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PERSPECTIVE

Life, Death and Energy: What Does Nature Select?

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ABSTRACT

Evolutionary biology is poised for a third major synthesis. The first presented Darwin's evidence from natural history. The second incorporated genetic mechanisms. The third will be based on energy and biophysical processes. It should include the equal fitness paradigm (EFP), which quantifies how organisms convert biomass into surviving offspring. Natural selection tends to maximise energetic fitness, $E = P_{\text{coh}}GFQ$, where P_{coh} is mass-specific rate of cohort biomass production, G is generation time, F is fraction of cohort production that is passed to surviving offspring, and Q is energy density of biomass. At steady state, parents replace themselves with offspring of equal mass-specific energy content, $E \approx 22.4 \text{ kJ/g}$, and biomass, $M \approx 1 \text{ g/g}$. The EFP highlights: (i) the energetic basis of survival and reproduction; (ii) how natural selection acts directly on the parameters of M ; (iii) why there is no inherent intrinsic fitness advantage for higher metabolic power, ontogenetic or population growth rate, fecundity, longevity, or resource use efficiency; and (iv) the role of energy in animals with a variety of life histories. Underlying the spectacular diversity of living things is pervasive similarity in how energy is acquired from the environment and used to leave descendants offspring in future generations.

1 | Introduction

Energy powers the universe. The motions of celestial bodies and continental plates, the growth and reproduction of plants and animals, and the development of human civilisation and economy are all powered by energy. Understanding the role of energy in plate tectonics and circulation of the oceans and atmosphere led to paradigm-shifting advances in the geological, oceanographic and climate sciences. The influence of energetics on the biological sciences has been mixed. A century of research on the underlying physics and chemistry transformed cellular and molecular biology. The 'molecular revolution' elucidated the biochemical processes of metabolism, revealed the chemical structure of DNA and molecular mechanisms of inheritance,

and allowed reconstruction of ancestry and descent dating back to the origin of life. At the same time, however, studies of evolution and natural selection largely ignored the role of energy, focusing instead on physiological, developmental, demographic, genetic and phylogenetic mechanisms of survival, growth and reproduction.

The modern science of evolutionary biology dates back to simultaneous publications by Darwin and Wallace (1858). Their theory was based on simple, arguably tautological, but powerful axioms: (i) parents produce more offspring than can survive; (ii) parents vary in heritable traits, (iii) parents with heritable traits that result in greater survival and reproduction leave more offspring with these traits in the next generation; (iv) the

result is descent with adaptive change. Subsequently, there have been two major syntheses. In the first, the *Origin of Species*, Darwin (1859) drew from his encyclopaedic knowledge of natural history to present empirical evidence for how heritable traits that enhance survival and reproduction are passed on to future generations, generating biodiversity and the tree of life. Darwin recognised that his theory was not yet complete and that his axiomatic logic and supporting evidence went only partway towards understanding the role of natural selection in the origin and maintenance of biodiversity. In the last chapter of his last edition (Darwin 1872) of *Origin of Species* he articulated the remaining challenge:

‘It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us. These laws, taken in the largest sense, being Growth with reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the conditions of life, and from use and disuse; a Ratio of Increase so high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less improved forms. Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone circling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved’.

Darwin’s theory was increasingly accepted as biologists filled out his framework with empirical examples and theoretical models. A second major synthesis in the 20th century incorporated advances in genetics, biochemistry and molecular biology. But studies of Darwinian fitness and evolution by natural selection continued to focus on organism- and population-level processes that affect survival and reproduction and cause adaptive heritable changes in succeeding generations (Barker 2009; Charlesworth 2015; Metz, Nisbet, and Geritz 1992; Orr 2009).

Despite its clear relevance, the role of energy in evolutionary processes has received little attention. In 1886 Ludwig Boltzmann noted, ‘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’. Alfred Lotka (1922) added, ‘In accord with (Boltzmann’s) observation is the principle that, in the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient in directing available energy into channels favourable to the preservation of the species’. Leigh Van Valen (1973, 1977, 1980) extended and elaborated. The supply of usable biomass is limited by the input of solar energy and the net primary production of ecosystems. The result is what Van Valen called a zero-sum game of competition for energy and Red Queen ecological and evolutionary dynamics (named after Lewis Carroll’s Red Queen who ‘takes all the running you can do, to keep in the same place’). As coexisting species respond to selection to increase their share of biomass energy by evolving traits that enhance resource uptake, competitive ability, predator avoidance, disease resistance, and so on, they continually interact and coevolve with other species. Some adapt and increase, or at least persist temporarily. Those that fail to do so ultimately go extinct.

