Universal rules of life: metabolic rates, biological times and the equal fitness paradigm

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Abstract

Here we develop and extend the equal fitness paradigm (EFP) of (Brown *et al.* 2018) as an important step in developing and testing a synthetic theory of ecology and evolution based on energy and metabolism. The EFP states that all species are equally fit at steady state, because all species allocate the same quantity of energy, ~22.4 kJ/g/generation to production of offspring. On the one hand, the EFP may seem tautological, because equal fitness across species is necessary for the origin and persistence of biodiversity. On the other hand, the EFP reflects universal laws of life: how biological metabolism – the uptake, transformation and allocation of energy – links ecological and evolutionary patterns and processes across levels of organization: from the structure and function of individual organisms, to the life history and dynamics of populations, to the coevolution of species in ecosystems. The physics and biology of metabolism have simultaneously facilitated the origin and maintenance of enormous biodiversity, so that the millions of species have idiosyncratic features of anatomy, physiology, behavior and ecology. However, there are universal constraints on biodiversity, so that all species share common features of metabolism that reflect the single origin and universal biophysical constraints of life.

Introduction

The diversity of life presents a fascinating duality. On the one hand, living things are amazingly diverse. Each of the millions of animal, plant and microbial species is unique. Each has distinctive features of anatomy, physiology, morphology, behavior and ecology that reflect its distinctive phylogenetic history and adaptations to environment. In other respects, however,

all living things are strikingly similar. They share fundamental features of structure and function that reflect the single origin of life and the biophysical constraints on subsequent evolution and diversification. Some of the shared traits are at molecular and cellular levels of organization, where they reflect the biochemical bases of inheritance and metabolism. Other shared traits are at whole-organism, population and ecosystem levels of organization. Many of these reflect unique species-specific features of metabolism – the uptake, transformation and allocation of energy. Emergent correlates and consequences of metabolism include scalings with body size and temperature, tradeoffs in physiology and life history, and features of ecosystem function and evolutionary diversification.

This duality of life can be understood, at least in part, as consequences of the equal fitness paradigm (EFP: Brown *et al.* 2018). Ever since Darwin, biologists have associated fitness with survival and reproduction. Because lifespan and fecundity differ across species from microbes to mammals by many orders of magnitude, the idea that all species have equal fitness may seem counterintuitive. But the EFP is a necessary condition for coexistence of species and maintenance of biodiversity. If fitness differs across species, the fittest survive, reproduce and dominate, and the others lose out and go extinct.

The EFP is based on the fact that energy is the ultimate limiting resource for living things. As Boltzmann (1886) perceptively wrote: “The “struggle for existence” of living beings is … for the possession of the free energy obtained, chiefly by means of the green plant, from the transfer of radiant energy from the hot sun to the cold earth.” The solar energy captured and converted into the organic molecules by green plants supplies essentially all the energy used by all organisms. The energy in the molecules is released and used to fuel the work of living in the processes of metabolism: assimilation, respiration and production. Assimilation is the uptake of energy from the environment. Autotrophic plants take up solar energy, carbon dioxide and oxygen in the process of photosynthesis and capture energy in organic molecules. Heterotrophic animals and microbes acquire biomass energy by consuming plants. Respiration is the biochemical transformation of biomass energy to fuel work, organic molecules are combined with oxygen, reduced to carbon dioxide and water, and energy is captured in ATP molecules. ATP is transported around the body, where it is converted to ADP, releasing energy to perform the work of digestion, excretion, activity, growth and reproduction. Finally, production is the transfer of biomass to offspring. Some assimilated biomass is not catabolized in respiration but passed on to the next generation in the form of offspring growth and parental investment in gametes.

Over a life cycle of one generation at steady state, parents on average exactly replace themselves with offspring, the birth rate of the population equals the death rate, and the number of individuals remains constant. Energy is a currency of biological fitness, because the traditional components of fitness – survival, growth and reproduction – can be defined biophysically in terms of the metabolic processes of assimilation, respiration and production. Energy balance at steady state requires that, in each generation, the energy assimilated from the environment is allocated between respiration and production, and gain in energy due to production is matched by loss of energy due to mortality (Fig. 1).

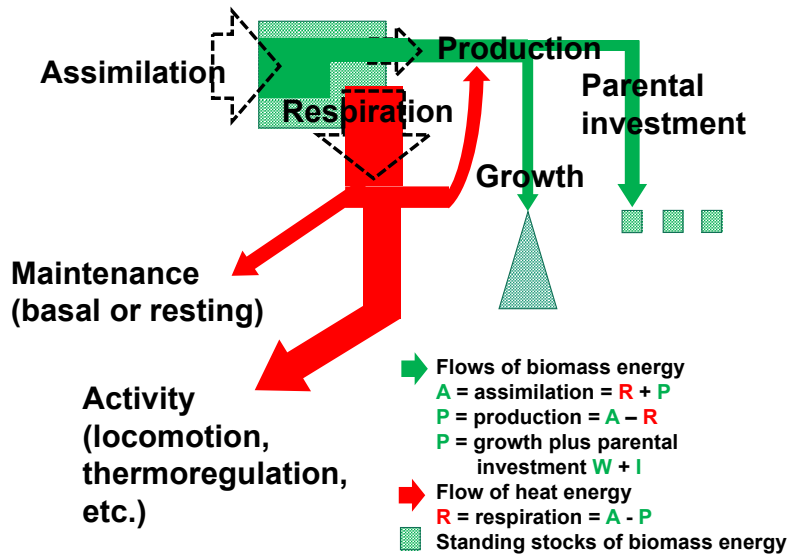

Fig. 1. Energy balance of an individual animal. Energy assimilated from food is allocated between respiration and production; energy captured in ATP by respiration is allocated between basal or resting metabolism and activity metabolism (which includes digestion, thermoregulation, growth, immune response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

The equal fitness paradigm (EFP)

