } j \in \{1,3\} \\ x_k + y_k & \text{for } j \in \{2,4\} \text{ with additive cooperation} \\ x_k \times y_k & \text{for } j \in \{2,4\} \text{ with multiplicative cooperation} \\ \sqrt{x_k \times y_k} & \text{for } j \in \{2,4\} \text{ with sub–multiplicative cooperation} \end{cases} \quad (8)$$

The difficulty d_j of a challenge depends on the challenge type. For an ecological or a cooperative challenge, the challenge difficulty is α, which depends on the ecological environment, which we assume is constant (this assumption can be relaxed in future extensions; Supplementary Information 9). In turn, the difficulty of a competitive challenge depends on the skill level of the individual's competitors. Since the mutant is rare, a mutant's competitors are residents, so the difficulty of a competitive challenge is the competence of the resident, $c(G_j(y_k, y_k))$. In general, the difficulty of a type-j challenge is

$$d_j(y_k) = \begin{cases} \alpha & \text{for } j \in \{1,2\} \\ c(G_j(y_k, y_k)) & \text{for } j \in \{3,4\} \end{cases} \quad (9)$$

We let the EEE from maternal provisioning when the individual is of age t be

$$\varphi(t) = \varphi_0 \exp(-\varphi_r t) \quad (10)$$

where φ_0 is the EEE from maternal provisioning at birth and φ_r measures the rate of decrease of maternal provisioning. The resulting equations for e_j for all cases considered can be found in Supplementary Information 2.3.

Evolutionary differential game. Let $R_0(u, v)$ be the expected lifetime number of offspring of a mutant with growth strategy u when the resident growth strategy is v. We assume that the population is kept at a constant size due to density-dependent competition through fertility rather than survival. Hence, an uninvadable growth strategy u^* maximizes the mutant's expected lifetime number of offspring when u^* is resident[34]. That is, an uninvadable growth strategy u^* satisfies

$$u^* \in \underset{u \in U}{\operatorname{argmax}} R_0(u, u^*) \quad (11)$$

where U is the set of feasible growth strategies. Assuming that the mortality rate μ is constant (which can be relaxed in future extensions; Supplementary Information 9) and that reproductive tissue is narrowly defined so that it is not involved in offspring maintenance (for example, defined as preovulatory ovarian follicles), the mutant's expected lifetime number of offspring when v is resident is

$$R_0(u, v) \propto \int_0^T \exp(-\mu t) x_r(t) \mathrm{d}t \quad (12)$$

Thus equation (11) poses a differential game problem: it is a 'game' between mutant and resident because the mutant's payoff ($R_0(u, v)$) depends on the resident strategy, it is 'differential' because it depends on differential equations (equations (1) and (2)), and it is 'evolutionary' rather than a typical differential game because only the mutant's payoff is maximized rather than both the mutant and resident's payoffs. Because equation (11) involves maximization with respect to functions (u) rather than points, this maximization poses an optimal control problem. We solve this problem numerically by finding a best response to the resident (optimal control problem), setting the best response as the resident, and iterating until convergence to a point at which the mutant and resident strategies are indistinguishable to a chosen extent. To do so, we use the software GPOPS[35].

Figure specifications. For Fig. 3a, b, plots are around only ecological challenges; that is, for a given plot, the remaining two P_j's are set to zero. For social challenges, the arrows in Fig. 3c describe the qualitative effect determined in Fig. 3a, b of increasing the proportion of a social challenge as the proportion of ecological challenge decreases; for ecological challenges, the arrows describe the qualitative effect of increasing the environmental difficulty α as found in Extended Data Fig. 3g, h. The patterns in Fig. 3a–c also hold around the best-fitting P^* for *H. sapiens*; that is, when for a given plot, the remaining two P_j's are set to the values of P^* (Extended Data Fig. 4b, c). The 'missing' dots in Fig. 3d are P_j combinations that did not converge to an uninvadable growth strategy (for example, owing to cycling solutions, suggesting possible evolutionary branching (female dimorphism) in brain size) or that were unreachable from lack of convergence of nearby runs (Supplementary Information 5). For Fig. 3a–e, cooperation is submultiplicative and for Fig. 3d, e, competence is exponential (see Extended Data Fig. 4 for all cases).

Figure 4a shows the hominin species for which we find a near-perfect adult fit (that is, for which the best adult fit is greater than the chosen threshold of $-D(\tau_a) = -0.05$; Extended Data Figs. 6–8). For Fig. 4a, cooperation is submultiplicative (respectively additive) for weakly (respectively strongly) decelerating EEE. In Fig. 4b, dots are the values for an average *H. sapiens* female as previously reported[21]. The resulting life periods in Fig. 4b are defined as 'childhood', when there has not been allocation to production of reproductive tissue from birth; 'adolescence', when there is allocation to production of somatic and reproductive tissues; and 'adulthood', when there is only allocation to production of reproductive tissue. The EEE from maternal provisioning at birth (part of the R parameters) in Fig. 4b is slightly smaller than its benchmark value to improve ontogenetic fit further without affecting adult fit (ontogenetic fit is $-E(D(\tau)) = -0.22$ using $\varphi_0^* = 0.5$ rather than -0.33 using the benchmark $\varphi_0 = 0.6$; Supplementary Information 6, 8).

Reporting summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

Code availability. Code that supports the findings of this study is available in Zenodo with the identifier https://doi.org/10.5281/zenodo.1197479.

Data availability. Data of predicted brain size, body size and skill level for the various challenge combinations as generated by this study and as used for Figs. 3, 4 and Extended Data Fig. 4, 6–8 have been deposited in Zenodo with the identifier https://doi.org/10.5281/zenodo.1197479. Complete numerical solutions, including growth strategies across the parameter sweep totalling 200 GB of data have been deposited in Zenodo with the identifier https://doi.org/10.5281/zenodo.1217123.

