

1 **Universal rules of life: Metabolic rates, biological times and the equal fitness paradigm**

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27
28 **Abstract** (171 words)

29 Here we review and extend the equal fitness paradigm (EFP) as an important step in developing
30 and testing a synthetic theory of ecology and evolution based on energy and metabolism. The
31 EFP states that all organisms are equally fit at steady state, because they allocate the same
32 quantity of energy, ~22.4 kJ/g/generation to production of offspring. On the one hand, the EFP
33 may seem tautological, because equal fitness is necessary for the origin and persistence of
34 biodiversity. On the other hand, the EFP reflects universal laws of life: how biological
35 metabolism – the uptake, transformation and allocation of energy – links ecological and
36 evolutionary patterns and processes across levels of organization from: i) structure and function
37 of individual organisms, ii) life history and dynamics of populations, iii) interactions and
38 coevolution of species in ecosystems. The physics and biology of metabolism have facilitated
39 the evolution of millions of species with idiosyncratic anatomy, physiology, behavior and ecology
40 but also with many shared traits and tradeoffs that reflect the single origin and universal rules of
41 life.

43 **Introduction**

44 Life presents a fascinating duality. On the one hand, living things are amazingly diverse.
45 Each of the millions of animal, plant and microbial species is unique. Each has distinctive
46 features of anatomy, physiology, morphology, behavior and ecology that reflect its distinctive
47 ecological niche and phylogenetic history. In other respects, however, living things are strikingly
48 similar. They share fundamental features of structure and function that reflect their common
49 ancestry and biophysical constraints on subsequent evolution and diversification. Some of the
50 shared traits are at molecular and cellular levels of organization, where they reflect the
51 biochemistry of inheritance and metabolism. Other shared traits are at higher levels of
52 organization, where they reflect general patterns and processes of physiological performance,
53 population dynamics, ecosystem organization and evolutionary diversification.

54 This duality – uniqueness and universality – of life is an outcome of evolution by natural
55 selection. Within a population, variation among genes and individuals results in differential
56 survival and reproduction and leads to descent with adaptive modification. Fitness is a central
57 concept in evolutionary biology: fitter individuals have higher survival or reproduction, passing
58 on their heritable traits to offspring. Ever since Darwin, theoretical biologists have struggled to
59 define fitness and empirical biologists have struggled to measure it. Indeed, biologists have
60 defined fitness in many different ways depending on the unit of measurement and level of
61 analysis (Box 1), but at root, it is the capacity to leave descendant individuals, genes and/or
62 quantitative heritable traits in the next generation. One corollary is that although fitness varies
63 among individuals within a population, it is nearly equal across species in ecological
64 assemblages. This equal fitness paradigm (EFP) is a consequence of competition for the limited
65 supply of usable energy in the biosphere (Boltzmann 1886; Lotka 1922; Van Valen 1977, 1980)
66 and constraints and tradeoffs in how it is allocated to production and survival (Burger et al.
67 Brown et al 2018; 2019a). The resultant near equal fitness of species is a necessary condition
68 for the origin and persistence of biodiversity.

69 For decades' synthesis across levels of biological organization and subdisciplines of
70 ecology and evolution were inhibited because they used different currencies (e.g., Brown 1981,
71 1995; but see Hutchinson 1959, 1965; Whittaker 1975; Peters 1983; Yodzis and Innes 1992;
72 Cohen et al, 1993; De Angelis 1995). Physiologists at the individual-organism level and
73 ecologists at the ecosystem level focused on metabolism and used biophysical $\frac{dE}{dt}$ currencies:
74 fluxes and stores of energy and materials. Ecologists at population and community levels
75 focused on population dynamics and used numerical $\frac{dN}{dt}$ currencies: numbers of individuals.
76 Synthesis was inhibited because it was far from straightforward to translate the biophysical data
77 and theories of physiological and ecosystem ecology into the numerical currencies of
78 demography and population and community ecology – and vice versa. Recently, however,
79 ecologists have begun to focus on energy metabolism to synthesize across subdisciplines and
80 levels of organization by linking the performance of individuals to emergent consequences for
81 niche relations, ecosystem organization and biodiversity. The EFP is the inevitable outcome of
82 competition and coevolution among species for the incident solar energy captured in biomass.

83

84 **An energetic definition of fitness**

85 Energy is the ultimate limiting resource for living things. As Boltzmann (1886)
86 perceptively wrote: “The “struggle for existence” of living beings is ... for the possession of the
87 free energy obtained, chiefly by means of the green plant, from the transfer of radiant energy

88 from the hot sun to the cold earth.” The solar energy captured and converted into the organic
89 molecules by photosynthesis in green plants supplies essentially all energy used by organisms.
90 The energy in the molecules is released and used to fuel the work of living in the processes of
91 metabolism: assimilation, respiration and production. Assimilation is the uptake of energy from
92 the environment. Autotrophic plants take up solar energy, carbon dioxide and oxygen and
93 capture the energy in organic molecules. Heterotrophic animals and microbes acquire biomass
94 energy by consuming plants. Respiration is the biochemical transformation of biomass energy to
95 fuel work: organic molecules are combined with oxygen, reduced to carbon dioxide and water,
96 and energy is captured in ATP molecules. ATP is transported around the body, where it is
97 converted to ADP, releasing energy to perform the work of digestion, excretion, activity, growth
98 and reproduction. Some assimilated biomass energy is not catabolized in respiration but
99 allocated to production and passed on to the next generation in the form of offspring growth and
100 parental investment.

101

102 Energy is arguably the most fundamental currency of biological fitness, because the
103 traditional components of fitness – survival, growth and reproduction – are all governed by the
104 physical laws of energy and mass balance. Energy balance requires that each generation
105 allocates the energy assimilated from the environment between respiration and production; the
106 energy allocated to production is partitioned between growth and reproduction. The gain of
107 energy due to production, is thus matched by loss of energy to mortality (see below and Fig.1).
108 One consequence of energy balance is that fitness can be expressed in terms of energy

$$109 \quad E = P_{coh}GFQ \quad (1)$$

110 where E is energetic fitness in kilojoules per gram per generation, P_{coh} , is the mass-specific rate
111 of biomass energy production (growth plus reproduction) of the cohort of offspring produced by
112 a parent in a lifetime in grams per gram per year, G is generation time in years, Q is the energy
113 density of biomass in kilojoules per gram, and F is the fraction of lifetime biomass production
114 that is passed through to **surviving** offspring in the next generation (Brown et al. 2018). So eq 1
115 defines the components of traditional Darwinian fitness – survival, growth and reproduction – in
116 terms of the physical currencies and metabolic processes of energy metabolism.

117 This relation can be simplified by recognizing that the energy density of biomass is
118 nearly constant across all living things: $Q \approx 22.4$ kJ/g dry weight (see below). Consequently, eq
119 1 can be rewritten in terms of mass balance

$$120 \quad \frac{E}{Q} = 1 = P_{coh}GF \quad (2)$$

121 where $\frac{E}{Q}$ is fitness in grams per gram per generation.

122 This biophysical characterization of fitness based on energy and mass balance (Fig 1
123 and seminal eqs 1 and 2) applies to all levels of biological organization from alleles, quantitative
124 traits and individuals within populations to species within communities, ecosystems and the
125 biosphere. Most traditional treatments of fitness focus on the population level where variation
126 among alleles, quantitative heritable traits, or individuals results in differential survival and
127 reproduction (Box 1). Such variation is the basis for evolution by natural selection. Individuals

128 with higher than average fitness have a higher probability of survival and reproduction and leave
129 more descendants in future populations, so heritable traits that confer such advantages
130 increase in frequency. This is consistent with energetic fitness; any differential survival
131 (generation time) or reproduction (production rate) is necessarily reflected in a change in
132 energetic fitness. When natural selection is operating – i.e., when a gene, trait or individual has
133 higher than average fitness – energetic fitness is greater than 1 and increases or decreases,
134 respectively, in the next generation. Expressing fitness in units of energy or mass instead of
135 alleles, heritable traits or individuals and relating traditional biological currencies to their
136 biophysical underpinnings is consistent with our understanding of fitness, natural selection and
137 evolution at the population level. It leads, however, to new insights and perspectives in ecology
138 and evolution at the levels of communities, ecosystems, and the biosphere.

139

140 Box 1 here

141

142 ***The equal fitness paradigm (EFP)***

143 Deeper insights into the biophysical underpinnings of ecology and evolution come from
144 invoking the assumption of population steady state and extending the concept of energetic
145 fitness to multiple levels of biological organization. This leads to the equal fitness paradigm
146 (EFP: Brown et al. 2018, Burger et al. 2019a). The steady state assumption is critical but also
147 realistic. At steady state parents replace themselves with an equal energy content, mass and
148 number of offspring each generation, so birth rates equal death rates, populations do not
149 increase or decrease, species coexist and biodiversity is maintained. Eqs 1 and 2 show that
150 species have equal energetic fitness because at steady state parents pass on 22.4 kJ/g of
151 energy or 1 g/g of biomass to surviving offspring each generation.

152 In some respects, the EFP is reminiscent of the Hardy-Weinberg equilibrium (Hardy
153 1908; https://en.wikipedia.org/wiki/Hardy%E2%80%93Weinberg_principle) in population
154 genetics. The HWE also makes the critical assumption of steady state as a proof that the
155 frequency of genes and genotypes in a population do not inherently change over time. When
156 first proposed, the HWE seemed counterintuitive to many geneticists, who assumed that the
157 frequencies of dominant genes would increase over generations. The HWE is also tautological
158 because it states, that at steady state, the frequencies of genes do not change. The HWE is
159 more than just a tautology, however. It plays a seminal role in population genetics and evolution,
160 because it provides the theoretical basis for quantifying the frequency of genes and genotypes
161 in populations and for predicting changes in these frequencies due to natural selection, genetic
162 drift and migration when the steady state assumption does not hold.

163 The EFP may also seem tautological, counterintuitive or both to biologists, who
164 traditionally have associated fitness with variation in survival and reproduction. Indeed,
165 components of fitness such as generation time and fecundity differ across species from
166 microbes to mammals by many orders of magnitude. Energetic fitness is constant across
167 species because there is a tradeoff between production rate, P_{coh} , and generation time, G , such
168 that in each generation at steady state, parents on average replace themselves with offspring
169 containing an equal quantity of biomass and 22.4 kJ/g of energy. The product, $P_{coh}GF$, is
170 constant, even though the three variables vary across species by many orders of magnitude.
171 The enormously varied patterns in life history strategies reflect a universal tradeoff in among the
172 pathways of energy allocation.