The EFP quantifies the energetic basis of biological fitness as

$$E = P_{coh}GQF \tag{1}$$

where E is energetic fitness in kilojoules per gram per generation, P_{coh} is the mass-specific rate of biomass energy production of the cohort of offspring produced by an average parent over one generation in kilojoules per gram per year, G is generation time in years, Q is the energy density of biomass in kilojoules per gram, and F is the fraction of biomass energy production that is passed through to surviving offspring in the next generation. Because Q is essentially constant ≈ 22.4 kJ/g dry weight (see below), eq 1 can be expressed in units of mass and simplified to give

$$1 = P_{coh}GF \text{ or } F = \frac{1}{P_{coh}G} \tag{2}$$

where P_{coh} is the mass-specific rate of biomass production at steady state of the offspring of an average parent in grams per gram per year, G is generation time in years, and F is the fraction of biomass production that is passed through to surviving offspring in the next generation. The EFP and its seminal eqs 1 and 2 apply to all levels of biological organization from individuals to ecosystems. The EFP (Brown et al. 2018) emphasizes that equal fitness is a necessary condition for the historical origin and current persistence of the millions of species that differ

enormously in taxonomy, anatomy, physiology, behavior and ecology. The EFP applies to all these organisms because there is a tradeoff between production rate and generation time: those organisms that replace parental biomass slowly require longer lifespans to do so.

Traditional definitions of fitness focus on unequal survival and reproduction among individual organisms within populations. Such differences are the basis for evolution by natural selection. Individuals with higher rates of survival and reproduction leave more descendants in future populations, and the heritable traits that confer such advantages increase in frequency. This is completely consistent with the EFP. When natural selection is operating, individuals with higher rates of biomass production or longer lifespans, have higher energetic fitness – higher values of E in eqs 1 and 2 – and leave more biomass energy contained in surviving offspring in subsequent generations. Note, however, that when natural selection is operating, the steady state assumption of the EFP does not hold and E is not equal. The steady state assumption is critical, but it is also realistic. Species coexist and biodiversity is maintained, because on average, parents replace themselves with an equal energy content, mass, and number of offspring each generation. Indeed, the EFP may seem tautological.

In this respect, the EFP is similar to the Hardy-Weinburg equilibrium (Hardy 1908; https://en.wikipedia.org/wiki/Hardy%E2%80%93Weinberg_principle) in population genetics which also makes the critical assumption of steady state. Because the frequency of genes and genotypes in a population do not change over time at steady state, the HWE is seemingly tautological. But when first proposed by G.H. Hardy, the HWE seemed counterintuitive to many geneticists, who thought that the frequencies of dominant genes would inherently increase over generations. The HWE plays a seminal role in population genetics and evolution, because it provides the theoretical basis for quantifying the frequency of genes and genotypes in populations and for predicting changes in these frequencies due to natural selection, genetic drift and migration when the steady state assumption does not hold.

The EFP may seem counterintuitive. Biologists intuitively associate fitness with variation in survival and reproduction, yet generation times and fecundity differ among species by many orders of magnitude. The EFP is more than just a tautology, because it specifies the biophysical basis of fitness. Energetic fitness is constant across species, because there is a tradeoff between production rate, P_{coh}, and generation time, G, so that at steady state parents replace themselves with 22.4 kJ/g of biomass energy each generation. The product, $P_{coh}GF$, is constant, even though the three variables vary among species by orders of magnitude. Much of the variation is related to body size and temperature. The standard metabolic theory of ecology (Brown et al. 2004) predicts the scalings of P_{coh} and G:

$$P_{coh} = P_0 m_A^{-\alpha} e^{-\frac{E_a}{kt}} \quad (3)$$

and

$$G = G_0 m_A^{\alpha} e^{\frac{E_a}{kt}} \quad (4)$$

where above P_{coh} is the mass-specific rate of cohort biomass production in grams per gram per year, P_0 is a normalization coefficient, G is generation time in years, m_A is adult body mass, α is the mass-scaling exponent, $e\ is$ the root of the natural logarithm, E_a is an "activation energy" which gives the temperature dependence, k is Boltzmann's constant, and t is the temperature in kelvin. These scaling relations apply both over ontogeny within species and across species. Standard metabolic theory predicts that α = 1/4 and $E_a \approx$ 0.65 eV, equivalent to a Q_{10} of approximately 2.5 (Brown et al. 2004; Sibly et al. 2012). The predicted equal-but-opposite scalings of production rate and generation time with body mass are well supported empirically (Fig. 2; see also Brown et al. 2018; Hatton et al. 2019). The values of the exponents, -0.26 and

0.24 for what Hatton et al. (2019) called “growth rate” and “lifespan” respectively, are very similar to the predicted values of -1/4 and 1/4. Consequently, the product, “lifetime growth” is nearly constant, ≈ 0 and independent of size and temperature (not shown here, but see Gillooly et al. 2001; Brown et al. 2004, Hatton et al 2019). There is, however, considerable variation around the fitted regression lines as discussed below.

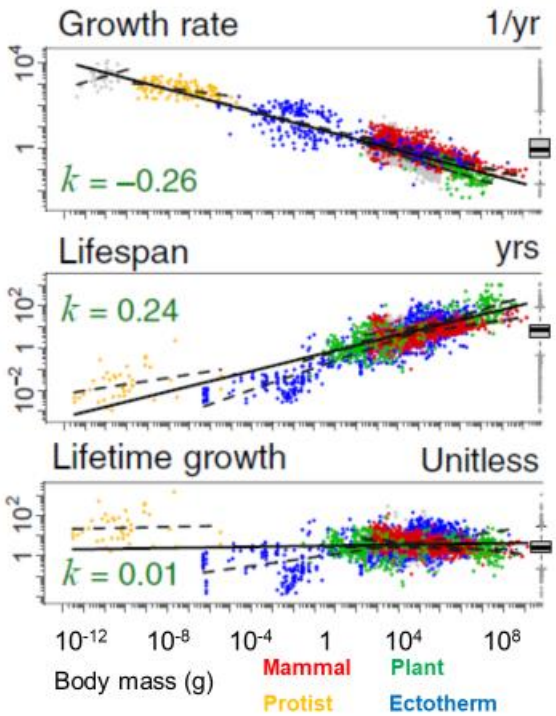

Fig. 2. Data from Hatton et al. (2019) showing the scalings of individual production rate, generation time, and individual lifetime production as a function of body mass for four major taxonomic/functional groups plotted on logarithmic axes. Note the close agreement between the fitted exponents and the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