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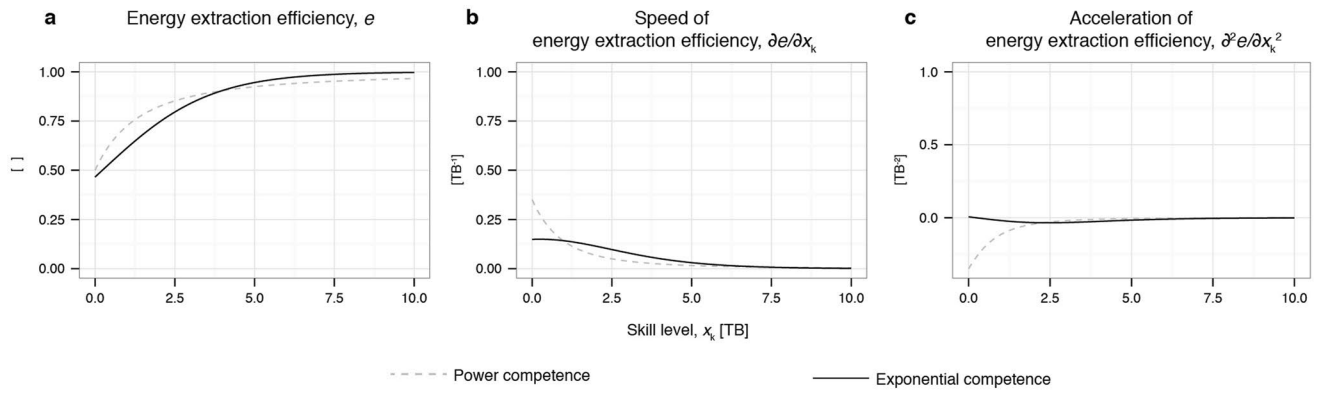
Extended Data Fig. 1 | Shape of EEE versus skill. a–c, Plots of EEE (e), its speed and acceleration with respect to skill level under power competence and exponential competence with only ecological challenges (that is, $P_1 = 1$) for the parameter values used and without maternal provisioning (that is, $\varphi = 0$, so that $e = S_1$). For comparison, the curves for power competence are displaced to the left by 1 unit because skill level at birth is 1 for power competence but 0 for exponential competence. **a, b,** e and its speed at birth and during young ages are smaller for exponential competence than for power competence. **c,** However, the acceleration in e at birth and at young ages is larger for exponential competence than for power competence.
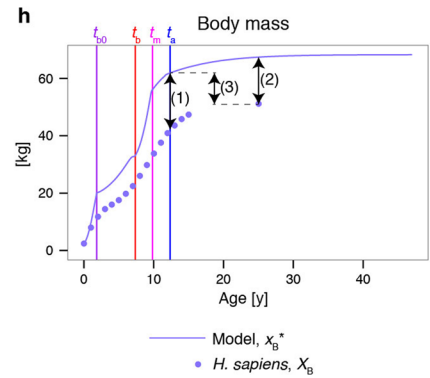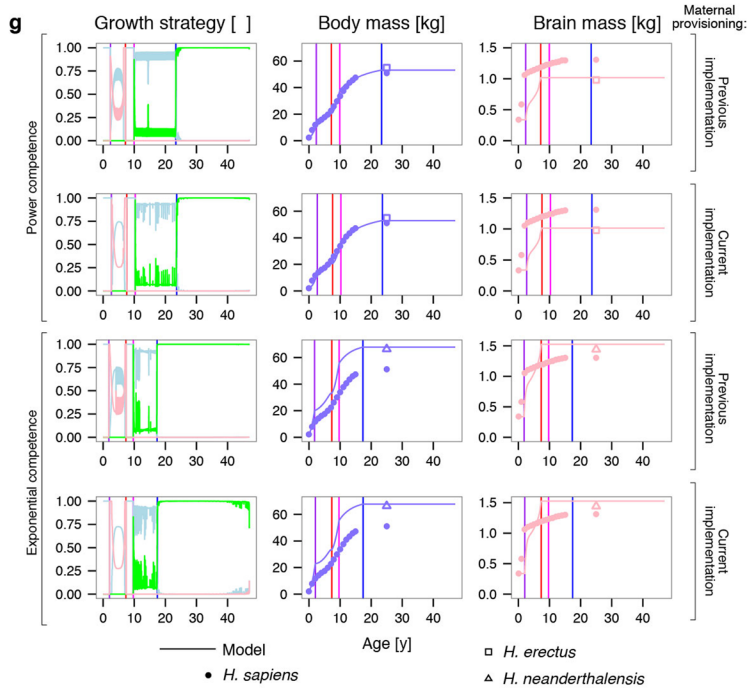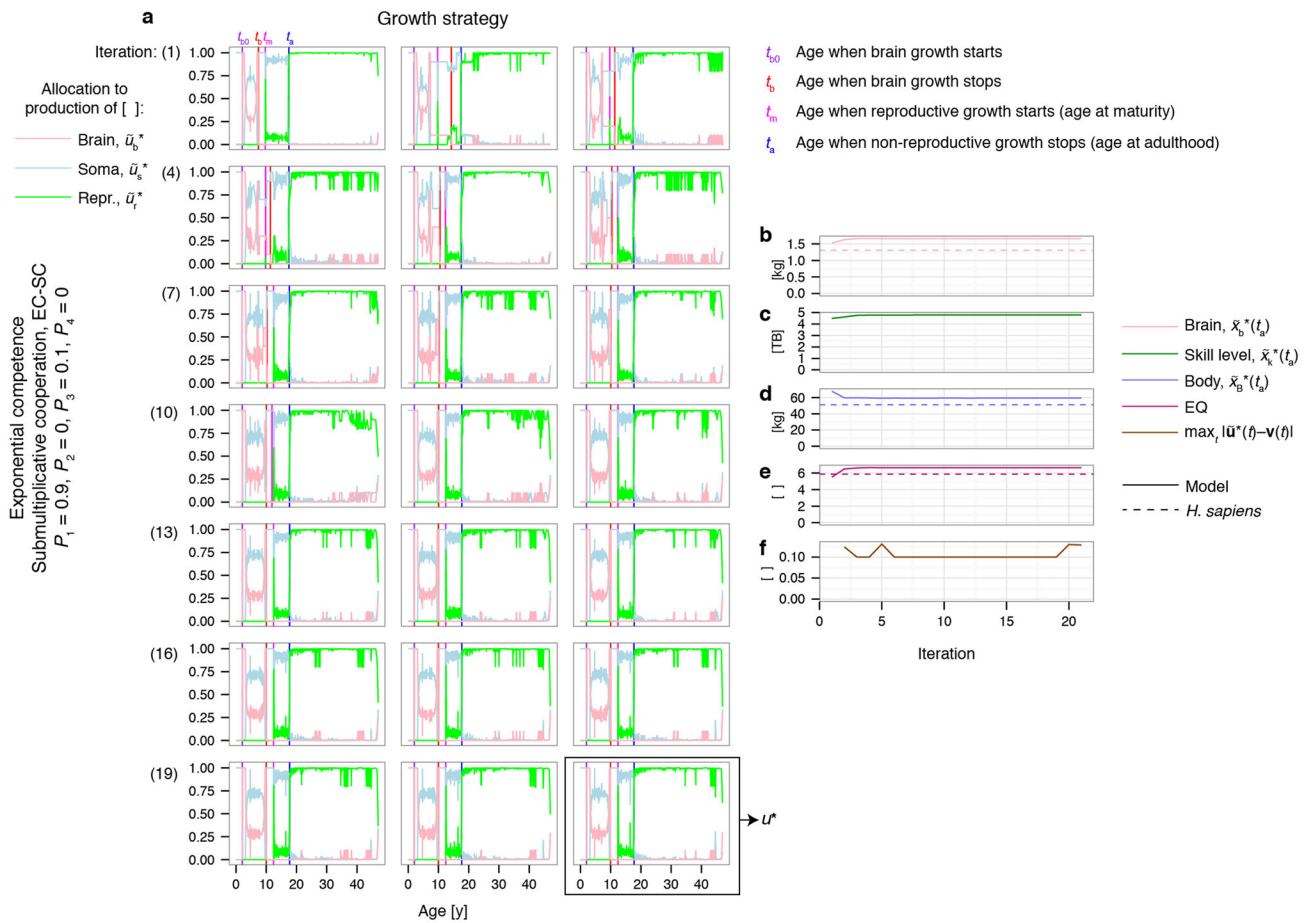
Extended Data Fig. 2 | See next page for caption.