173 Much of the variation is related to body size and temperature. The standard metabolic
174 theory of ecology (Brown et al. 2004) predicts the scalings of P_{coh} and G :

$$175 P_{coh} = P_0 m_A^{-\alpha} e^{-\frac{E_a}{kt}} \tag{3}$$

176 and

$$177 G = G_0 m_A^\alpha e^{\frac{E_a}{kt}} \tag{4}$$

178 where above P_{coh} is the mass-specific rate of cohort biomass production in grams per gram per
179 year, P_0 is a normalization coefficient, G is generation time in years, m_A is adult body mass, α is
180 the mass-scaling exponent, e is the root of the natural logarithm, E_a is an “activation energy”
181 which gives the temperature dependence, k is Boltzmann’s constant, and t is the temperature in
182 Kelvin. These scaling relations apply both over ontogeny within species and across species.
183 Standard metabolic theory predicts that $\alpha = 1/4$ and $E_a \approx 0.65$ eV, equivalent to a Q_{10} of
184 approximately 2.5 (Brown et al. 2004; Sibly et al. 2012a).

185 These equal-but-opposite scalings of production rate and generation time with body
186 mass are well supported empirically (e.g., by Hatton et al. 2019). Their values of the exponents,
187 -0.26 and 0.24 for what they called “growth rate” and “lifespan” respectively, are very similar to
188 the predicted values of -1/4 and 1/4 for what we call “production rate” and “generation time”.
189 Consequently, the product, their “lifetime growth” or our “energetic fitness” is nearly constant, \approx
190 0 and independent of body size (and also temperature: not shown here, see Gillooly et al. 2001;
191 Brown et al. 2004, 2018; Hatton et al. 2019; Burger et al. 2019a).

192 There is, however, considerable variation. Some of this due to lack of standardization
193 and measurement error. Testing the EFP (eqn 1) requires consistent definitions and
194 standardization of parameters (Box 2). Even when standardization and assumptions are met,
195 however, there is still biologically relevant variation remaining in the four parameters of the EFP.
196 Equation (1) provides a quantitative framework to unravel this variation. First, the relative
197 constancy of E and, Q is striking given the diversity of life. Second, traditional metabolic scaling
198 theory predicts most of the variation in P_{coh} and G with body size and temperature as (Brown et
199 al. 2004; Sibly et al. 2012a). Variation across taxa and functional groups generally offset,
200 resulting in relatively invariant scaling exponents and normalization constants. Third, there is
201 additional systematic variation in Q and F , which is not accounted for by body size and
202 temperature. Some of this is apparently due to variation in fecundity and parental care (see
203 below). Fourth, variation in heritable traits within a population is subject to natural selection and
204 niche evolution. It can lead to temporal and spatial variation when the steady state assumption
205 does not hold. We elaborate in the following sections after summarizing a metabolic theory of
206 life history (Burger et al. 2019a).

207

208 Box 2 Definitions and Standardizations here

209

210 **Metabolism and life history**

211 The concept of energetic fitness integrates physics and biology, metabolism and life
212 history. It addresses how the energetic performance of individual organisms affects their
213 contributions to future generations, interactions with other species and the abiotic environment
214 and coevolutionary dynamics. The life history is the schedule of survival and reproduction over a
215 lifetime; it determines the contributions of genes, traits and individuals to fitness in the next

216 generation. It is subject to the physical laws of energy and mass balance and the biological laws
217 of demography and population dynamics.

218 **1) Energy balance of an individual.**—All organisms obey the physical laws of energy and
219 mass balance (Lotka 1922; Odum 1971; Kooijman 2000). Figure 1 diagrams the energy balance
220 of an individual animal in terms of the uptake, transformation and expenditure of metabolic
221 energy.

222 i) Assimilation: Animal metabolism is fueled by consumption and assimilation of food. As
223 Boltzmann pointed out (see above), the energy used by organisms comes ultimately from the
224 sun and fixed in the organic molecules by photosynthesis in plants. Animals take up biomass
225 energy from the environment by consuming and assimilating plants or other food from animals
226 (and from solar energy in plants). The energy acquired from assimilation is processed and
227 transformed within the body and allocated between respiration and production.

228 ii) Respiration: Most of the energy acquired by assimilation is expended on respiration. The
229 organic molecules in food are eventually broken by oxidative metabolism to yield the waste
230 products carbon dioxide, water and heat, which are released back into the environment. Usable
231 energy is temporarily stored in ATP, which is subsequently metabolized to perform the physical
232 work of living: maintenance, growth and activity. Respiration is what Kleiber (1932) and
233 subsequent physiologists refer to as “metabolism” or “metabolic rate”.

234 Animal physiologists often use standardized conditions in the laboratory to measure
235 different levels of metabolic performance: i) basal or resting metabolic rates (BMR or RMR), the
236 respiration rate of an inactive, fasting individual in its thermoneutral zone (growing animals and
237 those engaged in thermoregulation, locomotion, feeding, territorial defense, courtship,
238 reproduction and immune response to pathogens have higher rates); ii) maximal metabolic rates
239 (VO_2 max), elevated respiration rates during activity or stress); and iii) field metabolic rate
240 (FMR), average respiration rates of free-living animals in nature. All of these levels of respiratory
241 metabolism are correlated to each other; they may differ in normalization coefficients, but scale
242 similarly with body mass: as $\sim m^{\frac{3}{4}}$ for whole-organism rates and $\sim m^{\frac{1}{4}}$ for mass-specific rates,
243 and with temperature (e.g., Peters 1983; Calder 1984; Schmidt-Nielson 1984; McNab 2002;
244 Speakman 1997; Gillooly et al. 2001; Savage et al. 2004; but see Nagy 1999, 2005; Glazier
245 2010; Speakman and Krol 2010). Since these measures of respiration do not include uptake
246 and expenditure for growth and reproduction, they do not represent energy balance for an
247 individual over its lifespan.

248 iii) Production: A fraction of the biomass acquired over the lifetime is not broken down in
249 respiration but stored temporarily in the body as production of “net new biomass”. The
250 macromolecules may be altered by metabolic biochemistry, but they are passed on with most of
251 their energy intact and allocated between somatic growth and parental investment in
252 reproduction.

253 As shown in Figure 1, mass-energy balance for an animal over its lifetime requires that
254 input equals output, so: i) assimilation, A_{ind} , or uptake from food; equals the sum of ii)
255 respiration, R_{ind} , for synthesis and expenditure of ATP plus iii) plus production, W_{ind} , for growth
256 and reproduction:

$$257 \quad A_{ind} = R_{ind} + W_{ind} = R_{ind} + (I_{ind} + H_{ind}) \quad (5)$$

258 where all rates are for whole-organism per generation. Production has two components: H_{ind} ,
259 biomass accumulated in the body as ontogenetic growth, and I_{ind} , parental investment in
260 reproduction in the form of gametes and post-fertilization nutrition (e.g., pregnancy, lactation
261 and feeding in mammals).

262 **2) Demography and life tables.**— All organisms are mortal. Life persists because parents
263 replace themselves with offspring in succeeding generations. The life history is the schedule of
264 survival, growth and reproduction over an entire life cycle of one generation. Animals exhibit a
265 spectacular diversity of life histories including sexual and asexual reproduction, semelparity and
266 iteroparity, determinate and indeterminate growth, and orders-of-magnitude variation in body
267 size of parent and offspring, fecundity and generation time. This variation notwithstanding,
268 however, the biological law of demography dictates that in sexual species at steady state, two
269 parents replace themselves over their lifetimes with two offspring; regardless of the number of
270 offspring born, which can vary from a few to billions, only two survive to reproduce and complete
271 the life cycle.

272 *i) Net reproductive rate:* Fundamental features of demography are typically presented in a life
273 table, which quantifies survival, l_x , and fecundity, f_x , as functions of age, x . The net
274 reproductive rate, $R_0 = \sum l_x f_x$, is a commonly used measure of fitness (Box 1). At steady state,
275 fitness is neutral, the population does not grow because the birth rate equals the death rate,
276 $R_0 = 1$, the fecundity of the average female is $N_0 = \sum_{x=G}^{x=0} f_x$, and the number of surviving
277 offspring, N , decreases with age from N_0 at $x = 0$ to 2 at $x = G$. There are hundreds of
278 published life tables for animal species with diverse life histories.

279 *ii) Metabolic life table:* A complete accounting of allocation of energy or mass to fitness over an
280 entire life cycle requires additional data on ontogenetic growth: i.e., body mass or energy
281 content of individuals of age x . Then it is possible to construct a metabolic life table (MLT; Brett
282 1983; Burger et al. 2020). Unfortunately, sufficiently complete and detailed data to construct an
283 MLT are available for only a few well-studied species. Furthermore, such information is not
284 available in large comparative databases such as FishBase (Froese and Pauly 2019),
285 AMNIOTE (Myhrvold et al. 2015), AnAGE (De Magalhães and Costa 2009), COMADRE
286 (Salguero-Gómez et al. 2016) or DEB (Marques et al. 2018) due to lack of standardization (Box
287 2) and steady-state assumptions. In Table 1 and Fig. 4 we present data on energetics and
288 demography for eight animal species with diverse life histories. Note that despite wide variation
289 in the underlying parameters, at steady state all of them obey the laws of energy-mass balance
290 and demography, and they have equal fitness with $E = 22.4$ kJ/g/generation.

291

292 Box 3 Scaling relations here

293

294 **3) Energy density of biomass.**—The EFP and its seminal equations 1 and 2 call attention to
295 the importance of Q , the energy density of biomass. Q is a biological constant: ≈ 22.4 kJ/g dry
296 weight (≈ 7 kJ/g wet weight). It varies less than 2-fold across organisms spanning 20 orders of
297 magnitude in body mass from microbes to mammals and trees (Brown et al. 2018). The value of
298 Q is determined by biochemistry, because biomass is composed of similar proportions of
299 carbohydrates (~ 17 kJ/g), proteins (~ 17 kJ/g), and lipids (~ 34 kJ/g). This was recognized more
300 than 50 years ago (e.g., Cummins and Wuychek 1967), but has gone largely unappreciated in
301 metabolic ecology. It is another universal characteristic of life at the molecular level – and one
302 with profound implications for biological energetics from physiology to ecosystem ecology.
303 Importantly, the constancy of Q allows the EFP and life history parameters to be expressed in
304 units of mass, which are more easily measured and readily available in the literature than units
305 of energy.