Definitions and standardization

Some of the residual variation is due to “error”: failure to rigorously define terms and make carefully standardized measurements. For decades biologists have used the terms metabolism, metabolic rate, growth, production and lifespan loosely, and the lack of rigor has carried over into macroecology, both in compilation of large electronic databases and development of theory. For example, Kleiber’s law of 3/4-power scaling of metabolic rate with body mass was based on what he called “basal metabolism” or simply “metabolism” and measured as “heat production” in units of Calories for 14 individual mammals and birds (Kleiber 1932). To standardize the terms commonly used in biological energetics and metabolic ecology and show their relationship to energy and mass balance (Fig. 1), we suggest the following definitions:

1) *Respiration rate*: This is what Kleiber called “metabolism” and “metabolic rate”. It can be measured directly as rate of heat production or indirectly as oxygen consumption, carbon dioxide production or ATP synthesis. All of these are typically closely correlated and scale similarly with body mass and temperature because of the stoichiometry of the underlying biochemistry. Respiration rate is typically reported as volume of oxygen consumed or carbon

dioxide produced per unit time or as power in units of j/sec or watts; it can be as expressed as a whole-organism rate, R_{ind}, or divided by body mass to obtain a mass-specific rate.

2) Multiple "metabolic rates": Animal physiologists often use standardized conditions in the laboratory to measure basal or resting metabolic rate (BMR or RMR), the respiration of an inactive, fasting individual in its thermoneutral zone. Growing animals and those engaged in activities such as thermoregulation, locomotion, feeding, territorial defense, courtship, reproduction, and immune response to pathogens have higher rates. Physiologists often measure such elevated rates as metabolic scope or maximal rates (VO_2 max). Most relevant to ecology is field metabolic rate (FMR), typically measured using doubly-labeled water to obtain the average respiration rate over a period of days for a free-living (but reproductively inactive) animal in nature (Speakman 1997). All of these levels of respiratory metabolism are correlated with each other, and to a first approximation they all scale similarly with body mass, $\propto m^{\frac{3}{4}}$ for whole-organism rates and $\propto m^{-\frac{1}{4}}$ for mass-specific rates, and with temperature, and differ only in normalization coefficients (Gillooly et al. 2001; Savage et al. 2004). These are all actually respiration rates, because they measure rates of oxidation of assimilated food, synthesis of ATP, and dissipation of heat, water and carbon dioxide. Since they do not include uptake and expenditure for growth and reproduction, they do not represent energy balance at steady state for an individual over its lifespan or a population over a generation.

3) *Individual-level assimilation, respiration and production:* As shown in Figure 1, mass-energy balance for an individual animal over its lifetime requires that assimilation, A_{ind}, or intake of energy from food must equal the sum of respiration, R_{ind}, plus individual production, W_{ind}, so

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

where all rates are for whole-organism per generation, I_{ind} is parental investment in reproduction in the form of gametes and post-fertilization nutrition (e.g., pregnancy, lactation and feeding in mammals), and H_{ind} is the biomass accumulated and stored in the body due to ontogenetic growth. Note that P_{ind} in eq 1 is mass-specific individual production, so $P_{ind} = \frac{W_{ind}}{m_A}$. Importantly, individual-level production is often measured in different ways for different taxa by different investigators, and consequently the values in most large electronic databases are not comparable. Often the values aim to approximate the "maximal production rate" of an individual in an exponentially growing population rather than at steady state (see below).

4) *Cohort-level assimilation, respiration and production*: The EFP is explicitly couched in terms of mass-energy balance for a non-growing population, or for the cohort of offspring produced by an average parent at steady state (Brown et al. 2018; Burger et al. 2019):

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

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

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

where N_d is the number of offspring dying at age x and m_d is the mass of those offspring when they die. Note that the mass-specific cohort biomass production of the EFP, $P_{coh} = \frac{W_{coh}}{m_A}$ (eqs 2 and 6) is not the same as mass-specific individual production, $P_{ind} = \frac{W_{ind}}{m_A}$ in eq 5, which has variously been called "individual production", "maximal production", "growth" or simply "production", because the latter do not include the reproductive investment and ontogenetic

growth of the parent and the growth of offspring that die before maturing and reproducing. The EFP is expressed in terms of a cohort or population at steady state (eqs 1 and 2), so that P is the production rate per generation and G is the generation time.

5) *Lifespan and generation time*: The EFP is explicitly formulated in terms of generation time, which we define as time from birth to death of an average parent that has replaced itself by leaving two surviving offspring (Fig. 3). This definition accommodates determinate and indeterminate growers, semelparous and iteroparous reproducers, informs how to measure adult size and is consistent with life history theory (Burger et al. 2019). Several different life history times are often reported in the literature and comparative databases: average (often not rigorously defined), total (from birth to death), reproductive (age from first to last breeding), and maximum lifespan, age at first breeding, and for both wild and captive animals. As shown in Figure 3, these are not directly comparable to each other or generation time, so using them indiscriminately can lead to confusion and serious errors.