Extended Data Fig. 2 | Method implementation. a, Typical result with convergence to an uninvadable growth strategy. For the ith best-response iteration, the growth strategy shown is the resident (v) whose best response ($\tilde{u}^*$) is shown next, which is the resident of the $i+1$th iteration. Convergence to a best response to itself (u^*) was declared visually, in this case, at iteration 21. **b–f,** Reporting variables across the best-response iterations in **a**. **b–e,** Resulting adult body mass, brain mass, skill level and encephalization quotient across iterations. These values tend to converge more quickly than the growth strategy (**a**). **f,** Rather than visually declaring convergence, convergence should ideally be declared when the difference between mutant and resident is below a chosen threshold. However, numerical jittering prevented the use of this criterion. For example, **f** shows the maximum of $|\tilde{u}^*(t)-v(t)|$ across t for each iteration in **a**. Without numerical jittering, this maximum should decrease as the growth strategy approaches a best response to itself. However, numerical jittering causes this maximum to be at least equal to the maximum mutation size $\delta=0.1$. The maximum of $|\tilde{u}^*(t)-v(t)|$ is occasionally greater than δ because $\tilde{u}^*$ and v have different partitions over t and we use the following approximation: for each t in the t partitioning of $\tilde{u}^*$, we find the closest t in the t partitioning of v and calculate the difference $|\tilde{u}^*(t)-v(t)|$ at these relatively close times; this may occasionally cause the difference to be the larger than δ when strategies change suddenly with t. Alternative measures of convergence were similarly inadequate (for example, $\Sigma_t\ |\tilde{u}^*(t)-v(t)|$). **g,** We implement maternal provisioning differently than before[24] to incorporate it when there are social challenges. The difference yields no detectable difference in predicted brain and body mass with only ecological challenges after slightly adjusting the EEE from maternal provisioning of a newborn (φ_0): before[24], $\varphi_0=0.6$ for power and $\varphi_0=0.8$ for exponential competence were used; here, $\varphi_0=0.4$ for power and $\varphi_0=0.6$ for exponential competence were used. **h,** Three ways to measure adult fit: (1) at the predicted age of adulthood ($x_{\mathrm{B}}^*(t_{\mathrm{a}})-X_{\mathrm{B}}(t_{\mathrm{a}})$); (2) at the observed age of adulthood ($x_{\mathrm{B}}^*(\tau_{\mathrm{a}})-X_{\mathrm{B}}(\tau_{\mathrm{a}})$); and (3) at the predicted age of adulthood for the prediction and at the observed age of adulthood for the observation ($x_{\mathrm{B}}^*(t_{\mathrm{a}})-X_{\mathrm{B}}(\tau_{\mathrm{a}})$). We use option 2.
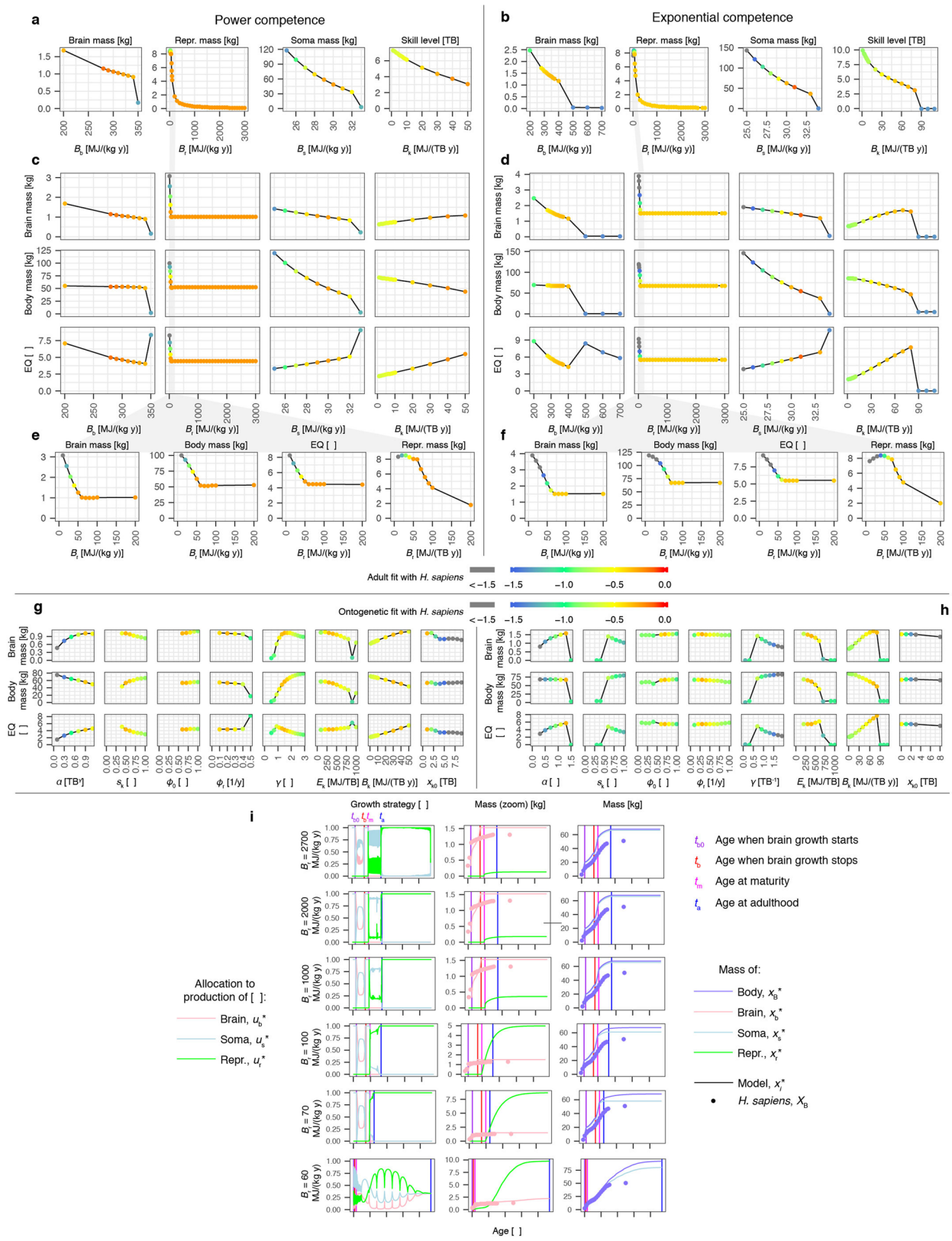
**Extended Data Fig. 3 |** See next page for caption.