306 **4) Production of a cohort.**— The EFP is explicitly couched in terms of mass-energy and
307 demographic balance of a non-growing population or the cohort of offspring produced by an
308 average parent at steady state (Brown et al. 2018; Burger et al. 2019a):

309 $A_{coh} = R_{coh} + W_{coh}$ (6)

310 where A_{coh} and R_{coh} are the total assimilation and respiration of all offspring produced by a
 311 female parent, and W_{coh} is the biomass of the entire cohort of offspring produced by the parent.
 312 So W_{coh} is the sum of the body masses of all offspring when they die, including the two that
 313 replace the parents. So

314 $W_{coh} = \sum_{x=0}^{x=G} N_d m_d$ (7)

315 where N_d is the number of offspring dying at age x and m_d is the mass of those offspring when
 316 they die. Note that the mass-specific cohort biomass production of the EFP, $\frac{E}{Q} = \frac{W_{coh}}{m_A}$ (eqs 2 and
 317 6) is not the same as $P_{ind} = \frac{W_{ind}}{m_A}$ in eq 5, which has variously been called “individual
 318 production”, “maximal production”, “growth” or simply “production”. These measures do not
 319 include the production attributable to a parent in the growth of offspring that die before maturing
 320 and reproducing.

321 **5) Efficiency of production.**—Rarely considered in treatments of life history is the quantity F in
 322 eqs. 1 and 2 (but see Brett 1986). $F = \frac{1}{P_{coh}G} = \frac{m_A}{2m_A+W}$ is the fraction of biomass energy
 323 produced in one generation that is incorporated into **surviving** offspring in the next generation,
 324 so it is a measure of efficiency of reproduction. Among the eight species in Fig. 4, values of F
 325 varied by more than an order of magnitude: from 0.013 to 0.032 in walleye pollock and copepod
 326 to 0.30 to 0.35 in chimpanzee and brown bat. [Note that F is not the same as the trophic
 327 efficiency $T = \frac{P_{coh}}{A_{coh}}$ of a species in the ecosystem, another consequential mass-energy balance.]

328 Especially relevant to ecology is the complementary fraction $(1 - F)$, the fraction of biomass
 329 produced by a cohort each generation that is lost to pre-reproductive mortality, left in the
 330 ecosystem, and mostly consumed by other organisms (predators and decomposers). Variation
 331 in F and $(1 - F)$ is closely related to the number and relative size of offspring. For example,
 332 mammals, which have extensive parental care and produce a few relatively large offspring pass
 333 on more than half of cohort production to the next generation; they are more efficient
 334 energetically than the fish and invertebrates that produce large numbers of tiny offspring but
 335 lose more than 90% (sometimes much more than 99%) of cohort production to pre-reproductive
 336 mortality in the ecosystem.

337 **6) Toward a more complete theory.**—A metabolic theory of life history is still a work in
 338 progress. Recent advances highlight the promise of a synthesis based on $\frac{dE}{dt}$ currencies and first
 339 principles of physics and biology (Burger et al. 2019a; Hatton et al. 2019; Burger et al. 2020). As
 340 exhibited in Fig. 4, animals exhibit wide variations in life histories. The EFP offers insights into
 341 the causes and consequences and the magnitudes and extents of this variation. Burger et al.
 342 (2019) showed how the basic life history tradeoffs – between generation time and production
 343 rate, offspring growth and parental investment, and number and size of offspring – are due to
 344 fundamental constraints of mass-energy balance and demography.

345 Other important patterns and processes remain to be explained. For example, there is
 346 necessarily a mechanistic linkage between growth and mortality, and more generally between
 347 the $\frac{dE}{dt}$ variables of metabolic ecology and the $\frac{dN}{dt}$ variables of demography and population
 348 dynamics. Progress will require both theoretical and empirical advances: new models of key
 349 processes and new compilations of data that address the issues of accuracy and
 350 standardization in (Box 1 and 2).

351

352 **Biological time and a general explanation for Kleiber's law**

353 The EFP raises questions about the nature of biological time. The equal but opposite
354 scaling of biological rates and times with body mass – as $m^{-\frac{1}{4}}$ and $m^{\frac{1}{4}}$, respectively (eqs 3 and
355 4) means that the product of rates and times is an invariant quantity: $m^{-\frac{1}{4}}m^{\frac{1}{4}} = m^0$. A classic
356 example is the product of heart rate and lifespan gives the number of heartbeats in a lifetime,
357 independent of body mass and nearly constant: ≈ 2 billion, across mammals from mice to
358 elephants. Similarly, the EFP gives energetic fitness as the invariant product, $E \approx 22.4$
359 kJ/g/generation, of production rate, P_{coh} , times generation time, G (eqs 1 and 2). The central
360 importance of generation time as a component of fitness and its equal but opposite scaling with
361 body size and temperature (eqs 1-4) suggests that it is a universal feature of life and an
362 alternative explanation for Kleiber's law: metabolic rate scaling as the 3/4-power of body mass.

363 Ever since Kleiber's (1932) seminal study, theoreticians have tried to explain why
364 metabolic processes scale with quarter powers of mass or volume rather than the third powers
365 that would be expected on the basis of Euclidean geometry. We propose that biological rates
366 scale with quarter powers of mass because time is the fourth dimension. This is well established
367 in theoretical physics but not generally extended to biology (but see Blum 1977; Ginzburg, and
368 Damuth 2008). We start with the observation that life is fundamentally four-dimensional. Three
369 are the standard dimensions of Euclidean geometry; the static characteristics of organisms'
370 scale as third powers of body volume: 1) length (e.g., of limbs, guts and nerves) scales as $L \propto$
371 $V^{\frac{1}{3}}$; 2) surface area (e.g., of skin, lungs, gills, guts and leaves) scales as $A \propto V^{\frac{2}{3}}$; and volume or
372 mass (e.g., of organelles and organs) scales as $m \propto V^{\frac{3}{3}} \propto V$. A fourth dimension, time, is
373 necessary to capture dynamics, and characteristic times of biological processes scale as $t \propto$
374 $m^{\frac{1}{4}}$. Empirical evidence indicates that biological times – spanning many orders of magnitude
375 from the milliseconds of biochemical reactions and muscle contractions at molecular and
376 cellular levels, to years of lifespans and population cycles at organism to ecosystem levels –
377 scale as the 1/4-power of body mass (Fig. 5: Lindstedt and Calder 1981; Peters 1983; Calder
378 1984; Brown et al 2004; Andersen et al. 2016; Hatton et al. 2019).

379 We suggest that fitness, an existential feature of life, is fundamentally four-dimensional
380 with fourth dimension reflecting the scaling of biological time. This leads to our hypothesis that
381 Kleiber's law, the $m^{3/4}$ scaling of respiration rate, is the result rather than the cause of the $m^{1/4}$
382 scaling of lifespan or generation time. Assuming that $G \propto m^{1/4}$ and substituting eq 4 into eq 2,
383 we have

384
$$\frac{1}{F} = CG = C_0 m^{-\alpha} G_0 m^{\alpha} = C_0 m^{-\alpha} G_0 m^{\frac{1}{4}} \quad (8)$$

385 and $\alpha = -1/4$ for mass-specific production rate. The other metabolic rates (assimilation, and
386 resting and active respiration) scale with similar exponents (but different normalization
387 coefficients), and whole-organism rates scale with $\alpha = 3/4$ as in Kleiber's law. This means that
388 the quantity of energy expended by a gram of tissue in a lifetime is approximately invariant,
389 independent of the size of the organism: $\propto m^{-1/4}m^{1/4} \propto m^0$ (e.g., Fig. 2; Andresen et al. 2002;
390 Speakman 2005; Atanasov 2007; Ginzburg, and Damuth 2008; Brown et al. 2018; Hatton et al.
391 2019; Burger et al. 2019a).

392 Our hypothesis that Kleiber's $m^{3/4}$ scaling of metabolic rate reflects the $m^{1/4}$ scaling of
393 biological time broadly and generation time in particular, is more general and widely applicable
394 than existing models based on vascular and other systems that supply metabolites and remove
395 wastes (e.g., West et al. 1997; West et al. 1999; Banavar et al. 2002, 2010; Aitkenhead et al.
396 2020). The 3/4-power scaling of respiration rate with body mass is pervasive across the animal
397 kingdom, occurring in diverse taxonomic and functional groups that have distinctly different
398 anatomies and physiologies for assimilating, transporting and excreting the substrates and
399 wastes of respiratory metabolism (e.g., Peters 1983; Brown et al. 2004). These include the guts,
400 lungs, gills, arteries, veins, tracheales, kidneys and Malpighian tubules of terrestrial, freshwater
401 and marine species. So, our explanation subsumes most existing network models by suggesting
402 that they are all solutions to the general problem of fueling metabolism: since time scales as
403 $m^{1/4}$, whole-organism production rate and other rates necessarily scale with quarter powers
404 (Gillooly et al. 2001, 2002; Savage et al. 2008; Banavar et al. 2010; Maino et al. 2014). This
405 leads to a general theory for scalings of animal form and function across: i) body mass from
406 milligrams to tonnes, ii) temperature from 0-60°C; iii) time from milliseconds to centuries, and iv)
407 level of organization from molecules and cells to populations and ecosystems.

408 ***The EFP and the Red Queen***

409 The diversity of species in ecological assemblages at all scales, from local populations
410 and communities to the global biota, is a corollary of the equal fitness paradigm: equal fitness is
411 a necessary condition for coexistence and persistence. Within species populations, however,
412 individuals vary in energetic fitness, E , and in heritable traits that determine the values of the
413 parameters in eq 1. An exception is the parameter $Q \approx 22.4$ kJ/g, which is nearly constant so
414 there is virtually no heritable variation for selection to act on. There are, however, orders-of-
415 magnitude variations in the other parameters: growth and reproduction (production rate, P_{coh}),
416 survival (generation time, G), and efficiency of production (F , the fraction of production passed
417 from parent to offspring). Why doesn't natural selection increase energetic fitness, E , by acting
418 on this variation and resulting in increases in these constituent parameters?

419
420 There are at least three inter-related reasons. First, is depletion of genetic variation.
421 Continual selection on any trait leads to reduced heritable variation and progressively slower
422 change in fitness. Second is ecological compensation (Calow and Sibly 1983). If there is
423 heritable variation for production rate, P_{coh} , survival, G , or reproductive efficiency, F , natural
424 selection will favor individuals and traits with higher values, they will increase in the population
425 and the population will grow. But such dynamics will be transient. Ultimately population growth
426 will be limited by some environmental factor (carrying capacity), the initial advantage will be lost,
427 and further increases will not occur. The third reason why energetic fitness and its component
428 traits do not increase indefinitely is because of Red Queen interactions and coevolution. As
429 Boltzmann (1886, see above) pointed out, the biomass energy produced by photosynthesis is
430 the ultimate limiting resource for living things. Van Valen (1973; 1980) characterized the
431 ecological and evolutionary dynamics of species in ecological assemblages as a "zero sum
432 game" of competition for energy. He coined the term Red Queen after the character in Lewis
433 Carroll's *Through the Looking Glass* who famously said "It takes all the running you can do, to
434 keep in the same place."