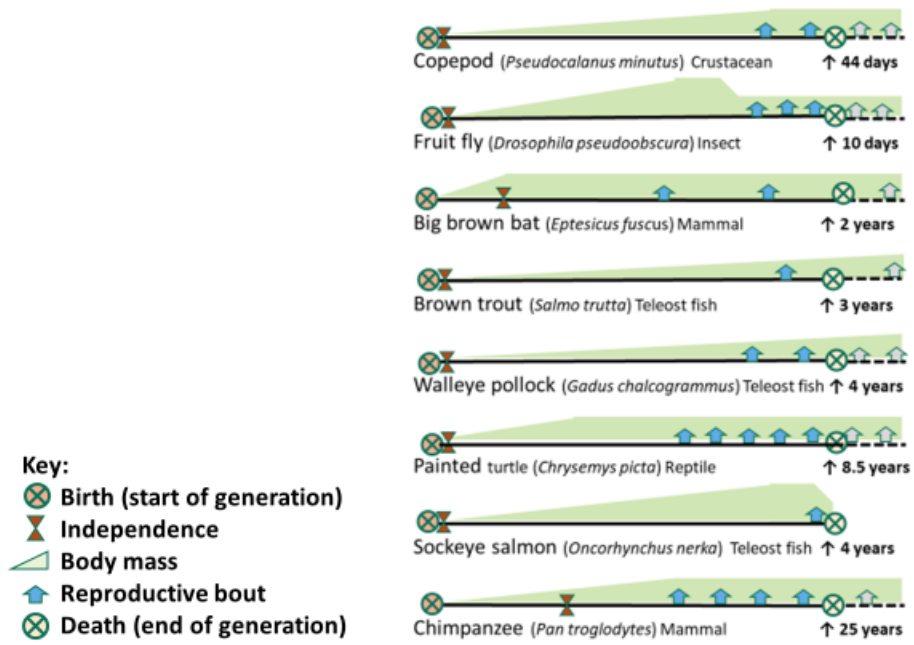

Fig. 3. Life history schedules for various animal species, showing the relation of generation time (solid line between ⊗ and ⊗; value given by ↑) to times of other events. We define generation time as time from birth to death of an average parent that replaces itself by leaving two surviving offspring. Note sockeye salmon is the only semelparous species, which dies after a single reproductive bout. In contrast in iteroparous species, some individuals live longer, continue to reproduce and sometimes grow beyond the average generation time defined here. Note that other life history times given in the literature and electronic databases, such as average, maximum and reproductive lifespans and age to first reproduction, are not the same as generation time. See also text on definitions and standardizations and Box 1.

6) *Normalized variables*: Theories of metabolic ecology can sometimes be simplified: i) by combining variables to create dimensionless ratios: one example is "lifetime reproductive effort:" $LRE = N_O\mu$, where N_O is the average number of offspring produced per lifetime and $\mu = \frac{m_O}{m_A}$ is the ratio of offspring mass to adult mass; (e.g., Charnov 1991, 1993; Burger et al. 2019; Hatton

et al. 2019; Morrow et al. 2019), and ii) by expressing rates and times as per generation rather than per unit clock time (Hou et al. 2008; Brown et al. 2018; Burger et al. 2019).

We hope that this effort at clarification and standardization will lead to caution in compiling and using large electronic databases in macroecology and to greater rigor and transparency in developing and evaluating metabolic theory.

The coefficients Q and F

The EFP and its seminal equation call attention to the importance of the two coefficients, Q and F. The energy density of biomass, Q ≈22.4 kJ/g dry weight (≈7 kJ/g wet weight), is a universal biological constant. It varies less than 2-fold across organisms spanning 20 orders of magnitude in body mass from microbes to mammals and trees (Brown et al. 2018). The value of Q is bounded, because biomass is composed of similar proportions of carbohydrates (~17 kJ/g), proteins (~17 kJ/g), and lipids (~34 kJ/g). This was recognized more than 50 years ago (e.g., Cummins and Wuychek 1967) but seems to have gone largely unappreciated. It is another universal characteristic of life at the molecular level – and one with profound implications for biological energetics from physiology to ecosystem ecology. Importantly, the constancy of Q allows parameters to be expressed in units of mass, which are more easily measured and readily available in the literature than units of energy.

Even less appreciated and at least equally important is the coefficient, F, the fraction of biomass produced in one generation that is incorporated into surviving offspring in the next generation. So F indexes the efficiency of lifetime reproduction. For a cohort or population at steady state, production must be balanced by mortality. At steady state, the biomass gained, the sum of the masses of the parents and all offspring when they die after having grown to varying extents, must equal the biomass lost in the sum of their body masses at death (eqs 2, 6 and 7).

Brown et al. (2018) attempted a preliminary empirical evaluation of F, which we build upon here. For asexual unicellular organisms that reproduce by mitotic fission, by definition F = 0.5: in each generation the cell doubles in size, divides, and one survives to replace the parent. For most organisms, accurate estimates of F requires a metabolic life table – the schedule of growth, reproduction and mortality as a function of age (Burger et al. 2020) – for which necessary data are not readily available in the literature. We have compiled such life tables for a selection of animals with contrasting life histories (Box 1). Across diverse taxa spanning many orders of magnitude in body mass, fecundity and lifespan, F varies by a factor of about 25, from 0.013-0.35. There seems to be a consistent pattern. Animals, such as mammals, where parents supply nutrition and care to rear a few relatively large offspring, have low rates of mortality and they pass a relatively large fraction of lifetime production (high F) through to the next generation. Animals such as teleost fish and invertebrates that produce many tiny offspring necessarily suffer higher mortality and leave a larger fraction of lifetime production in the ecosystem and have low F.

Toward a metabolic theory of life history

The facts that all organisms are subject to the same biophysical laws and share common structures and functions at molecular and cellular levels suggest the potential to construct a synthetic theory of life history that roots the population-level phenomena of demography and population dynamics in individual-level energetics and physiology. Historically, synthesis between levels of organization and subdisciplines of ecology and evolution were inhibited because they used different currencies. Physiologists at the individual-organism level and ecologists at the ecosystem level used metabolism and $\frac{dE}{dt}$ currencies: fluxes and stores of energy and materials. Ecologists at population and community levels used population dynamics

and $\frac{dN}{dt}$ currencies: numbers of individuals and species (see Brown 1981, 1995; De Angelis 1995). Recent advances in metabolic theory highlight the promise of a synthetic theory of life history based on first principles of bioenergetics and $\frac{dE}{dt}$ currencies (Burger et al. 2019, Burger et al. 2020; Hatton et al. 2019).