Extended Data Fig. 3 | Effects of Q and R parameters. a, b, Effects of maintenance costs (B_i) on the corresponding tissue mass or skill level. Each B_i tends to decrease the value $x_i^*(\tau_a)$ for the corresponding i, but not necessarily for the other i (see **c, d**). **c, d**, Effect of B_i on adult brain mass, body mass and encephalization quotient. With power competence (**c**), when $B_b = 310$ and 340 MJ kg^{-1} per year (y), the predicted adult brain mass is $x_b^*(\tau_a) = 1.0298$ and 0.9133 kg, respectively. With exponential competence (**d**), when $B_b = 310$, 340 and 370 MJ kg^{-1} y^{-1}, the predicted adult brain mass is $x_b^*(\tau_a) = 1.542$, 1.3973 and 1.2767 kg, respectively. **e, f**, Effects of B_r when B_r is small. When B_r varies between 70 and $2,700$ MJ kg^{-1} y^{-1}, B_r has no detectable effect on adult brain mass and encephalization quotient. **g, h**, Ontogenetic fit with *H. sapiens* around the used values for each of the R parameters (except δ). The ontogenetic fit is approximately maximized around the benchmark values chosen previously[24], which are also used here (except for φ_0 given our improved implementation of φ). **i**, Effect of B_r on the predicted life history with exponential competence. In the left column, from top to bottom, as B_r decreases, the allocation to the growth of reproductive tissue during adolescence increases (u_r^* between t_m and t_a) and adolescence shortens. In the central column, the increased allocation to the growth of reproductive tissue increases the mass of reproductive tissue, but brain mass does not change with B_r for $B_r \geq 70$ MJ kg^{-1} y^{-1}. In the right column, as the mass of reproductive tissue increases, body mass increases slightly, which is more noticeable for $B_r \leq 100$ MJ kg^{-1} y^{-1}. An exceedingly small B_r (<70 MJ kg^{-1} y^{-1}) disrupts the predicted life history, which with $B_r = 60$ MJ kg^{-1} y^{-1} is severely different from that of *H. sapiens* (for example, there is brain growth late in life and reproductive growth from birth). Similar results arise for even smaller B_r. In **a–i** there are only ecological challenges and we use the previous[24] definition of φ.
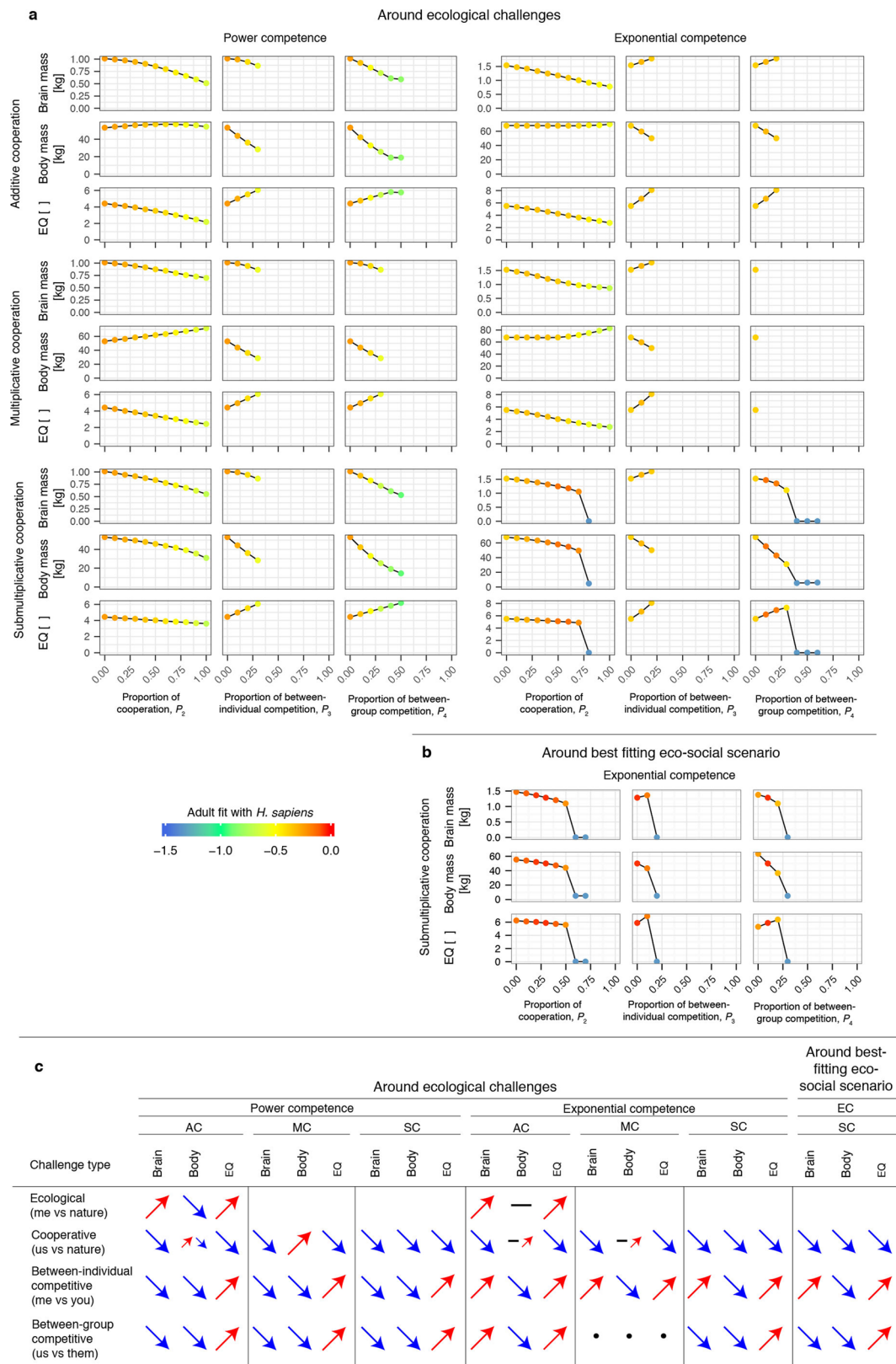
Extended Data Fig. 4 | Effects of challenge types on brain size.
a, **b**, Outer rows are for the cooperation cases that were considered; outer columns are for the competence cases. **a**, Around the pure ecological scenario (that is, in a given plot for P_j as P_1 decreases, the remaining two P_j's are set to zero). **b**, Around the best fitting scenario for *H. sapiens* (that is, in a given plot for P_j as P_1 decreases, the remaining two P_j's are set to the best fitting P^* found in Fig. 3d. **c**, Summary of the qualitative effects of challenge types on brain size. For social challenges, the direction of