435
436 A simplified characterization of the Red Queen zero sum game is diagrammed in Fig. 6.
437 The overall supply of usable biomass energy is set by net primary production of the ecosystem
438 (Hutchinson 1959). There is continual selection on each species, subject to the Malthusian-
439 Darwinian dynamic (MDD: Brown 1995; see also Nekola et al. 2013), to increase its share. The

440 energy used by each species is set jointly by its intrinsic biological traits and local environmental
441 conditions (e.g., Violle et al. 2012; Enquist et al. 2015; Burger et al. 2019b). Together, these
442 define the unique ecological niche. Selection leads to the divergence of traits, such as body
443 size, food requirement, territorial and antipredator behavior, etc., and the dispersion of niches
444 along axes of environmental variation, such as temperature, nutrients, physical structure,
445 predation risk, etc. (Whittaker 1970; Hall et al. 1992; Blonder et al. 2014). Moreover, as any
446 species increases in abundance, its biomass becomes a more attractive resource for
447 consumers: predators, parasites and pathogens. The collective result of the ecological
448 interactions and coevolution of species is that all the biomass energy produced in the
449 ecosystem tends to be used. At fine scales of time and space the niches and abundances are in
450 constant flux as each species competes in the zero-sum game. At larger scales, however, there
451 is an approximate steady state as increases in some species are balanced by decreases in
452 others and biodiversity is maintained. At steady state the fitness of all species is very nearly
453 equal: each is close to its carrying capacity and none exhibits more than a temporary advantage
454 in space and time.

455
456 At this steady state the energetic fitness of each species is very close to the canonical
457 22.4 kJ/g/generation of the EFP (eq 1). This value is set by the biophysical laws of metabolism
458 and life history, enforced by tradeoffs in physiology and behavior that limit the share of NPP that
459 can be acquired by any given species and reinforced by the Red Queen zero sum interactions
460 among species. As indicated above, the steady state hides complex non-equilibrium dynamics
461 at smaller scales, where the component species fluctuate in abundance and their traits evolve
462 adaptively in response to the abiotic environment and biotic interactions. When the environment
463 changes and new resources become available, native species shift their niches or alien species
464 colonize and exploit them. Some species are able keep up, but any increase in production and
465 abundance is temporary, ultimately checked by ecological compensation and the Red Queen at
466 the 22.4 kJ/g/generation steady state of the EFP. Other species are less successful; they fall
467 behind in the zero-sum game, decrease in abundance and ultimately go extinct unless rescued
468 by environmental change or new adaptations.

469
470 One consequence of these complex ecological and evolutionary dynamics is the
471 enormous variation in the abundance, distribution and ecological niches of coexisting species.
472 Darwin (1882, 6th ed. p. 62) perceptively observed: “The most flourishing, or, as they may be
473 called, the dominant species – those which range widely, are the most diffused in their own
474 country, and are the most numerous in individuals....”. Since then many authors have
475 addressed such variation, not only in abundance and distribution (e.g., Preston 1948; MacArthur
476 1957; Brown 1984, 1995; Williams 1964; Hubbell 2001; Harte 2011), but also in impacts on the
477 physical structure, energy and nutrient flows, and species diversity of ecosystems (e.g., priority,
478 pioneer, climax, foundational, engineer, keystone and apex predator species; e.g., Paine 1966;
479 McNaughton and Wolf 1970; Dayton 1975; Lawton and Jones 1995; Schramski et al. 2015;
480 Fukami 2015; Brandl et al. 2019; Enquist et al. 2020). This inequality in ecological relationships
481 is another consequence of the EFP. Ecological communities are filled to capacity with nearly
482 equally fit species, but their fitnesses are exactly equal only when populations are constant and
483 natural selection is not operating. During departures from steady state, a small change in
484 extrinsic environment or heritable trait can have a large effect on fitness and trigger large shifts
485 in abundance, distribution, community composition and ecosystem processes. This
486 interpretation is consistent with the well-documented “individualistic” responses of communities
487 to climate change and invading species (e.g., Graham and Grimm 1990; Brown et al. 1997;
488 Jackson and Overpeck 2000; Sax and Brown 2000; Williams et al. 2004; Sax et al. 2007).

489 Throughout its history, biology has focused on biodiversity – describing the unique
490 anatomy, physiology, behavior and ecology of life stages and species, and organizing them into
491 hierarchical groups based on shared features of structure, function and phylogenetic history.
492 This endeavor has always included a healthy tension between empiricists, who focused on the
493 variation and endeavored to quantify and organize it, and theoreticians, who focused on the
494 repeated patterns and sought to “explain” them in terms of biophysical laws and mathematical
495 equations.

496 This review and synthesis presents our vision for a still unfinished theoretical framework
497 based on energy. We are indebted to pioneers who laid groundwork over a half-century ago:
498 Boltzmann (1886), Thompson (1917), Lotka (1922), and Odum (1971). More recently, others
499 have done related work; some have contributed directly or indirectly to our work and others
500 have challenged it. We cannot review or even cite them all here, but some common themes and
501 still unresolved differences are in Box 4.
502

503 Box 4: Related work in metabolic ecology
504

505 ***The Road Forward: Testing and extending the EFP***

506 Recent decades have seen an explosion of interest in biological scaling and metabolic
507 ecology. Regardless whether measured from the pioneering studies of Thompson, Lotka and
508 Kleiber, the synthetic treatments of Peters, Schmidt-Nielsen, and Calder, or more recent work
509 on metabolic scaling, DEB and MTE, the progress has been impressive. This broad research
510 program has the common themes of theory based on first principles of physics, chemistry and
511 biology, and empiricism based on compilation, analysis and interpretation of more and better
512 data. On the one hand, there is optimism that these studies are leading to universal rules of life
513 based linking the biological performance of individual organisms to their consequences for
514 ecosystem ecology and global biodiversity. On the other hand, there is sobering realization of
515 how much more work will be required to turn this vision into reality.

516 We do not presume to predict or prescribe the future. We do, however, provide our
517 perspective on a few concrete steps that could be taken. Some of these are primarily
518 theoretical. Progress will depend largely on extending the existing frameworks to develop
519 models and make predictions about heretofore little explored phenomena. Others are more
520 empirical. Progress will depend largely on applying new and better data to deductively
521 distinguish between existing alternatives and inductively inspire unification and new ones.

522 ***A) Variations in life history.***— Both DEB and MTE rely on mass-energy balance to elucidate
523 patterns and processes of life history. At present, however, there appears to be a gap between
524 the “big picture” framework of MTE and EFP and the more detailed models (e.g., more
525 parameters) of DEB. Neither theory has yet developed and tested models to address important
526 aspects of such related phenomena as:

527 i) The “two-fold cost of sex”: Most animals reproduce sexually, so a female parent produces two
528 offspring to replace herself and her mate in the next generation. Some of these animals have
529 closely related parthenogenetic species: there is no sexual reproduction, offspring develop from
530 unfertilized eggs, and a female parent produces only one female offspring than surviving to
531 replace herself in the next generation. The resulting so-called “two-fold cost of sex” (e.g.,

532 Doncaster et al. 2000), expressed in terms of mass-energy balance, means that the lifetime
533 cohort production, P_{coh} in eqs 1 and 2 should be two times higher in a sexual species compared
534 to an otherwise equivalent parthenogenetic one. Yet at steady state, both must have equal
535 fitness. The apparent resolution to this puzzle is that it represents another example of ecological
536 compensation. The two-fold advantage of a new parthenogen is only temporary; its population
537 growth is ultimately checked by environmental limiting factors and other adaptive advantages of
538 sexual reproduction and the resulting genetic variation come into play (see reviews by
539 Doncaster et al. 2000; Lehtonen et al. 2012). The EFP and the pervasiveness of sexual
540 reproduction implies that the energy cost and fitness benefit of sex is 22.4 kJ/g/generation, the
541 “extra” energy required to produce a surviving male offspring.

542 ii) “Parental care”: DEB and MTE highlight insights gained by applying mass-energy balance
543 and biophysical dE/dt currencies to analyses of life history. Most of the relevant fitness traits
544 can be converted from the dN/dt variables of demography and population ecology to units of
545 mass or energy. So, for example, it is relatively straightforward to define parental investment as
546 the biomass or energy content of gametes plus any direct nutritional contribution prior to
547 offspring independence (such as lactation in mammals and feeding in altricial birds). But there
548 can be complications. An obvious example is the effect on energetic fitness of internal gestation
549 and live birth in giving unborn offspring mortality similar to the mother (e.g., in sharks, mammals,
550 and some reptiles, compared to teleost fish, amphibians, and birds). A more complicated
551 problem is how to quantify the energetic fitness due to parents and members of social groups
552 “teaching” and grooming offspring and protecting them from predators and parasites. Such
553 parental care has seemingly been a major influence on allocation of production, values of F
554 ($1 - F$), and evolution of life histories in taxa such as primates and mouth-brooding cichlid fish.

555 iii) Exceptions that prove the rule: Conceptual frameworks and formal models are often useful
556 even when they fail: assumptions do not hold, additional factors or parameters are required, or
557 data appear to refute predictions. As mentioned above, the steady state assumption of EFP is
558 often violated, especially at small space and time scales. This does not invalidate the concept of
559 energetic fitness; the mechanistic foundations of the EFP (eqs 1 and 2), and the prediction that
560 ecological and evolutionary dynamics tend to result in nearly equal fitness across species (Fig.
561 2). It does, however, mean that models with more functions and parameters will likely be
562 required in instances. It should be informative to test the EFP by applying it to exceptional
563 cases, such as parthenogenetic species; parasites, insects and amphibians with complex life
564 cycles; cyclical populations; and colonizing and declining species.

565 iv) Experimental tests: DEB, MTE and EFP share the key assumption of mass-energy balance.
566 But like the Hardy-Weinberg equilibrium (HWE), their greatest contribution may be applications
567 and extensions to predict dynamic responses when the steady state assumption does not hold.
568 Examples from applied environmental sciences include harvested populations of game and
569 ocean and freshwater fish, control of pests and colonizing invasive species, and management
570 interventions to conserve endangered species and ecosystems. There are also opportunities to
571 conduct controlled, manipulative experiments for direct tests of theoretical predictions using
572 both wild animals and model laboratory organisms, such as rats and mice, fruit flies, the
573 nematode *C. elegans*, and numerous unicellular eukaryotic and prokaryotic. There is a sizeable
574 literature on experimental selection on dN/dt life history traits, but abundant scope for
575 experiments to test effects of selection on the parameters of energetic fitness. The EFP predicts
576 that selection to increase P_{coh} , G , and F should result in increased energetic fitness. It is readily

577 apparent that artificial selection on domesticated animals has resulted in substantial increases
578 in rates of biomass production (growth and hence P_{coh}) for human food consumption, and this
579 has resulted in tradeoffs in traits that affect G and survival in the wild.