The life history is the schedule of survival, growth and reproduction over the life cycle. As exemplified in Box 1, animals exhibit a spectacular diversity of life histories including sexual and asexual, semelparity and iteroparity, determinate and indeterminate growth, and orders-of-magnitude variation in relative offspring size, fecundity and generation time. The EFP offers insights into the causes and consequences, and the magnitudes and extents of the variation. Burger et al. (2019) showed how the basic life history tradeoffs – between generation time and production rate, offspring growth and parental investment, and number and size of offspring – are due to "two fundamental constraints: 1) a demographic constraint on mortality so that, regardless of the number of offspring produced, only 2 survive to complete a life cycle of one generation; and 2) a mass–energy balance constraint so that in each generation energy acquired by assimilation from the environment is expended on respiration and production, and energy allocated to production matches energy lost to mortality." The basic patterns of life history (Box 1) are well explained by theory. Large fish and invertebrates, which produce miniscule larvae that feed themselves, must produce many of them to offset the mortality as they grow to maturity. Mammals and birds, with high investment, nourishing and protecting their offspring until they have grown to near-adult size, can produce fewer of them, because they suffer less mortality.

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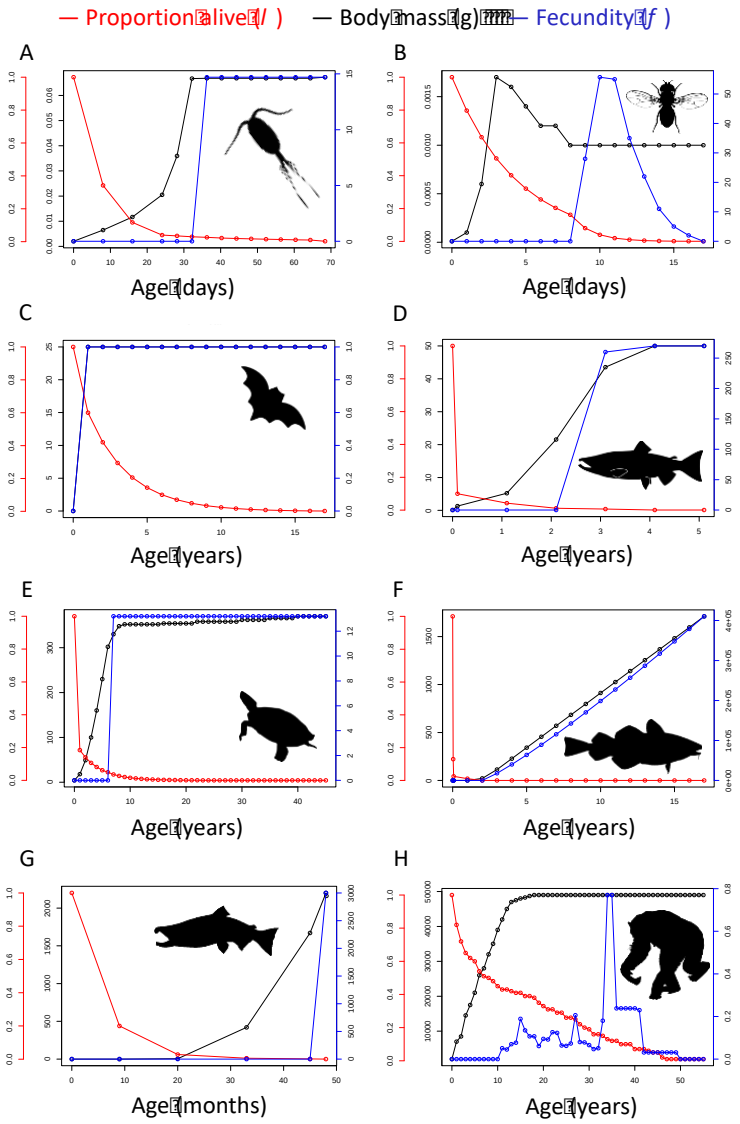

Table 1: Values of life history parameters for the animal species illustrated in the figure. All traits vary by more than two orders of magnitude across the eight species, but the variation is constrained. Large teleost fish produce thousands of miniscule larvae that suffer high mortality as they grow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

Common name	Scientific name	Taxon	Adult mass	Offspring mass (at independence)	Normalized offspring mass	Avg # of offspring per female per lifetime	Growth	Normalized growth	Parental investment	Normalized parental investment	Fraction of production to growth or investment	Generation time	Biomass lost to mortality	Fraction of production to offspring
			mA	mO	μ = mO/mA	NO	H = mA - mO	H/mA =(mA-mO)/mA	I = NOmO	I/mA = (NOmO)/mA	Growth/investment = H/I	average life span	W	F = mA/(2mA + W)
Units			g	g	dimensionless ratio	number	g	dimensionless ratio	g	dimensionless ratio	dimensionless ratio	days	g	dimensionless ratio
Copepod	*Pseudocalanus minutus*	Crustacean	0.000067	0.000002	0.0029940 12	14.7	0.000666	0.99700598 8	0.000294	0.04401197 6	22.65306122	42	0.000293	0.228
Fruit fly	*Drosophila pseudoobscura*	Insect	0.001	0.00001	0.010000	30	0.00099	0.999	0.0003	0.3	3.3	9	31.370	0.032
Big brown bat	*Eptesicus fuscus*	Mammal	25	24.9	0.996000	3.9	0.100	0.004	97.11	3.8844	0.00102976	730	98.7	0.253
Brown trout	*Salmo trutta*	Teleost fish	43.55	0.09	0.001679	135	53.510	0.99832089 6	12.15	0.22667910 4	4.404115226	1095	310.7	0.140
Walleye pollock	*Gadus chalcogrammus*	Teleost fish	119.5	0.00028	0.000002	64762	119.500	0.99999765 7	18.13336	0.15174359 8	6.590048397	1460	88879	0.013
Painted turtle	*Chrysemys picta*	Reptile	350	4.14	0.011829	34.3	345.860	0.98817142 9	142.002	0.40572	2.435599499	3100	2402.6	0.146
Sockeye salmon	*Oncorhynchus nerka*	Teleost fish	2200	0.13	0.000059	3000	2199.870	0.73329	390	0.17727272 7	5.640692308	1460	33396.8	0.066
Chimpanzee	*Pan troglodytes*	Mammal	49000.0	21000	0.42857142 9	3.4	28000.0	0.57142857 1	71400	1.45714285 7	0.392156863	9125	140000	0.350