We suggest that evolutionary biology is on the cusp of a third synthesis: one based on energy and the pioneering contributions of Boltzmann, Lotka, Van Valen and others. This still-incomplete synthesis is addressing Darwin’s challenge to understand how the biodiversity of the tangled bank has been ‘produced by laws acting around us’. A recent addition is the equal fitness paradigm (EFP: Brown, Hall, and Sibly 2018; Brown et al. 2022; Burger, Hou, and Brown 2019; Burger et al. 2021). The EFP holds that at steady state, species are equally fit because they allocate an equal quantity per gram of energy and biomass to surviving offspring.

Here we go beyond earlier treatments of the EFP to probe more deeply into how energy, materials and information are taken up from the environment and passed on to surviving offspring, thereby maintaining unbroken lineages of ancestry and descent that extend back to the origin of life billions of years ago (Bartholomew 2005). In contrast to traditional treatments in terms of demography, life history, physiology and evolutionary ecology, we reformulate Darwinian fitness and evolution by natural selection in terms of biophysical currencies and metabolic processes. We show how this theory not only raises new questions but also offers new perspectives on old ones that have challenged biologists since Darwin.

2 | Background

To survive, reproduce and persist for millennia, organisms must acquire a share of biomass energy and use it to leave surviving offspring. To persist in the face of competition, predation, parasitism and disease, they must interact and coevolve with coexisting species. These processes require that energy be taken up from the environment and transformed into the biological currencies of survival, growth and reproduction. Species that fail to do so ultimately go extinct and are replaced by others with successful innovations.

2.1 | Energy Balance

We start with the assertion that Darwinian fitness is a physical property that can be measured in units of energy or mass. Fitness

is embodied in the biomass energy synthesised originally from solar energy by plants. Biomass is assimilated from the environment and used for ontogenetic growth and parental investment to produce offspring. The utilisation of energy for survival, growth and reproduction obeys the law of energy balance (Kooijman 2010; Appendix S1). Biomass energy produced by photosynthesis is transformed in metabolism, and allocated between respiration, to fuel the biological work of living, and production, to leave offspring in the next generation; the assimilated energy is ultimately returned to the environment in the form of heat and non-living mass. An initial parental investment of energy and materials in gametes, followed by postzygotic nutrition and care in some species, fuels survival, growth and development of offspring from fertilisation to independence. After independence from parental inputs, offspring assimilate biomass from the environment and use it for survival, growth and reproduction. When organisms die, the biomass produced during their lifetimes is recycled in the ecosystem.

2.2 | Steady State of Equal Fitness

Organisms are mortal, but populations persist and biodiversity is preserved when birth rates equal death rates and parents are replaced by an equal number, energy content and biomass of surviving offspring. It may seem counterintuitive, but species as different in ecology, physiology and life history as Greenland shark and bluefin tuna are equally fit (Figure 1; Burger et al. 2021; Sibly et al. 2018). By definition, at steady state there is no directional selection on heritable traits that affect survival and reproduction. Natural selection occurs during departures from steady state when parents leave more or fewer surviving offspring than replacement.

The assumption of steady state provides a baseline for the simplest case, from which such departures can be assessed.

3 | The Equal Fitness Paradigm

The equal fitness paradigm (EFP) was introduced by Brown, Hall, and Sibly (2018) and elaborated upon in three subsequent publications (Brown et al. 2022; Burger, Hou, and Brown 2019; Burger et al. 2021). The theory provides a biophysical explanation based on energy, for why not only sharks and tunas (Figure 1), but also microbes, insects, mammals and trees are all equally fit. Biodiversity is generated and maintained by a trade-off between incorporation of biomass into offspring as production and loss of biomass to the environment as mortality. At steady state, all species invest an equal quantity of energy (ca. 22.4kJ/g) and biomass (ca. 1g/g) to leave surviving offspring in the next generation.

3.1 | Composition of Biomass

The EFP goes beyond traditional definitions of fitness in biological terms of survival and reproduction. It redefines fitness in terms of the stocks and fluxes of energy and biomass passed on to surviving offspring (Figure 2). This production includes parental investments of gametes and nutrition in offspring prior to independence (e.g., birth, weaning, fledging), and self-fuelled growth of offspring from independence through reproductive maturity until death. These biophysical currencies consist of biomass energy, other chemical constituents of protoplasm, genetic material with its encoded information, a functioning infrastructure of organelles and cells, and a biological clock that runs from fertilisation to death.