580 **B) Biodiversity and applied ecology.**—The EFP has utility in understanding the general rules
581 of life with applications to systems science, human and applied ecology based from first
582 principles of physics, chemistry and biology and the compilation, analysis and interpretation of
583 new data. These include:

584 *i) Body size spectra and energy equivalence.* – The empirical observation that in general small
585 organisms are abundant and large ones are rare led to the concept of the biomass spectrum.
586 Pioneering papers by Sheldon (Sheldon and Prakash 1972; Sheldon et al. 1977) showed that in
587 pelagic marine ecosystems the number of individual organisms across all trophic levels scales
588 approximately as the inverse of body mass, $N_i \propto m_i^{-1}$, so the total biomass of the “particles” is
589 independent of body size: $N_i m_i^{-1} \approx 0$ (e.g., Jennings 2005; Andersen et al. 2016). A related
590 pattern within a trophic level is that population density scales as the inverse of Kleiber’s rule, so
591 total rates of energy use (assimilation and respiration) are independent of body size: $N_i \propto$
592 $m_i^{-3/4}$, $R_i \propto m_i^{3/4}$, and $N_i R_i = m_i^{-3/4} R_i^{3/4} \propto m_i^0$ (e.g., Damuth 1981; White et al. 2007; Isaac et
593 al. 2013).

594 *ii) Trait space.* – As shown in Fig. 4, the temporal sequence and quantitative allocations to
595 ontogenetic growth and parental investment vary enormously across species, yet all of them
596 have equal energetic fitness. It is obvious that these observed patterns are only a subset of the
597 possible combinations, and most of them do not have equivalent fitness. This raises interesting
598 questions about the trait space of life history parameters (e.g., Blonder et al. 2015; Morrow et al
599 2018) and how they interact with dynamic environments to form communities (e.g., Enquist et
600 al. 2015; Burger et al. 2019b). How can they be combined, transformed, and reduced to a
601 subset of traits arrayed along quantitative axes that accounts for most of the observed
602 variation? Presumably such an analysis will reveal absolute constraints, relative tradeoffs, other
603 important patterns and lead to insights into the biophysical underpinnings, ecological relations
604 and evolutionary processes. It should help to answer questions such as: Why the strategy of
605 producing enormous numbers of miniscule eggs that develop on their own and suffer enormous
606 mortality has apparently facilitated the success of teleost fish as they invaded the oceans,
607 diversified explosively and largely replaced sharks and rays after the K-T mass extinction? and
608 How to explain the sometimes large differences in allocation to ontogenetic growth and parental
609 investment by the two sexes of the same species (e.g., Sibly et al. 2012b).

610 *iii) Ecosystem energetics.* – MTE has been applied to link metabolism of individual organisms
611 to the structure and dynamics of ecosystems, resulting in deductive tests of theoretical
612 predictions and discovery of new empirical patterns. For example, body size and temperature
613 play major roles in the structure of food webs (e.g., Brown et al. 2005; Schramski et al. 2015;
614 Grady et al. 2019; Hatton et al. 2019). The EFP makes specific predictions linking energy flows
615 from individual performance and population life history to ecosystem energetics. The parameter
616 F and $(1 - F)$ are closely related to the number and relative size of offspring. For example,
617 mammals, which have a few relatively large offspring pass on more than half of cohort
618 production to the next generation; whereas fish and invertebrates that produce large numbers of
619 tiny offspring but lose more than 90% (sometimes much more than 99%) of cohort production to
620 pre-reproductive mortality in the ecosystem (e.g., Brandl et al. 2019). These new insights from

621 the EFP have implications for understanding ecosystem dynamics in space and time and the
622 energetic ramifications throughout ecosystems during temporary departures from steady-state
623 populations.

624 *iii) Human ecology:* DEB, MTE and their underpinnings in biophysical laws have been applied to
625 human ecology – in particular, to correlates and consequences of energy use by humans over
626 the historical transition from aboriginal hunter-gatherers in approximate steady state with their
627 environment to the modern agricultural-industrial-technological societies whose unsustainable
628 practices are transforming the biosphere (Burger et al. 2012). Interdisciplinary studies, at the
629 interface between the biophysical science of ecology and the social sciences of economics and
630 sociology, highlight the roles of energy and other resources on the growth, socioeconomic
631 development, and environmental impacts of modern humans (e.g., Brown et al. 2011; Nikola et
632 al. 2013; Syvitsk et al. 2020). A particularly interesting example is how the urban transition – the
633 increasing concentration of humans in cities – can be understood in terms of a combination of
634 biological constraints inherited from primate ancestors and modern technological innovations
635 (e.g., Burger et al. 2017; Burger and Fristoe 2018; Burger et al. 2019c).

636 **Conclusion: Toward a modern ecological synthesis**

637 The mid-20th Century saw the development of the Modern Evolutionary Synthesis – a
638 unified body of theory that incorporated the newly discovered biological laws of inheritance to
639 explain patterns and processes of variation and change in living and fossil organisms. The
640 Hardy-Weinberg Equilibrium, by assuming steady state and incorporating laws of Mendelian
641 genetics, played a major role. Similarly, we see the Equal Fitness Paradigm, by assuming
642 steady state and incorporating biophysical laws, playing a seminal role in a Modern Ecological
643 Synthesis – a unified body of theory that explains patterns and processes of interactions
644 between organisms and their environments in terms of the struggle for free energy. Such a
645 theory has the potential to incorporate and integrate some of the most fundamental features of
646 living things: i) metabolism, the intake, processing and expenditure of energy and materials by
647 organisms; ii) scalings of physiological and life history rates and times with body mass and
648 temperature; iii) universal features of demography and population dynamics; iv) flows of energy
649 and materials through ecosystems; and v) origin and maintenance of biodiversity. Some of the
650 seminal questions and predictions are given in Box 5. Much remains to be done to achieve
651 unification, but the rate of recent progress provides grounds for optimism.

652

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661

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1047 **Box 1. Natural selection and alternative definitions of fitness (words 706)**

1048 Ever since Darwin's theory of evolution by natural selection, biologists have struggled to
1049 define fitness. Most definitions assume that fitness is the quantity that is maximized or optimized
1050 by natural selection. Natural selection operates on variation among genes, quantitative traits
1051 and individuals **within** a single species population. When natural selection is operating, there is
1052 a departure from steady state. Fitter individuals leave more descendent heritable traits and
1053 descendants in the next generation.

1054 Several measures of fitness are well-established in the literature of life history,
1055 evolutionary and physiological ecology.

1056
1057 **1) Rate of increase.**—One is based on the premise that natural selection tends to maximize the
1058 rate of increase in heritable traits that enhance reproduction or survival, and of individuals
1059 possessing such traits. Two measures are commonly used: i) the population growth rate, $r =$
1060 $1/N \, dN/dt$, where N is the number of copies or individuals; and ii) the net reproductive rate,
1061 $R_0 = \sum l_x f_x$, where l_x is survival and f_x is fecundity as a function of age x) (e.g., Charlesworth
1062 1973, 1994; Charnov and Schaffer 1973; Stearns 1977, 1992; Charnov 1991, 1993; Sibly 1991,
1063 2002; Brown and Sibly 2006). These are typically applied to quantify rates of change per unit
1064 clock time (r) or per generation (R_0) in the frequency of an allele, quantitative trait, genotype or
1065 phenotype within a population during departures from steady state when natural selection is
1066 operating.

1067 **2) Maximum power.**—An alternative suggestion is that selection tends to maximize metabolic
1068 or reproductive power. This has been called the maximum power principle (MPP) and attributed
1069 primarily to Alfred Lotka and H.T. Odum (Lotka 1922, Odum and Pinkerton 1955, Odum 1971;
1070 see also Brown et al 1993; Hall 1995). Power is measured in units of energy per time (e.g., J/s
1071 or watts). Biological power, expressed as rate of respiration or production, increases with body
1072 mass, scaling $\propto m^{3/4}$. But larger more powerful animals are not necessarily fitter.

1073
1074 **3) Resource use efficiency.**—Physiological ecologists have frequently used resource use
1075 efficiency (RUE) – of carbon, water, a nutrient or some other limiting resource – as a measure of
1076 performance, with the implication that natural selection tends to maximize RUE (DeLucia and
1077 Schlesinger 1991; Chapin et al. 1997; Sterner and Elser 2002; Funk and Vitousek 2007;
1078 Hodapp et al. 2019; Vitousek 1982). Efficiency is the unitless ratio: $REU = output/input$,
1079 measured for example, in g/g or kJ/kJ. However, greater REU does not mean that more efficient
1080 organisms are necessarily fitter.

1081
1082 **4) Lifetime reproductive effort.**—Our energetic fitness, E , has similarities to the lifetime
1083 reproductive effort, LRE, of Charnov (1991, 1993; Charnov et al. 2007), in that both E and LRE
1084 are predicted to be approximately constant: independent of body size, fecundity, lifespan and
1085 other life history traits. Charnov's model uses the net reproductive rate, R_0 , as the measure of
1086 fitness and makes assumptions about how component variables scale with body mass. The big
1087 difference between LRE and E is that the former does not explicitly incorporate growth and pre-
1088 reproductive mortality of offspring (W_{coh} , eg 7). Consequently, the prediction of nearly constant
1089 LRE seems to hold only for animals such as mammals and lizards (Charnov and Ernest 2006;
1090 Warne and Charnov 2008), which produce a few relatively large offspring with relatively little
1091 growth and mortality after independence. The EFP can be viewed as a more general theory that
1092 subsumes Charnov's model of constant lifetime reproductive effort as a special case.

1093 The above definitions differ from the energetic fitness, E , of the EFP. The EFP was
1094 developed by Brown et al. (2018) to account for the nearly constant value of $E \approx 22.4$
1095 kJ/g/generation (eqs 1 and 2) across species in different taxa, functional groups and
1096 environments. The EFP, like the Hardy-Weinburg equilibrium, uses the assumption of steady
1097 state to establish a baseline from which to quantify departures. Therefore, the EFP is distinct
1098 from but consistent with definitions of fitness that focus on evolution of traits due to natural
1099 selection. The EFP does not contradict the proposition that natural selection can act to increase
1100 the above measures of fitness (r , R_0 , metabolic power, RUE or L), but only during departures
1101 from steady state when the more or less fecund, long-lived, powerful or efficient variant
1102 temporarily has higher energetic fitness.