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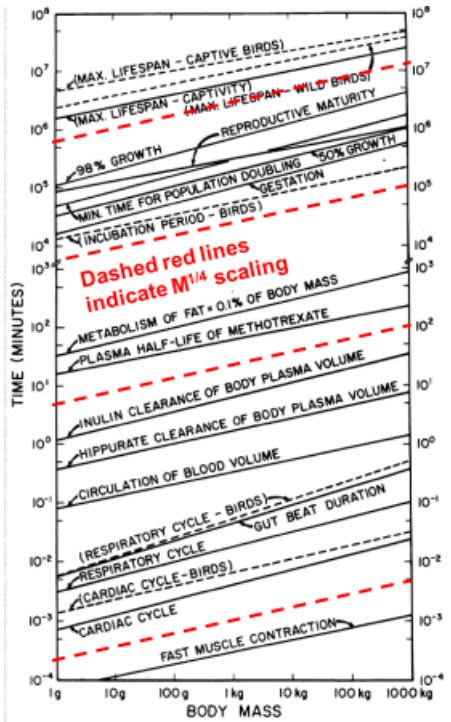


Fig. 3. Data and analysis from Lindstedt and Calder (1981) showing that biological times scale as the 1/4 power of body mass. The authors have plotted the characteristic times of biological processes spanning 12 orders of magnitude, from milliseconds to centuries, in mammals and birds spanning 6 orders of magnitude in body mass from shrews and hummingbirds to elephants and ostriches. For reference, we have plotted dashed red lines indicating $m^{\frac{1}{4}}$ scaling.

The fundamental role of biological time offers a different way of explaining Kleiber's 3/4-power law and other quarter-power scalings. Assuming from above that life is fundamentally four dimensional, with the numerator reflecting the three-dimensional geometry of living things and the denominator incorporating the 1/4-power scaling of time, and substituting eq 4 into eq 2, we have

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

So α = -1/4 and $\frac{1}{F} = C_0 G_0$,

This derivation of the metabolic mass-scaling exponent, α, is consistent with the equal-but-opposite quarter-power scalings of mass-specific respiration rate, $\propto m^{-\frac{1}{4}}$, and lifespan, $\propto m^{\frac{1}{4}}$, so that the quantity of energy expended by a gram of tissue in a lifetime is approximately the same, regardless of the size of the organism $\propto m^0$ (e.g., Fig. 2; Blum 1977; Andresen et al. 2002; Speakman 2005; Atanasov 2007; Ginzburg, and Damuth 2008; Brown et al. 2018; Hatton et al. 2019). These scalings led to the rate of living theory, which suggests that ageing is regulated by energy metabolism, so that shorter lifespans are due to higher metabolic rates (for

reviews see Pearl 1928; Speakman 2005; Selman et al. 2012; Hou and Amunugama 2015). It is becoming increasingly clear, however, that although oxidative respiration generates free radicals and other byproducts that cause molecular and cellular damage and contribute to aging and mortality. However, this cannot be the only cause. Lifespan also affects evolution of metabolism, growth, reproduction and mortality rates. It takes longer to build and reproduce a larger organism, and so it must grow and resist aging for longer than a smaller organism.

Our explanation for Kleiber's 3/4-power law based on the 1/4-power scaling of time is more general than models based on vascular and other systems that supply metabolites and remove wastes (e.g., West et al. 1997; Banavar et al. 2002, 2010; Aitkenhead et al. 2020). The 3/4-power scaling of respiration rate with body mass is pervasive across the animal kingdom, occurring in diverse taxonomic and functional groups that have distinctly different systems for assimilating, transporting and excreting the substrates and wastes of respiratory metabolism (e.g., Peters 1983; Brown et al. 2004). These include the guts, lungs, gills, arteries, veins, tracheoles, kidneys, and malpighian tubules of terrestrial, freshwater and marine species. These organ systems have distinctly different geometric structure and biophysical processes. So, our explanation for Kleiber's law subsumes network models by suggesting that these are all solutions to the general problem of supplying resources at rates proportional to the 3/4-power of volume or mass (see also Savage et al. 2008; Banavar et al. 2010; Maino et al. 2014). It unifies a general theory for scalings of metabolic rates and biological times across the diversity of animal form and function spanning: i) body masses from milligrams to tonnes, ii) time scales from milliseconds to centuries, and iii) levels of organization from molecules and cells to populations and ecosystems. It leads to a general theory for scalings of metabolic rates and biological times that applies to levels of organization from molecules and cells to populations and ecosystems and to the diversity of animals from unicellular eukaryotes to vertebrates.