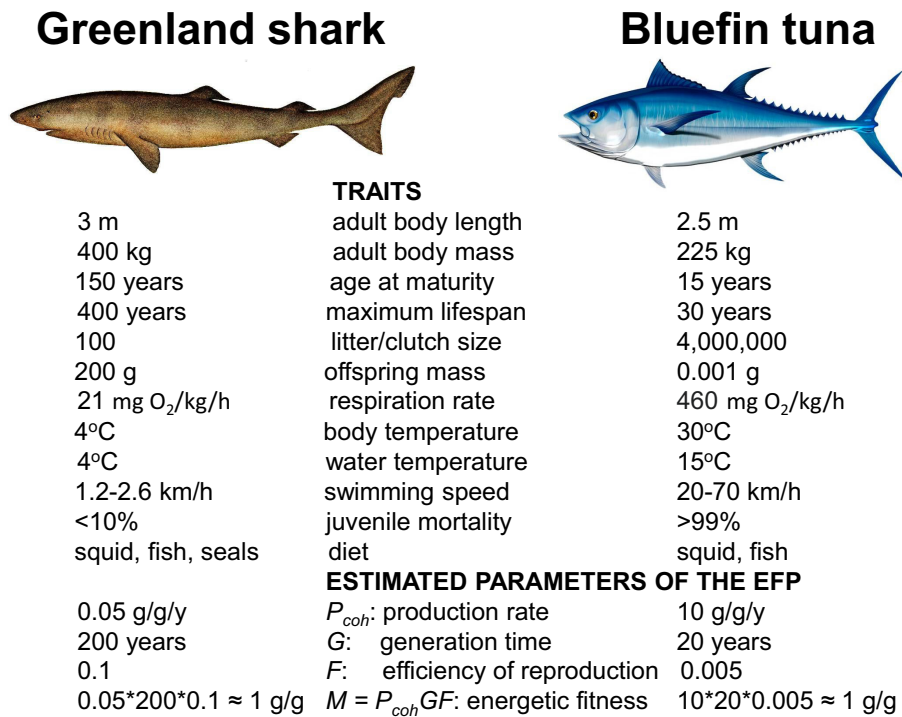


FIGURE 1 | Models of life history traits and EFP parameters for Greenland shark (*Somniosus microcephalus*) and bluefin tuna (*Thunnus thynnus*), two marine apex predators of similar size which differ conspicuously in anatomy, physiology, behaviour and ecology. Estimates of the parameters P_{coh} , G and F show why energetic fitness $M \approx 1$ and sharks and tunas are equally fit. Based on Sibly et al. (2018); https://en.wikipedia.org/wiki/Atlantic_bluefin_tuna; https://en.wikipedia.org/wiki/Greenland_shark.