1103

1104

1105 **Box 2: Definition and standardization of metabolic variables (409 words)**

1106 The sections on energy balance and life tables highlight the importance of carefully defining and
1107 measuring the relevant variables. This has often not been done in past studies of biological
1108 scaling, metabolic ecology and in compiling the electronic databases that have been used in
1109 empirical analyses. Failure to do so can result in both systematic deviations and random errors.
1110 Relevant issues include:

1111 i) Assimilation: We define assimilation rate as the rate of uptake of energy or matter from the
1112 environment: i.e., absorption from the gut or across the body surface. In complex metazoan
1113 animals, assimilation is ingestion of food minus excretion of feces – an important clarification,
1114 because assimilation is often **assumed** to be some constant fraction of gross food consumption.

1115 ii) Respiration: If not rigorously defined and carefully measured, variation in reported respiration
1116 rates can reflect the influence of uncontrolled factors, including the biochemical composition of
1117 biomass, the oxidation pathway (e.g., aerobic vs anaerobic metabolism), level of activity (e.g.,
1118 basal, resting, maximal or field metabolic rates), and other states (e.g., thermoregulation, stress
1119 or reproduction). For example, maximal respiration rates during physical activity (VO_2max) can
1120 vary several fold, both across species depending on “athleticism” (e.g., sedentary sloth vs
1121 athletic spider monkey) and within individuals depending on intensity and duration of activity
1122 (e.g., 100 m dash vs 100 km ultramarathon). Reported maximal and field respiration rates are
1123 often simply **assumed** to be some constant multiple of basal or resting rates.

1124 iii) Production: Reported “production rates” in the literature and electronic databases have often
1125 been measured inconsistently, i.e., as either growth or parental investment rather than both
1126 components (e.g., Peters 1983; Ernest et al. 2005; Sibly and Brown 2007; Brown et al 2018;
1127 Hatton et al. 2019).

1128 iv) Lifespan and generation time: Several different life history times are often reported in the
1129 literature and comparative databases for specific taxa: average (often not rigorously defined),
1130 total (from birth to death), reproductive (from first to last breeding), and reflecting closer to
1131 maximum lifespans from birth to death for both wild and captive animals (e.g., Myhrvold et al.
1132 2015; De Magalhães and Costa 2009). These are not directly comparable to each other or to
1133 generation time, so using them indiscriminately can lead to confusion and serious errors. For
1134 example, it is often **assumed** that generation time is the reciprocal of lifespan ($G = 1/t_{life}$), but
1135 this is only true when t_{life} is the average time from birth to replacement reproduction, which
1136 requires a life table for accurate determination.

1137 **Box 3: Scaling relations (578 words)**

1138 For centuries, natural scientists have been intrigued by the variation in forms and
1139 functions of animals. With the advent of more modern methods of measurement and analysis,
1140 pioneers such as D'Arcy Thompson (1917), Huxley (1932), Kleiber (1932), and Brody (1945)
1141 and successors such as McMahon and Bonner (1983), Peters (1983), Calder (1984), and
1142 (Schmidt-Nielsen 1984) delved into these relationships, showing that relatively simple equations
1143 can describe how diverse anatomical, physiological, behavioral and ecological traits scale with
1144 body size and temperature. In this paper, we have followed standard metabolic theory used in
1145 the scaling relations in eqs 3 and 4 (above). We recognize that throughout the history of
1146 biological scaling there has been debate about: i) the theoretically predicted or empirically
1147 estimated values of the exponents and normalization coefficients and ii) the magnitudes and
1148 sources of the remaining variation.

1149 i) Scaling exponents: There is a longstanding debate about whether in eqs 3 and 4 the scaling
1150 exponent, $\alpha = 1/4$ or $1/3$. Ever since Kleiber's (1932), most investigators have favored the
1151 quarter-power even though the mechanistic basis remained obscure (e.g., Peters 1983;
1152 McMahon and Bonner 1983; Calder 1984; Schmidt-Nielsen 1984; Brown et al. 2004; Sibly et
1153 al. 2012a). But a few advocated a geometric third powers in part because heat is dissipated
1154 from the body surface which scales as $m^{2/3}$ (e.g, Rubner 1883; Heusner 1991; Glazier 2005,
1155 2010; Speakman and Król 2010). There has also been debate whether a simple Boltzmann
1156 exponential term is adequate to characterize temperature dependence, or some more
1157 complicated expression should be used (e.g., see Gillooly et al. 2001; Knies and Kingsolver
1158 2010).

1159 ii) Normalization coefficients: Often there is statistically significant variation in the normalization
1160 coefficient: e.g., the values of P_0 and G_0 in eq 3 and 4. Sometimes this is due to lack of
1161 standardization of definitions or measurements. For example, failure to standardize level of
1162 activity (e.g., time and speed of running or swimming) can lead to misinterpretation of the
1163 apparent differences (Speakman and Król 2010). Sometimes variations in normalization
1164 coefficients are "real" differences in metabolic performance among individuals (e.g., in
1165 respiration rates between the larval, pupal and adult life history stages of holometabolous
1166 insects; e.g., Llandres et al. 2015) or between species (e.g., in production rates and lifespans
1167 between birds and mammals).

1168 iii) Error: Failure to rigorously define terms and standardize measurements results in error
1169 variation because the data are not comparable (see box Box 3). Such variation can increase the
1170 magnitude of "unexplained" variation or introduce systematic bias (e.g., for biomedical example
1171 see Dhurandhar 2015; Allison et al. 2016). Increased use of large databases and informatics is
1172 contributing enormously to macroecology and other areas of biology. But careful standardization
1173 and accurate measurement will be required to have confidence in empirical studies, regardless
1174 of whether they are inductive patterns or formal deductive tests of hypotheses.

1175 iv) Statistical analyses: Technological advances – in hardware, software and 'big data' – have
1176 been accompanied by an explosion of statistical methods to characterize the magnitudes and
1177 sources of variation and distinguish among alternative models and hypotheses. We will just
1178 point out that statistics as a sub-discipline of mathematics, and its applications to other sciences
1179 are continually changing. There is no single "correct" method or "right" answer, and the best
1180 choice will likely change in a few years. The challenge is to continue to ask new questions and
1181 to expect only better – but always imperfect – answers. The EFP synthesized herein provides a
1182 unified framework to guide these questions.

1183

1184 **Box 4: Related work in metabolic ecology (750 words)**

1185 **1) Scaling relations.**—As pointed out above, it has long been recognized that many traits scale
1186 predictably with body size and temperature. In the mid-1980s, following the pioneering studies
1187 of Kleiber (1932), Brody (1945), Hemmingsen (1960) and others, four important books
1188 attempted to synthesize the state of the science (Bonner and McMahon 1983; Peters 1983;
1189 Calder 1984; and Schmidt-Nielsen 1984, but see Heusner 1982, 1991). Each book presented a
1190 unique perspective, but there was consensus that metabolic rate and related processes scale
1191 as quarter-powers of body mass. But in the absence of a general theory, and interest ebbed.
1192 When West et al. (1997) purported to explain Kleiber’s law of $m^{3/4}$ scaling of “metabolic rate” in
1193 terms of the structure and function of the fractal-like vascular networks that distribute metabolic
1194 resources, it was followed a flurry of supporting and critical studies. Points of contention
1195 included: i) vascular networks that violate critical assumptions of the WBE model (e.g.,
1196 Bannavar et al. 2002, 2010; Chown et al 2007, White et al. 2011; Seymour et al. 2019;
1197 Aitkenhead et al. 2020); ii) variation in the parameters of fitted regression equations (e.g.,
1198 Darveau et al 2002; Kozłowski et al. 2003; Kozłowski and Konarzewski 2004; Glazier 2005,
1199 2010; Etienne et al. 2006; Apol et al. 2008; Dodds 2010); and iii) different statistical methods for
1200 analyzing data and evaluating hypotheses (e.g., Isaac and Carbone 2010; Kearney and White
1201 2012; Uyeda et al. 2019; White et al. 2019). Many studies, and relevant theoretical and
1202 empirical issues, are addressed in Sibly et al. (2012).

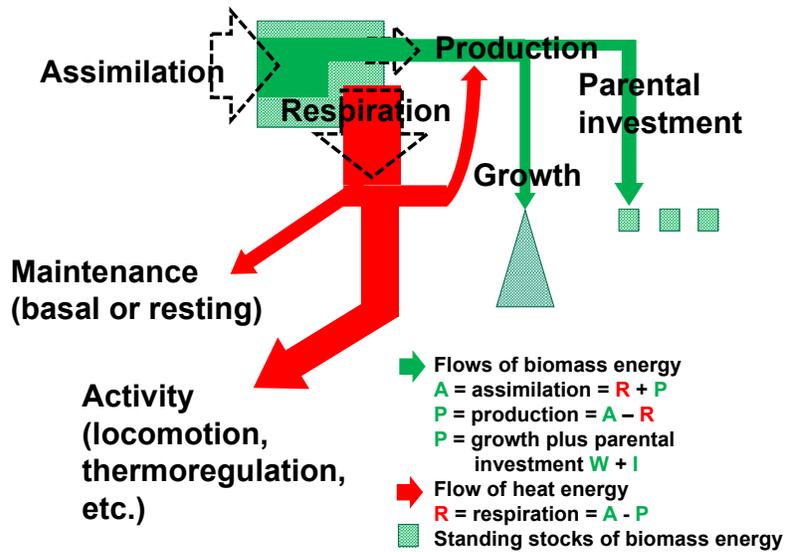
1203 In this paper, we circumvent many of these controversial issues by suggesting that the
1204 whole family of quarter-power scalings reflects the importance to fitness of generation time and
1205 the very general $m^{1/4}$ scalings of biological times. We attribute this insight primarily to Linsdtedt
1206 and Calder (1981; see also Calder 1984). Like most ideas in science, however, it has its
1207 antecedents (e.g., Blum 1977; Bleuweiss et al. 1978; Richardson and Rosen 1979) and
1208 successors (e.g., Hainsworth 1981; Ginzburg and Damuth 2008; Colyvan and Ginzburg 2010).