Natural selection and alternative definitions of fitness

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

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

Rate of increase.—One suggestion is that natural selection tends to maximize the rate increase of a heritable trait that enhances reproduction or survival. The population growth rate, $r = \frac{1}{N}\frac{dN}{dt}$ (where N is the number of copies of a focal allele) and the net reproductive rate, $R_0 = \sum l_x f_x$ (where l_x is survival and f_x is fecundity as a function of age x) have both been used as measures of fitness (e.g., Charlesworth 1973, 1994; Charnov and Schaffer 1973; Stearns 1973, 1977, 1992; Charnov 1991, 1993; Sibly 1991, 2002; Brown and Sibly 2006). They have usually been applied to measure rates of change per unit clock time (r) or per generation (R_0) in the frequency of an allele or heritable quantitative trait within a population during departures from steady state when natural selection is operating.

Maximum power.—An alternative suggestion is that selection tends to maximize metabolic or reproductive power. This has been called the maximum power principle (MPP) and attributed

primarily to Alfred Lotka and H.T. Odum (Lotka 1926, Odum and Pinkerton 1955, Odum 1971; see also Brown et al 1993; Hall 1995). Power is measured in units of energy per time (e.g., J/s or watts). Biological power, expressed as rates of respiration and production, increases with body size, scaling $\propto m^{\frac{3}{4}}$. But the resulting variation in power does not result in larger, more powerful animals being fitter.

Resource use efficiency.—Physiological ecologists have frequently invoked efficiency of resource use (RUE) – of carbon, water, a nutrient or some other limiting resource – as a measure of performance, with the implication that natural selection tends to maximize RUE (Vitousek 1982; DeLucia and Schlesinger 1991; Chapin et al. 1997; Sterner and Elser 2002; Funk and Vitousek 2007; Hodapp et al. 2019). Efficiency is the unitless ratio: $REU = \frac{output}{input}$. or g/g/generation (eq 1). However, the sometimes-wide variation in REU does not result in more efficient animals being necessarily fitter than less efficient ones.

Lifetime reproductive effort.—Our energetic fitness, E, is somewhat similar to the lifetime reproductive effort, LRE, of Charnov (1991, 1993; Charnov et al. 2007), in that both E and LRE are predicted to be approximately constant, independent of body size, fecundity, lifespan and other life history traits. Charnov's model uses the net reproductive rate, R_0, as the measure of fitness and makes assumptions about how component variables scale with body mass. The big difference between LRE and E is that the former does not explicitly incorporate growth and mortality of offspring. Consequently, the prediction of nearly constant LRE seems to hold only for animals such as mammals and lizards (Charnov and Ernest 2006; Warne and Charnov 2008), which produce a few relatively large offspring with relatively little growth and mortality after independence. The EFP can be viewed as a more general theory that subsumes Charnov's model of lifetime reproductive effort as a special case.

The above definitions differ from the energetic fitness, E, of the EFP. The EFP was developed by Brown et al. (2018) to account for the nearly constant value of $E \approx 22.4$ kJ/g/generation (eqs 1 and 2) across species in different taxa, functional groups, and environments. The EFP, like the Hardy-Weinburg equilibrium, uses the assumption of steady state to establish a baseline from which to quantify departures. In both the EFP and HWE at steady state fitness is equal and natural selection is not operating. The EFP explicitly enforces the physical laws of thermodynamics and energy/mass balance to quantify fitness as the rate of change per generation in the quantity of physical energy passed on to surviving offspring. So, it defines fitness in terms of Boltzmann's (1886, see above) characterization of the Darwinian struggle for existence as the struggle to assimilate photosynthate and pass it on to surviving offspring. It focuses the variation in fitness across and within species explicitly in energetics.

Because of its reliance on the assumption of steady state, the EFP is distinct from but consistent with definitions of fitness that focus on evolution of traits due to natural selection during departures from steady state. The EFP does not contradict the proposition that natural selection can act to increase the above measures of fitness: r, R_0, metabolic power, RUE or L. But it emphasizes important caveats. Natural selection tends to increase these traits only during departures from steady state when the more or less fecund, long-lived, powerful or efficient variant also has higher energetic fitness. So, there is always potential selection to increase E. But energetic fitness cannot increase indefinitely, because at steady state the maximum value is

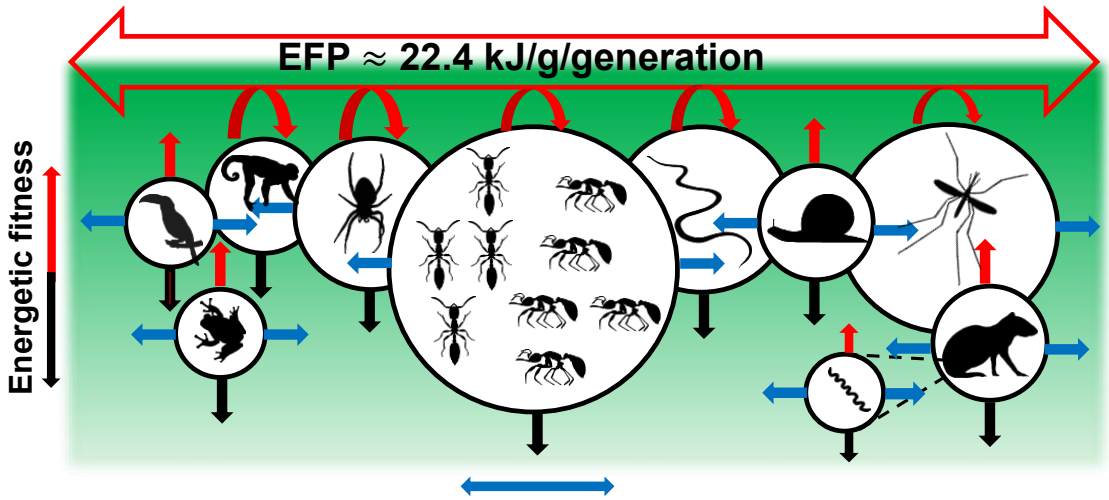
E = 22.4 kJ/g per generation. This constant value is enforced by biophysical constraints and ecological interactions among species.

Red Queen dynamics and their ecological consequences

The enormous diversity of species in ecological assemblages at all scales, from local ecological communities to the global biota, is a consequence of ecological interactions and coevolution among diverse taxa with near-equal fitness.