the arrows is taken from **a**, **b**. For ecological challenges, the direction of the arrow is taken from Extended Data Fig. 3g as the environmental difficulty α increases. A dash ($-$) indicates an approximately invariant relationship and a dot ($\cdot$) indicates insufficient data points for identifying a relationship. The arrows in Fig. 3c are taken from this summary, in which, for social challenges, the arrows are those of submultiplicative cooperation. AC, additive cooperation; EC: exponential competence; MC, multiplicative cooperation; SC, submultiplicative cooperation.
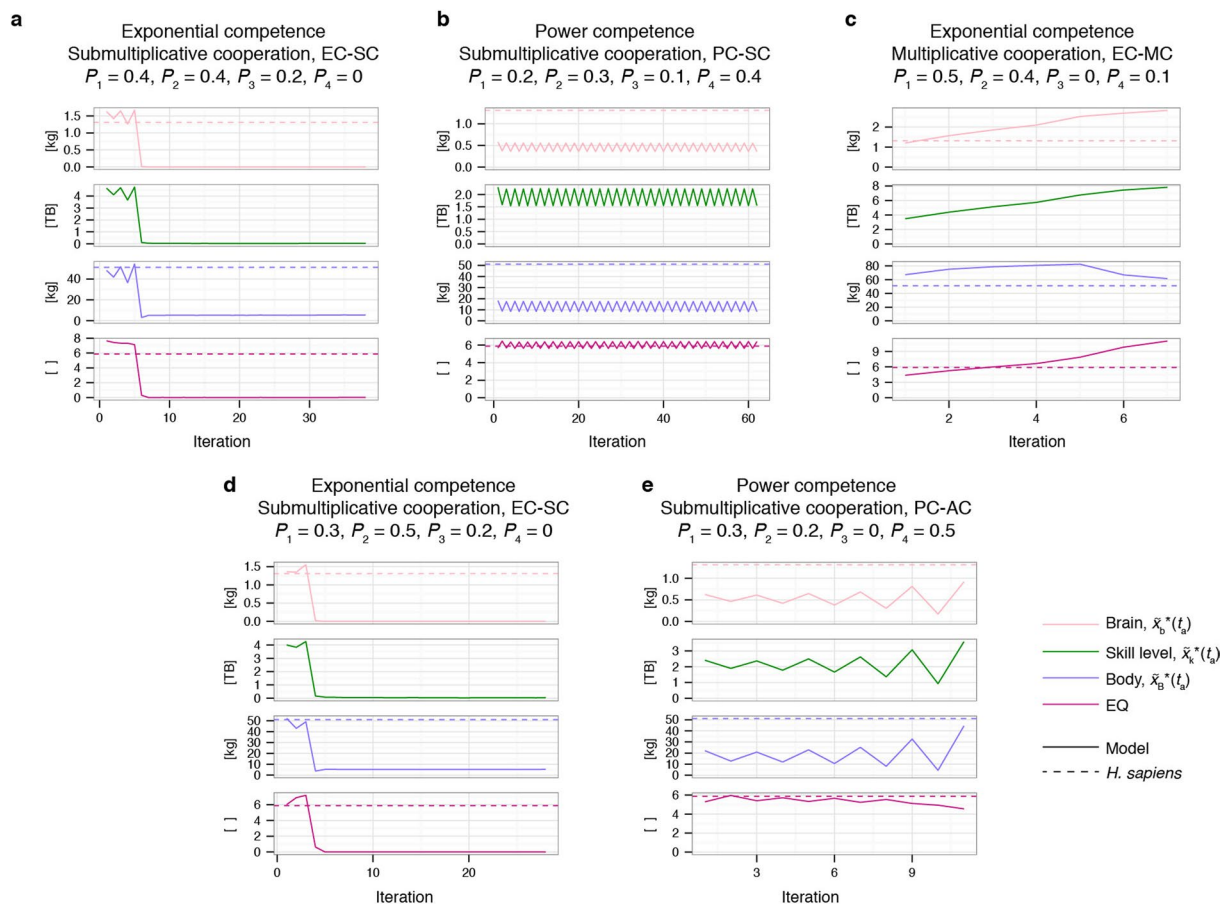
Extended Data Fig. 5 | Typical results when there is convergence to no brain growth or when there is no convergence to an uninvadable growth strategy. a–e, Adult values over best-response iterations for cases of no brain growth or no convergence to an uninvadable strategy. **a**, Amplifying cycle leads to no brain growth. **b**, Stable cycle. **c**, Arms race that ends when the solver warns that the optimal control problem (OCP) may be infeasible. This might arise if the best response to the last iteration necessarily involves a substantially different growth strategy, which is not allowed in the optimization as the best response is constrained to be sufficiently similar to that in the previous iteration. It is possible that such substantially different best response involves either no brain growth (for example, as seen under purely ecological challenges when the environmental difficulty is exceedingly high[24] (Supplementary Information 4.4)) or substantially more allocation to brain growth (which appears unlikely given the energetic constraints). **d**, A short arms race in encephalization quotient that leads to no brain growth. **e**, Amplifying cycle that ends when the solver warns that the OCP may be infeasible.
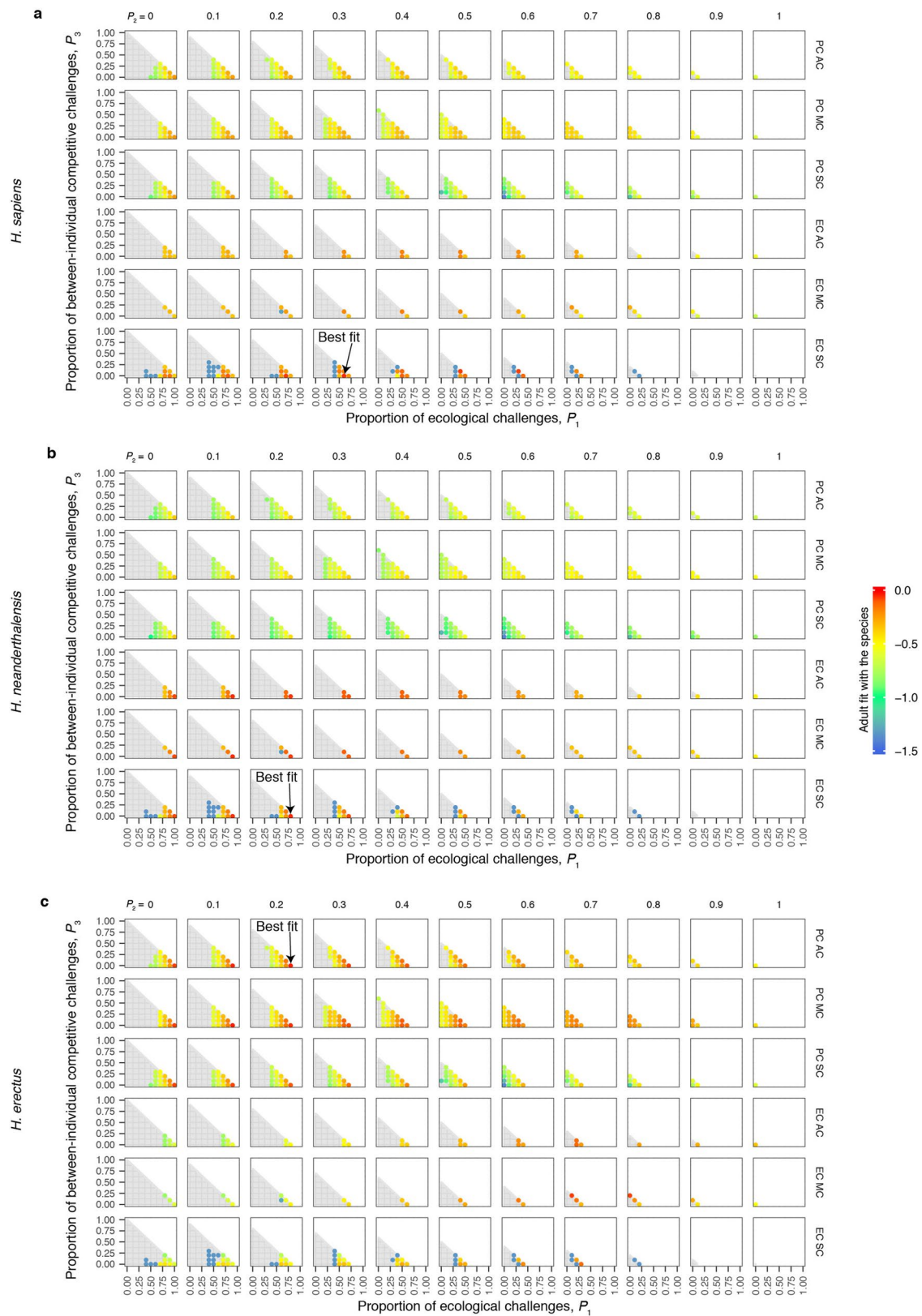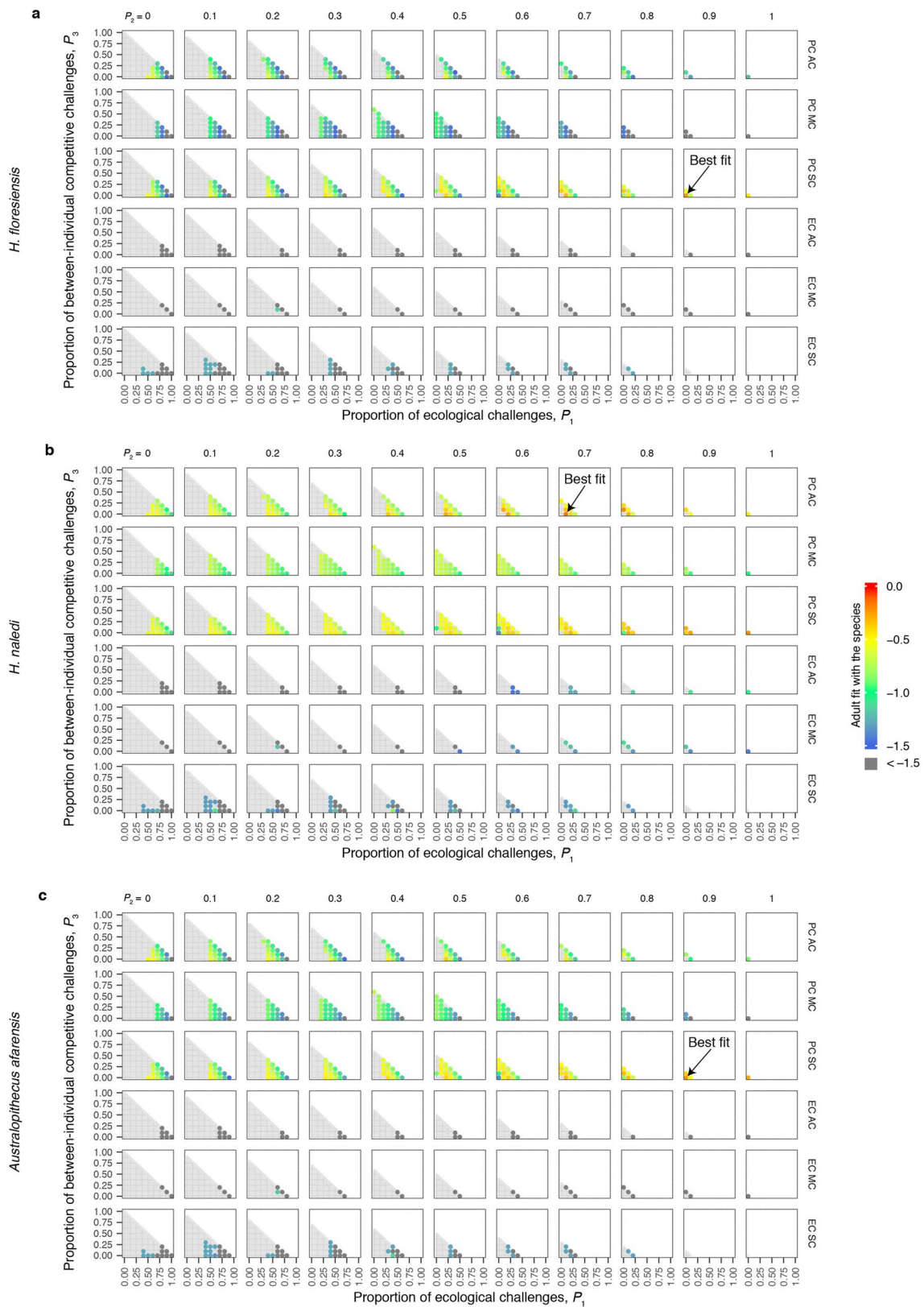
Extended Data Fig. 6 | Identification of best-fitting scenarios across hominins. Adult fit of predicted adult brain and body mass with those observed in a given species across parameter values for all cases considered. Each dot's colour gives the adult fit, $-D(\tau_a)$, for the corresponding parameter combination and case. **a**, *H. sapiens*. **b**, *H. neanderthalensis*. **c**, *H. erectus*.
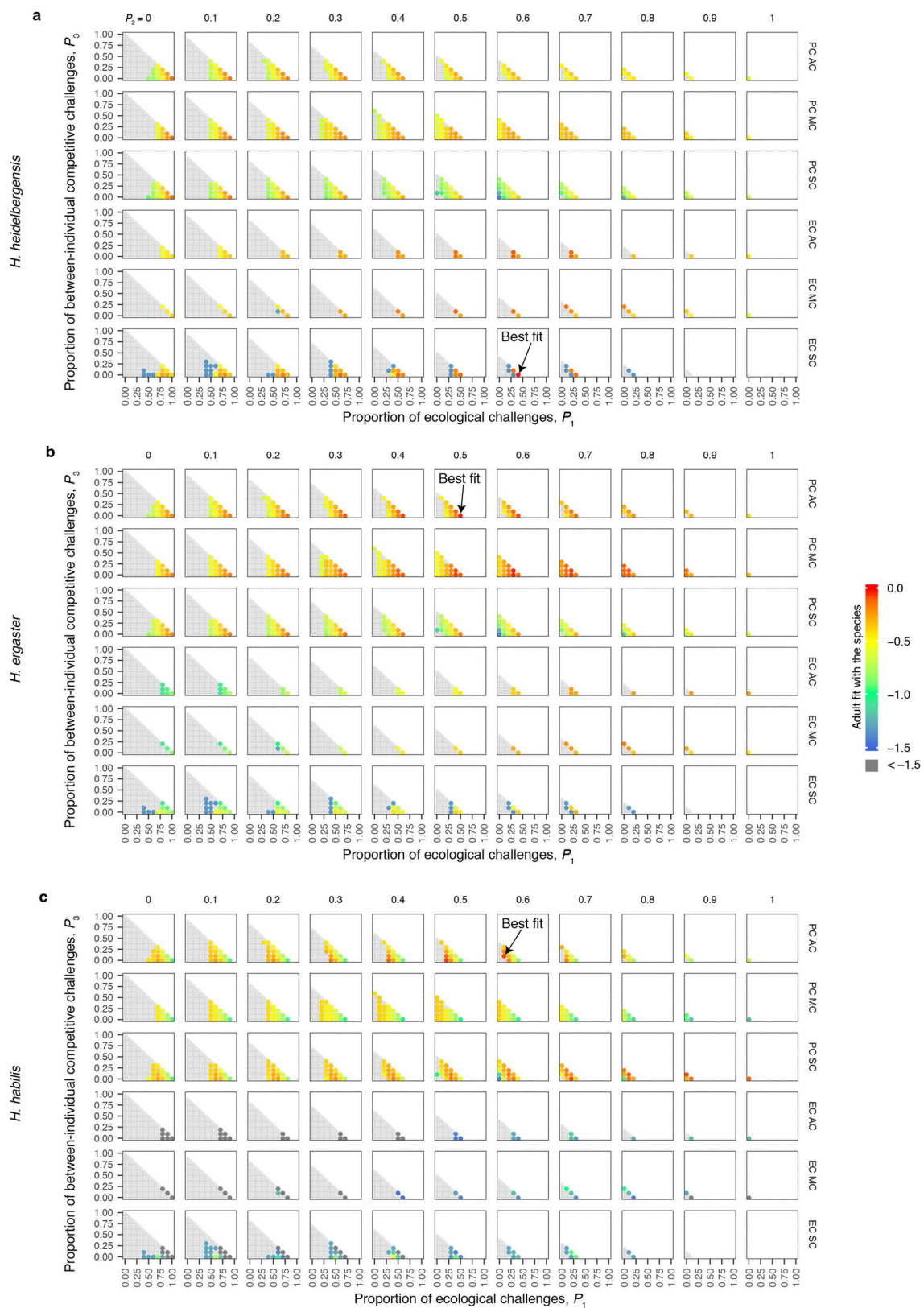
Extended Data Fig. 7 | Identification of best-fitting scenarios across hominins, continued. See legend of Extended Data Fig. 6 for details.
a, *H. heidelbergensis*. **b**, *H. ergaster*. **c**, *H. habilis*.