1209 **2) Rate of living.** – The EFP shows some resemblance to ‘rate of living’ or ‘pace of life’ theories
1210 (Rubner 1908; Pearl 1928). Recent versions posit that ageing is caused by energy metabolism:
1211 higher metabolic rates lead to shorter lifespans, because oxidative respiration generates free
1212 radicals and other byproducts that cause molecular and cellular damage and contribute to
1213 aging, senesce and mortality (for reviews and divergent assessments see Pearl 1928;
1214 Speakman 2005; Speakman and Król 2010; Selman et al. 2012; Hou and Amunugama 2015). It
1215 is becoming increasingly clear, however, that cause and effect are intertwined: metabolism does
1216 affect lifespan, but lifespan also affects metabolism, especially production. It takes longer to
1217 build and reproduce a larger, more complex organism, and so it must grow and resist aging and
1218 extrinsic mortality for longer than a smaller, simpler organism.

1219 **3) Dynamic energy budgets.**— The body of work on dynamic energy budgets (DEB) by
1220 Kooijman and collaborators (e.g., Kooijman 1986; 2000; 2010; Nisbet et al. 2000, 2010, 2012;
1221 Sousa et al. 2008; 2010; Freitas et al. 2010; Maino et al. 2014) is a longstanding research
1222 program that paralleled work on a metabolic theory of ecology (MTE; Brown et al. 2004, 2018;
1223 Sibly et al. 2012a; Burger et al. 2019a). It may not be the “most comprehensive metabolic theory
1224 of life existing to date” (Jusup et al. 2017), but DEB has much in common with MTE. Both aim to
1225 elucidate fundamental rules of life based on mass-energy balance, other laws of physics and
1226 chemistry, and first principles and established facts of biology. Both provide an integrated
1227 framework of models and data. But there are differences in content and applications. DEB is
1228 more based on the biochemical and physiological details of metabolism, invokes some different
1229 assumptions, includes more parameters in its models, and has been more applied to practical
1230 problems of environmental policy and management. MTE has been more based on simple
1231 assumptions and models with fewer parameters, more focused on scaling relations and other

1232 phenomena of whole organisms, and more extended to address ecological and evolutionary
1233 patterns and processes at ecosystem, community, geographic and evolutionary scales. We do
1234 not, however, see any inherent conflict between DEB and MTE. The relative merits of
1235 alternative assumptions and models can be debated and resolved, and more and better data
1236 collected and compiled to test and extend the theories (e.g., Fig 3,4 & Appendix 1; see also
1237 Marques et al. 2018). To a large extent, the perceived merits and demerits of the two theories
1238 are matters of subjective taste, not objective science.

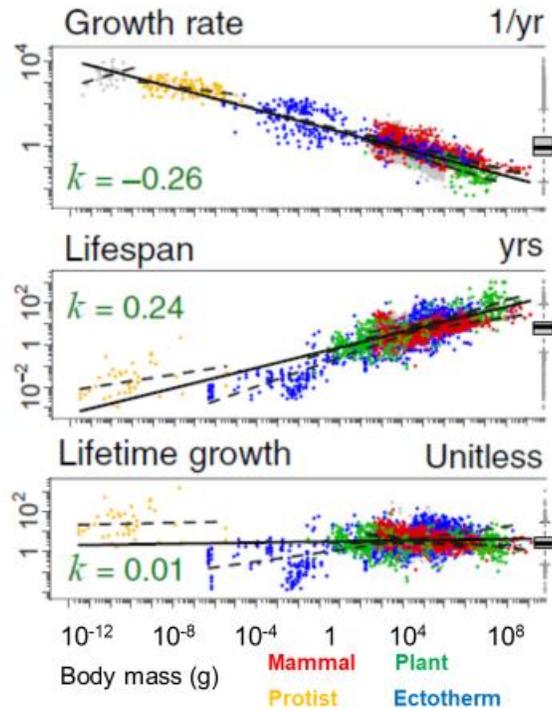
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1240

1241 Fig. 1. Energy balance of an individual animal. Energy assimilated from food is allocated
 1242 between respiration and production; energy captured in ATP by respiration is allocated between
 1243 basal or resting metabolism and activity metabolism (which includes digestion,
 1244 thermoregulation, growth, immune response to pathogens, and locomotor, feeding, territorial
 1245 defense, courtship and mating behaviors). Biomass energy passed to the next generation as
 1246 production is allocated between offspring growth and parental investment in gametes and
 1247 nutrition. Over the lifespan of an average individual at steady state, energy taken up from the
 1248 environment in assimilation is returned to the environment in mortality and heat as metabolism.

1249

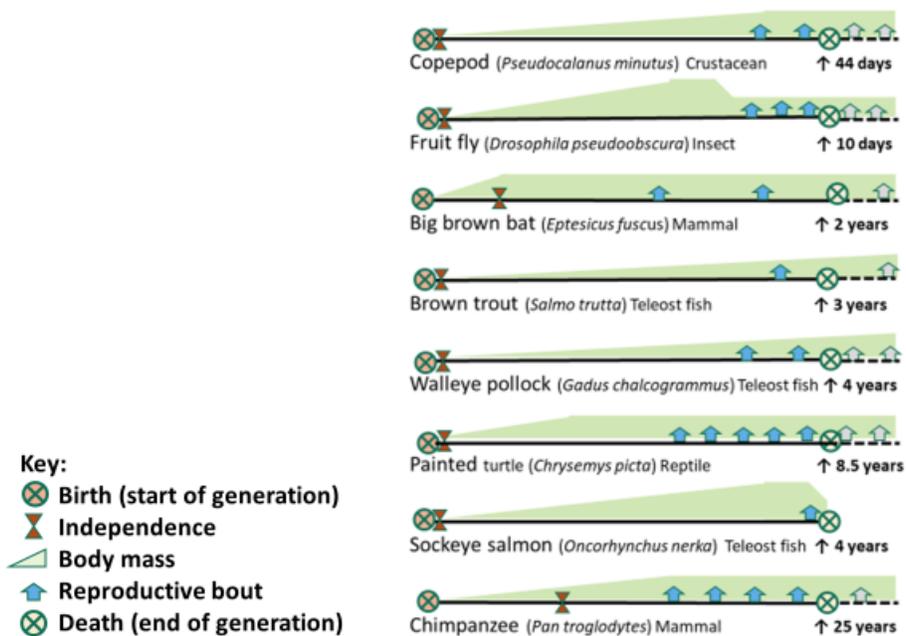


1250

1251 Fig. 2. Data from Hatton et al. (2019) showing the scalings of individual production rate,
 1252 generation time, and individual lifetime production as a function of body mass for four major
 1253 taxonomic/functional groups plotted on logarithmic axes. Note the close agreement between the
 1254 fitted exponents and the predicted values: -0.26 vs -0.25, 0.24 vs 0.25 and 0.01 vs 0.00,
 1255 respectively. Note gray points are bacteria.

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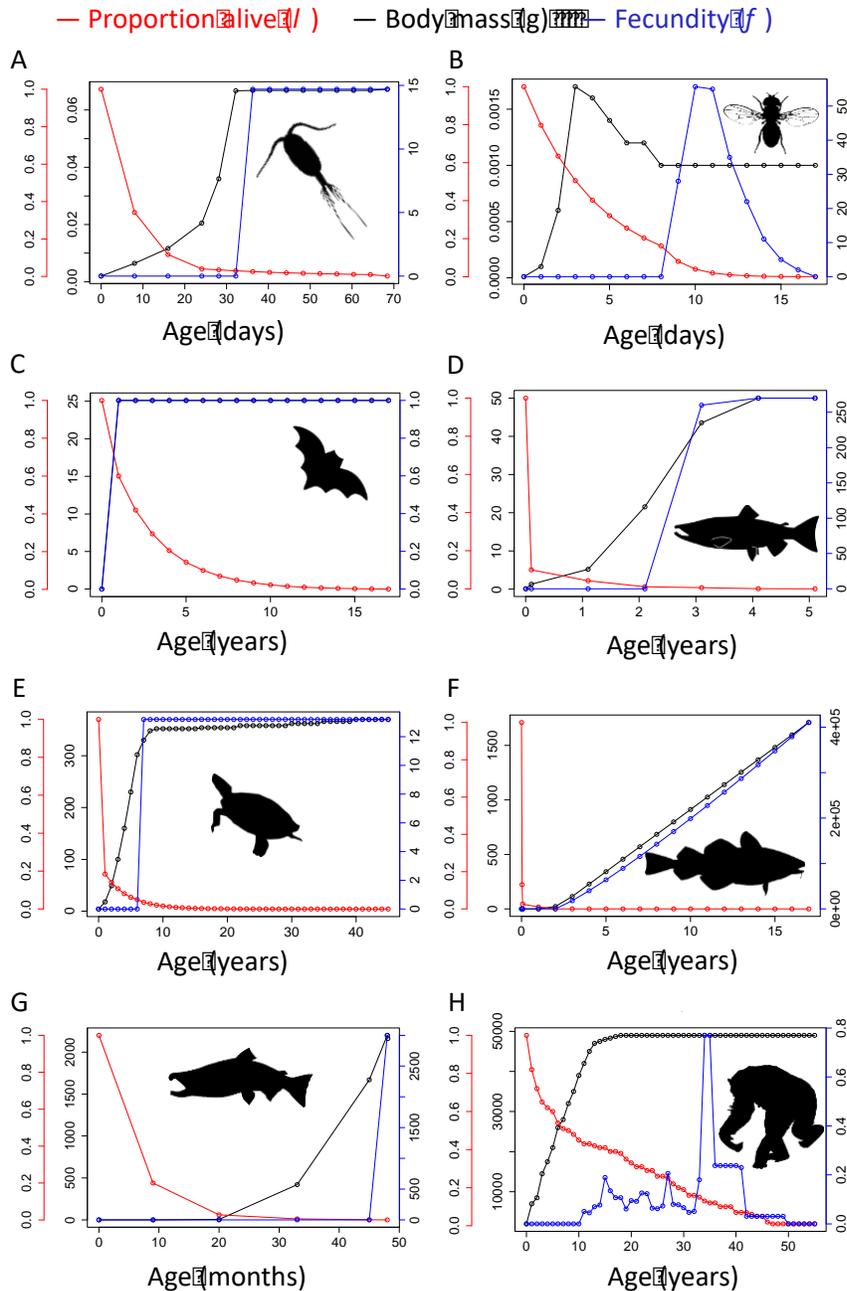
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1258

1259 Fig. 3. Life history schedules for various animal species, showing the relation of generation time
 1260 (solid line between ⊗-birth and ⊗-death value given by ↑) to times of other events. We define
 1261 generation time as time from birth to death of an average parent that replaces itself by leaving
 1262 two surviving offspring. Note sockeye salmon is the only semelparous species, which dies after
 1263 a single reproductive bout. In contrast in iteroparous species, some individuals live longer,
 1264 continue to reproduce and sometimes grow beyond the average generation time defined here.
 1265 Note that other life history times given in the literature and electronic databases, such as
 1266 average, maximum and reproductive lifespans and age to first reproduction, are not the same
 1267 as generation time. See also text on definitions and standardizations.