Within each species' population, natural selection favors individuals with heritable traits that increase Darwinian fitness. As Boltzmann (1886; see quotation above) noted, the biomass energy produced by photosynthesis is the ultimate limiting resource for living things. "The struggle for existence" is the struggle to obtain a share of this usable energy. Fitter **individuals** have higher E in eqs 1 and 2, because they produce more biomass energy per gram per lifetime and leave more surviving offspring in the next generation. So, natural selection tends to increase the frequency of more productive genotypes **within** a population. But increased production and resulting population growth is ultimately checked by the limited availability of usable energy. Once the number of individuals reaches the carrying capacity set by the environmental energy supply, the population stops growing because energy gain due to increased production is balanced by energy loss due to increased mortality. This tradeoff, which (Calow and Sibly 1983) call ecological compensation, is a steady state where natural selection no longer results in increased production.

The maximum rate of production at this steady state carrying capacity – the canonical E ≈ 24 kJ/g/generation – is set by the fundamental biophysical constraints inherent in the EFP, reinforced by Red Queen interactions among species. Leigh Van Valen (1973) coined the term Red Queen after the character in Lewis Carroll's *Through the Looking Glass* who famously said "It takes all the running you can do, to keep in the same place." Van Valen (1980) characterized the ecological and evolutionary dynamics of species in ecological assemblages as a "zero sum game" of competition for a share of usable energy. A simplified characterization of the Red Queen zero sum game is diagrammed in Figure 4. The supply of usable energy is set by net primary production (NPP) of the local ecosystem. To a first approximation, all of this biomass energy is used. Numbers of individuals and species increase in response to the Malthusian-Darwinian dynamic (Brown 1995; see also Nekola et al. 2013) until the steady state where population growth is limited by the carrying capacity and addition of new species due to colonization and speciation is balanced by loss of species due to extinction (Van Valen 1980; Ernest and Brown 2001; Ernest et al. 2008). This is the steady state of the EFP.



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

Fig. 4. Schematic diagram representing diverse yet equally fit species. The joint effects EFP energetics and Red Queen interactions on the assembly of a hypothetical ecological community. As they compete for usable energy the coexisting species (represented by the circles) continually diversify in biological traits and environmental requirements along niche axes (blue arrows). Some species are able to obtain a larger share of usable energy (size of circle), increase in abundance and energetic fitness (red arrows), and push up against the maximum steady state value of E = 22.4 kJ/g/generation. Other species are unable to keep up in the zero sum Red Queen game, decrease in abundance, and eventually go extinct (black arrows). Icons reused under Public Domain phylopic.org with special credits to Sarah Werning (Capuchin), Gareth Monger (Spirochete) and (Birgit Lang) Spider under https://creativecommons.org/licenses/by/3.0/

Tradeoffs in physiology and behavior limit the share of NPP that can be acquired by any given species. This share is set jointly by intrinsic biological traits and dynamic local environmental conditions (Enquist et al. 2015; Burger et al. 2019). Together, these define the unique ecological niche of each species. Selection on traits – such as body size, food requirement, territorial and antipredator behavior, etc. – results in dispersion of niches along axes of environmental variation – such as temperature, nutrients, physical structure, predation risk, etc. (Whittaker 1970; Hall et al. 1992; Blonder et al. 2014). At steady state, the community is full to capacity with species, each assimilating a share of the NPP and producing sufficient offspring biomass to persist (Van Valen 1980; Ernest and Brown 2001). But this idealized steady state hides complex underlying non-equilibrium dynamics as the species play the zero-sum game. Species fluctuate in abundance and their traits evolve adaptively in response to the abiotic environment and biotic interactions. When new resources become available, native

species shift their niches or alien species colonize and exploit them. Some species are able keep up, but any increase in productivity and abundance is necessarily temporary, ultimately checked by ecological compensation at the 22.4 kJ/g/generation steady state of the EFP. Other species are less successful; they fall behind in the Red Queen race, decrease in abundance, and ultimately go extinct unless rescued by environmental change or new adaptations.

One consequence of these complex dynamics is enormous variation in the abundance, distribution and ecological roles of coexisting species. Darwin (1882, 6th ed. p. 62) perceptively observed: "The most flourishing, or, as they may be called, the dominant species – those which range widely, are the most diffused in their own country, and are the most numerous in individuals…." Since then many authors have addressed variation, not only in abundance (e.g., Preston 1948; MacArthur 1957; Brown 1984, 1995; Williams 1964; Hubbell 2001; Harte 2011) but also in important roles of species in the physical structure, energy and nutrient flows, and species diversity of ecosystems (e.g., pioneer, climax, foundational, engineer, keystone and apex predator species; e.g., Paine 1966; McNaughton and Wolf 1970; Dayton 1975; Lawton and Jones 1995; Schramski et al. 2015; Enquist et al. 2020).

This inequality in ecological relationships is entirely consistent with the EFP. Ecological communities are filled to capacity with near equally fit species, but their fitnesses are only exactly equal when populations are constant and natural selection is not operating. During departures from steady state, a small change in extrinsic environment or heritable trait can have a large effect on fitness and trigger large shifts in abundance, distribution, community composition, and ecosystem processes. This interpretation is consistent with the well-documented "individualistic" responses of communities to climate change and invading species (e.g., Graham and Grimm 1990; Brown et al. 1997; Jackson and Overpeck 2000; Sax and Brown 2000; Williams et al. 2004; Sax et al. 2007).

The EFP has additional, still largely unexplored implications for the ecology of communities and ecosystems and for the origin and perpetuation of biological diversity. We see promising opportunities to apply a theoretical framework, based on first principles of physics and biology and using the dE/dt currencies of metabolic ecology, to address longstanding questions about the roles of abiotic conditions, biotic interactions, colonization, speciation and extinction in the assembly of ecological communities.

Conclusion: Toward a modern ecological synthesis

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

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