**Extended Data Fig. 8 | Identification of best-fitting scenarios across hominins, continued.** See legend of Extended Data Fig. 6 for details. **a**, *H. floresiensis*. **b**, *H. naledi*. **c**, *Australopithecus afarensis*. The best adult fit is −0.24 (**a**), −0.14 (**b**) and −0.23 (**c**).
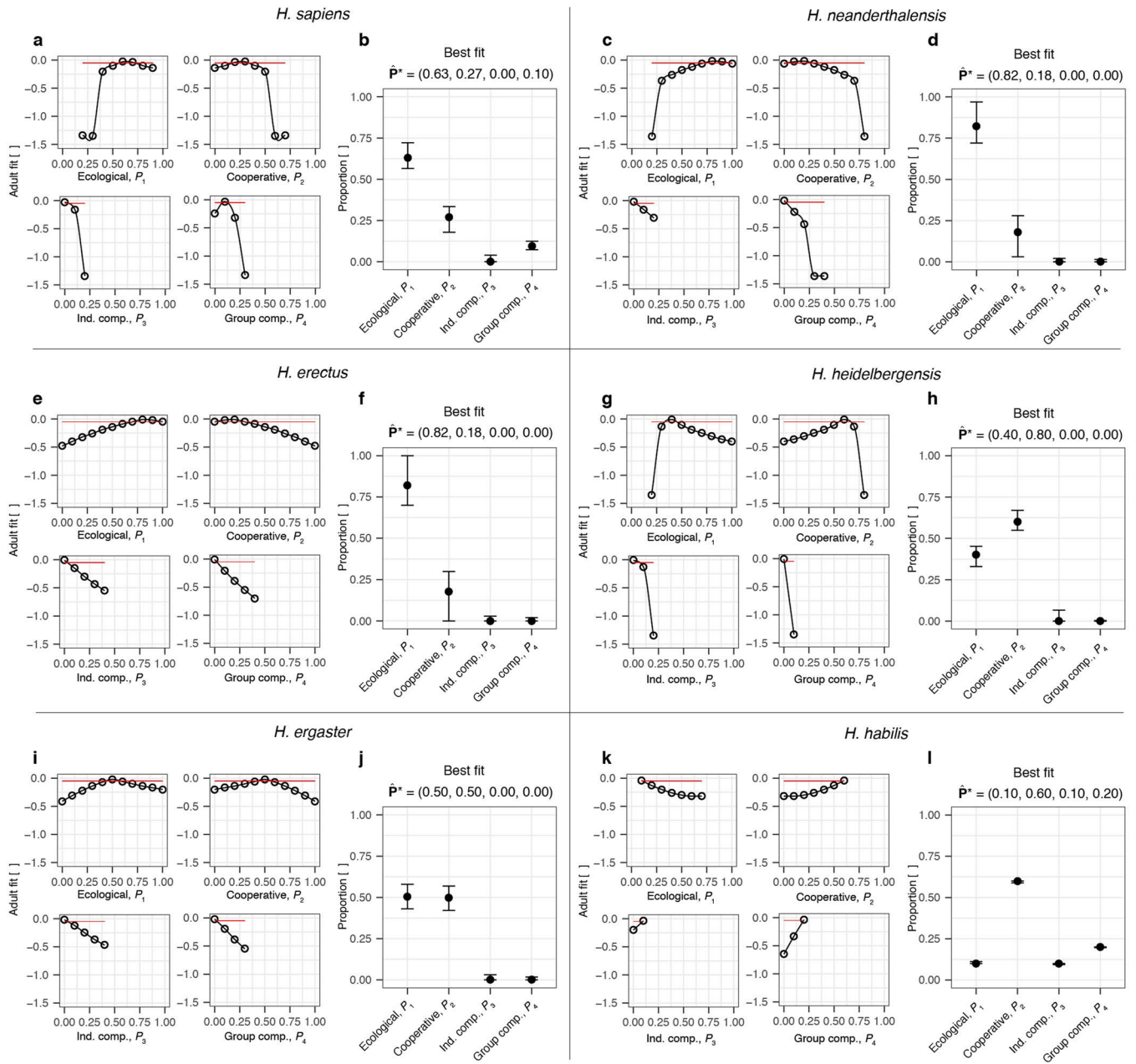
Extended Data Fig. 9 | High fit intervals for best-fitting scenarios across hominins. Here we show high fit intervals around the best fitting scenarios across hominins having a best adult fit greater than −0.05. **a, c, e, g, i, k,** For the top left plot, as P_1 increases, P_2 decreases, whereas for the remaining plots as P_2, P_3 and P_4 increase, P_1 decreases; for a given plot, the remaining P_j are set to the corresponding $\mathbf{P^*}$ shown in Fig. 4a (that is, plots are around $\mathbf{P^*}$). The dots are the adult fit and the lines are interpolated values using a monotone Hermite spline (splinefun with