1268



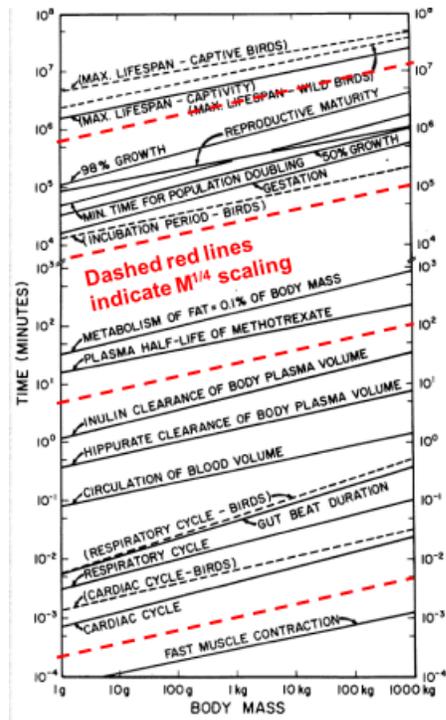
1269

1270 Fig. 4: Metabolic life histories of eight animal species chosen based on data availability and to
 1271 represent a diversity of taxa, body sizes and lifestyles. Included here are values for teleost fish
 1272 including sockeye salmon, which grow for four years and then have just one bout of
 1273 reproduction (data from Brett 1983; Brett 1986; Furnell and Brett 1986; Larkin McDonald 1968);
 1274 and marine walleye pollock (data from Hinckley 1987; Houde 1989; Houde 1997 [used for larval
 1275 stages]; Houde and Zastrow 1993; Smith 1979) and fresh-water brown trout (data from Brown
 1276 1946; Horton 1961; Dartmoor wild trout project 2016), which continue to grow and reproduce
 1277 throughout life; mammals such as the big brown bat (data from O'Shea et al. 2010; O'Shea et
 1278 al. 2011) and chimpanzee (data from Hill et al. 2001; Bronikowski et al. 2016), which provide
 1279 nutrition and parental care to produce a few large offspring; a reptile, painted turtle (data from

1280 Wilber 1975a,b), which is relatively long-lived and produces a clutch of eggs each year; and two
1281 very small invertebrates a marine copepod (data from McLaren 1974; Frost 1989; Hunley and
1282 Boyd 1984) and terrestrial fruit fly (data from Church and Robertson 1966; Rosewell and
1283 Shorrocks 1987; Roberston and Sang 1944; Smith 1958; Tantawy and Vetukiv 1960), which
1284 both lay miniscule eggs but have very different patterns of growth and mortality. Life histories of
1285 eight species, depicted as trajectories over the lifespan for: growth (body mass), survival
1286 (number of offspring alive), and fecundity (number of offspring per female). Note the scales of
1287 the axes, which indicate the magnitude of variation within and between species. (See
1288 supplemental data). Icons reused from phylopic.org under
1289 <https://creativecommons.org/licenses/by/3.0/> with following credits: Chimpanzee T. Michael
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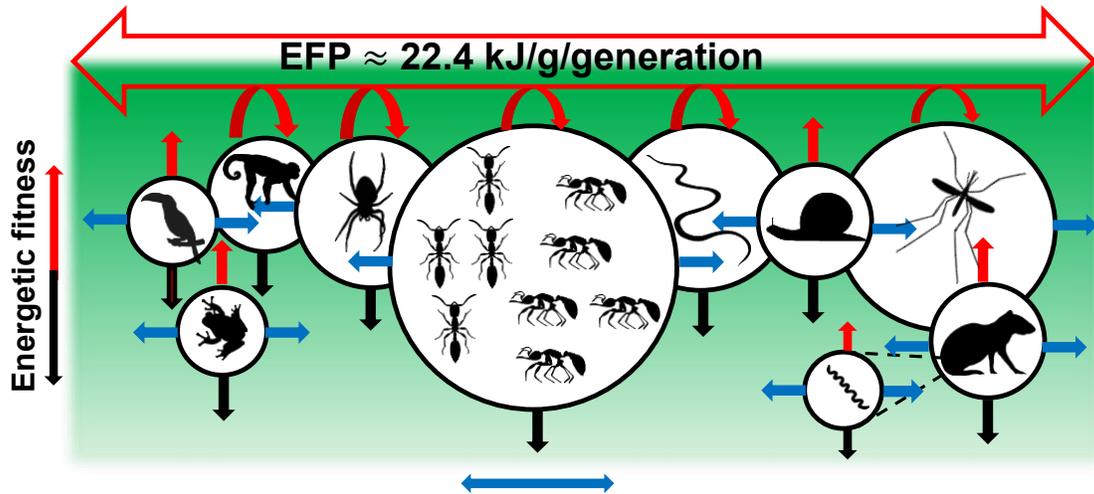
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1294

1295 Fig. 5. Data and analysis from Lindstedt and Calder (1981) showing that biological times
1296 scale as the 1/4 power of body mass. The authors have plotted the characteristic times
1297 of biological processes spanning 12 orders of magnitude, from milliseconds to centuries,
1298 in mammals and birds spanning 6 orders of magnitude in body mass from shrews and
1299 hummingbirds to elephants and ostriches. For reference, we have plotted dashed red
1300 lines indicating $m^{\frac{1}{4}}$ scaling.

1301



Trait distribution:

Body size, Assimilation rate, Activity respiration, Growth, Production rate, Generation time, Fecundity, Mortality, Semelparous/iteroparous, Parental care

Niche axes:

Temperature, Water, Nutrients, Competitors, Predators, Parasites, Disease

1302
1303

1304 Fig. 6. Schematic diagram representing diverse yet equally fit species. The joint effects EFP
 1305 energetics and Red Queen interactions on the assembly of a hypothetical ecological
 1306 community. As they compete for usable energy the coexisting species (represented by the
 1307 circles) continually diversify in trait distributions and environmental requirements along niche
 1308 axes (blue arrows). Some species are able to obtain a larger share of usable energy (size of
 1309 circle), increase in abundance and energetic fitness (red arrows), and push up against the
 1310 maximum steady state value of $E = 22.4$ kJ/g/generation. Other species are unable to keep up
 1311 in the zero sum Red Queen game, decrease in abundance, and eventually go extinct (black
 1312 arrows). Icons reused under Public Domain phylopic.org with special credits to Sarah Werning
 1313 (Capuchin), Gareth Monger (Spirochete) and (Birgit Lang) Spider under
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1315

1316 Appendix 1: Values of life history parameters for the animal species illustrated in Figure 3. All
 1317 traits vary by more than two orders of magnitude across the eight species, but the variation is
 1318 constrained. Large teleost fish produce thousands of miniscule larvae that suffer high mortality
 1319 as they grow to maturity. Tiny invertebrates (copepod and fruit fly) produce smaller numbers of
 1320 comparably-sized larvae that suffer lower mortality because of shorter generation times.
 1321 Mammals (bat and chimpanzee) invest extensive nutrition and care to produce a few relatively
 1322 large offspring which suffer relatively low mortality.

Com mon name	Scienti fic name	Taxo n	Adult mass	Offs prin g mas s (at inde pen den ce)	Norm alized offsprin g mass	Avg # of offs prin g per fem ale per lifet ime	Gro wth	Norm alized growt h	Par ental inve stme nt	Norm alized parent al invest ment	Fracti on of produ ction to growt h or invest ment	Gener ation time	Bio ma ss lost to mor talit y	Fracti on of produ ction to offsprin g
			m_A	m_O	$\mu = m_O/m_A$	N_O	$H = m_A - m_O$	$H/m_A = (m_A - m_O)/m_A$	$I = N_O m_O$	$I/m_A = (N_O m_O)/m_A$	Growt h/invest ment = H/I	averag e lifesp an	W	$F = m_A/(2 m_A + W)$
Units			g	g	dimen sionle ss ratio	nu mb er	g	dimen sionle ss ratio	g	dimen sionle ss ratio	dimen sionle ss ratio	days	g	dimen sionle ss ratio
Cope pod	<i>Pseud ocalanus minutus</i>	Crus tace an	6×10^{-4}	2×10^{-6}	2.99×10^{-3}	14.7	6.6×10^{-4}	9.97×10^{-1}	2.94×10^{-5}	4.40×10^{-2}	2.27×10^1	42	2.9×10^{-4}	2.28×10^{-1}
Fruit fly	<i>Drosophila pseudoobscura</i>	Insect	1×10^{-3}	1×10^{-5}	1×10^{-2}	30	9.9×10^{-4}	9.99×10^{-1}	3×10^{-4}	0.3	3.3	9	3.1×10^1	3.2×10^{-2}
Big brown bat	<i>Eptesicus fuscus</i>	Mammal	25	24.9	9.96×10^{-1}	3.9	0.1	4×10^{-3}	97.1	3.88	1.03×10^{-3}	7.3×10^2	98.7	2.53×10^{-1}
Brown trout	<i>Salmo trutta</i>	Teleost fish	4.36×10^1	0.09	1.68×10^{-3}	135	5.3×10^1	9.98×10^{-1}	12.15	2.27×10^{-1}	4.40	1.2×10^3	3.1×10^2	1.40×10^{-1}
Walleye pollock	<i>Gadus chalcogrammus</i>	Teleost fish	1.2×10^2	2.8×10^{-4}	2×10^{-6}	6.4×10^4	1.2×10^2	1	1.81×10^1	1.52×10^{-1}	6.59	1.46×10^3	8.8×10^3	1.3×10^{-2}
Painted turtle	<i>Chrysemys picta</i>	Reptile	3.5×10^2	4.14	1.18×10^{-2}	34.3	3.4×10^2	9.88×10^{-1}	1.42×10^2	4.06×10^{-1}	2.44	3.1×10^3	2.4×10^3	1.46×10^{-1}
Sockeye salmon	<i>Oncorhynchus nerka</i>	Teleost fish	2.2×10^3	0.13	5.9×10^{-5}	3×10^3	2.2×10^3	7.33×10^{-1}	3.9×10^2	1.77×10^{-1}	5.64	1.46×10^3	3.3×10^4	6.6×10^{-2}
Chimpanzee	<i>Pan troglodytes</i>	Mammal	4.90×10^4	2.1×10^4	0.43	3.4	2.8×10^4	0.57	7.14×10^4	1.46	3.92×10^{-1}	9.13×10^3	1.4×10^5	3.50×10^{-1}

1323