method monoH.FC in R). The red line is $-D(\tau_a) = -0.05$. **b, d, f, h, j, l,** The whiskers are the high fit intervals where adult fit is greater than −0.05 and the dots are the estimated $\hat{\mathbf{P}}^*$ giving the best adult fit for the species in the interpolation. The cases of competence and cooperation are as found in Extended Data Figs. 6, 7. Note that for *H. habilis*, the high fit intervals may be wider as the adult fit is increasing at the end of the values of P_2, P_3 and P_4 for which uninvadable growth strategies were obtained.
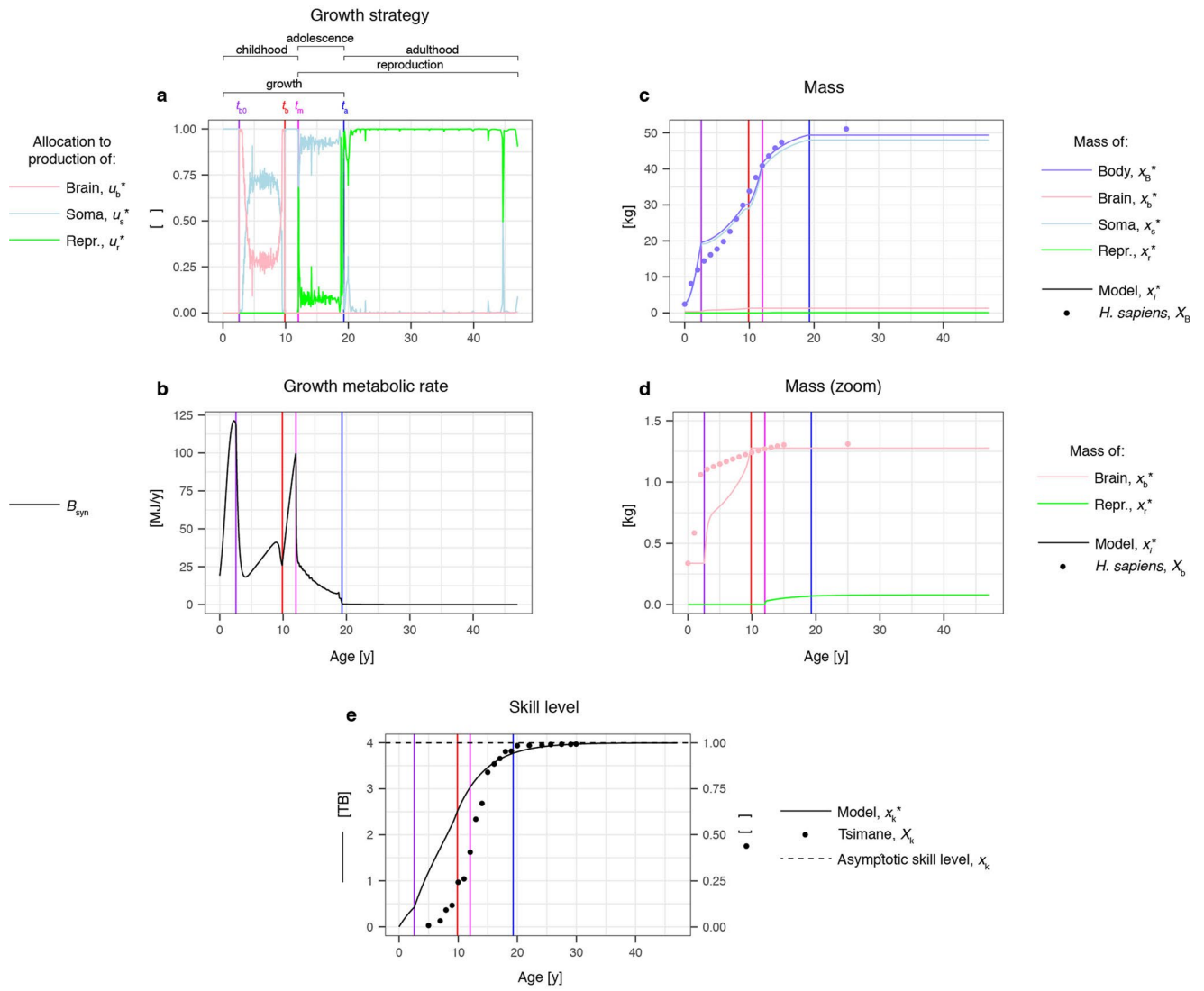
Extended Data Fig. 10 | Detailed life history resulting from the best-fitting scenario for *H. sapiens*. Plots correspond to Fig. 4b. **a**, The growth strategy generating the life history. **b**, The resulting growth metabolic rate. **c**, **d**, The mass of all tissues. **e**, The skill level. For comparison with the model's predicted skill level, x_k^*, the black dots in **e** are the observed cumulative distribution of self-reported acquisition ages of food production skills in female Tsimane horticulturalists[36].

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For final submission: please carefully check your responses for accuracy; you will not be able to make changes later.

▶ Experimental design

1. Sample size

   Describe how sample size was determined.

   > We used previously published data for parameter estimates and observed (or empirically estimated) brain and body mass for various Homo species. Thus, sample sizes were those of the original publications as cited in the paper.

2. Data exclusions

   Describe any data exclusions.

   > We discarded results that did not converge to a growth strategy that was a best response to itself. This is because our method only applies to cases where the growth strategy converges to a best response to itself.

3. Replication

   Describe the measures taken to verify the reproducibility of the experimental findings.

   > Numerical solutions were consistently replicated with the software and hardware specified in the Supplementary Information. Replication using other software or hardware may require modification of the solver setup to obtain stable costate estimation as described in the Supplementary Information section 5. Analyses leading to Fig. 3 and 4 can be replicated without optimal control software using the data deposited in Zenodo with the identifier https://doi.org/10.5281/zenodo.1197479

4. Randomization

   Describe how samples/organisms/participants were allocated into experimental groups.

   > This is not relevant to our study, which finds approximate numerical solutions to deterministic optimal control problems.

5. Blinding

   Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

   > Blinding is also not relevant to our study as it involved no data collection.

   Note: all in vivo studies must report how sample size was determined and whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a	Confirmed	
☒	☐	The <u>exact sample size</u> (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☒	☐	A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐	A statement indicating how many times each experiment was replicated
☒	☐	The statistical test(s) used and whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☒	☐	Test values indicating whether an effect is present *Provide confidence intervals or give results of significance tests (e.g. P values) as exact values whenever appropriate and with effect sizes noted.*
☒	☐	A clear description of statistics including <u>central tendency</u> (e.g. median, mean) and <u>variation</u> (e.g. standard deviation, interquartile range)
☐	☒	Clearly defined error bars in <u>all</u> relevant figure captions (with explicit mention of central tendency and variation)

See the web collection on statistics for biologists for further resources and guidance.

▶ Software

Policy information about availability of computer code

7. Software

Describe the software used to analyze the data in this study.

> Numerical solutions were run with the licensed software GPOPS 2.3, run in MATLAB R2015b, in a 32-cpu machine running Linux Debian 8.9.
>
> Custom computer code was written in MATLAB R2015b and R version 3.3.1 and is available in Zenodo with the identifier https://doi.org/10.5281/zenodo.1197479.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

▶ Materials and reagents

Policy information about availability of materials

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a third party.

> All materials are readily available in the Supplementary Information, Zenodo (computer code and resulting predictions), from the authors (complete numerical solutions over the parameter sweep), or from specified commercial sources (GPOPS).

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

> No antibodies were used.

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

> No eukaryotic cell lines were used.

b. Describe the method of cell line authentication used.

> No eukaryotic cell lines were used.

c. Report whether the cell lines were tested for mycoplasma contamination.

> No eukaryotic cell lines were used.

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.

> No commonly misidentified cell lines were used.

▶ Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. Description of research animals

Provide all relevant details on animals and/or animal-derived materials used in the study.

No animals were used.

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

The study did not involve human research participants.