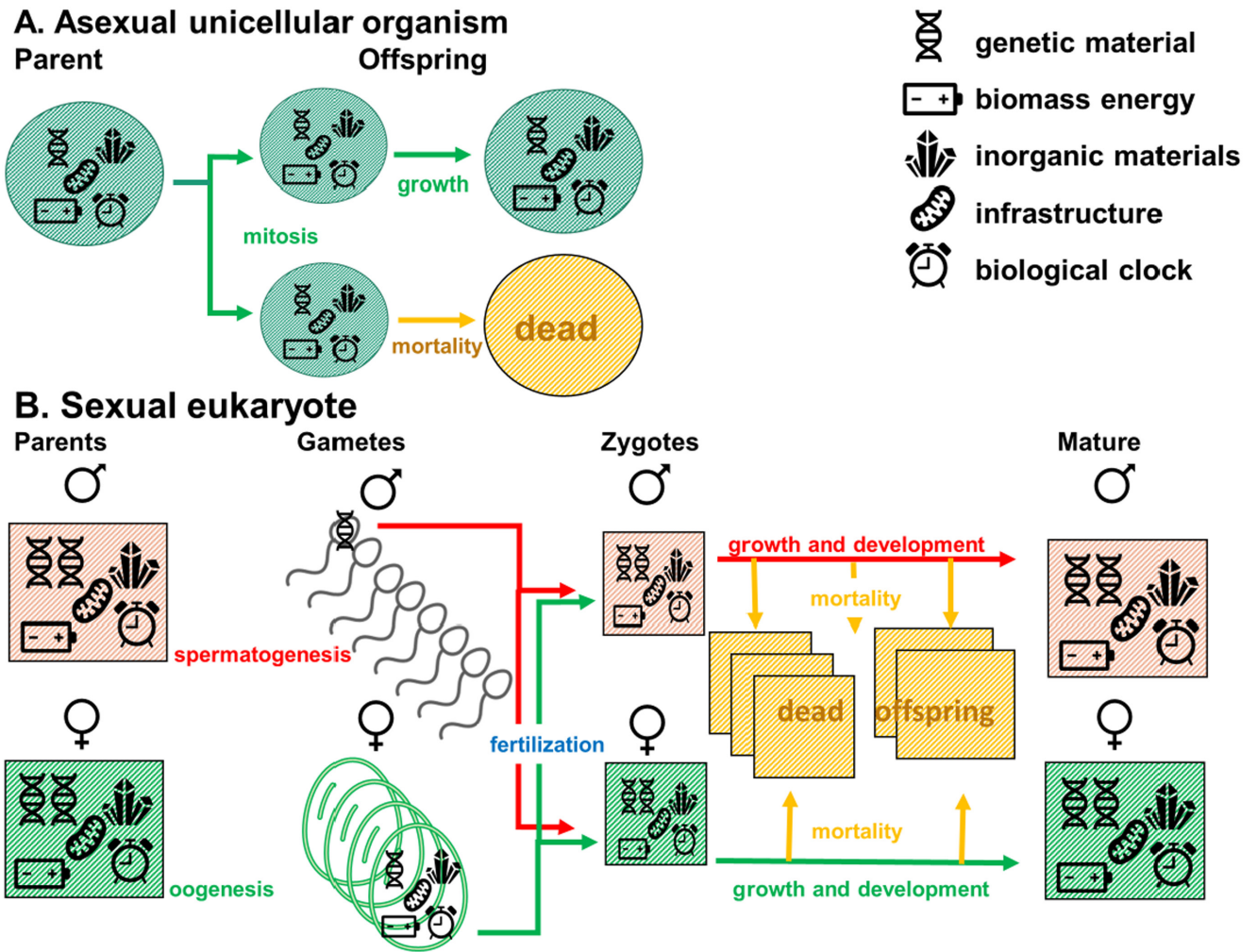


FIGURE 2 | A simplified diagram showing how the five biological currencies of fitness (biomass energy, inorganic materials, biological infrastructure, genetic information and biological clock) are passed from parents to offspring in (A) asexual prokaryotes and (B) sexual eukaryotes.

These currencies are packaged together in eggs and sperm, united in zygotes at fertilisation, and passed on to the next generation in the bodies of surviving offspring.

3.2 | The Basic Equation

The EFP quantifies energetic fitness, E , in terms of energy passed on to surviving offspring in the next generation. It is expressed in the basic equation

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

3.3 | Parameters of the EFP and Metabolic Life Tables

The parameters of Equation (1) are precisely defined in biophysical terms, but to apply and test the theory, they must be measured empirically: that is, quantified in the kinds of data collected by practicing biologists. For utility, all four parameters can be compiled and analysed in a metabolic life table (MLT: Brett 1983; Burger, Hou, and Brown 2019; Van Valen 1975). A MLT is similar to a traditional demographic life table, but in addition to the number of

surviving offspring, it contains energy content or body mass of offspring as a function of age. Ideally for sexual organisms, it includes an entire cohort of two parents and their offspring of both sexes. A challenge is that in practice it is difficult to obtain complete and accurate measurements of some critical parameters for free-living populations in nature. Even incomplete MTEs are available for only a few species: for example, the tropical palm, *Euterpe globosa* (Van Valen 1975) and sockeye salmon, *Oncorhynchus nerka* (Brett 1983). Standard demographic statistics and life history traits are often measured and analysed for only the female half of a population. But as shown for the example of red deer (Appendix S2), the parameters of the EFP often differ substantially between males and females. For these reasons, it is a challenge to rigorously ‘test’ the EFP using currently available data.

For this reason, the cases presented here should be regarded as simplified examples with estimated parameters for populations of the relevant species. We have tried to realistically represent the organisms and cited sources, but we have often relied on reviews in Wikipedia and elsewhere rather than the detailed data and multiple citations in the original literature. And we have adjusted values somewhat to meet assumptions of the models (e.g., energy, mass and demographic balance at steady state). We urge

others to regard these examples with caution, correct the values if warranted, and—most importantly—collect and publish accurate and relevant data. We hope that increased attention to the EFP and applications of new technologies will ultimately provide high-quality metabolic life tables for at least some model species.

In the meantime, however, we can specify how the parameters of the EFP should be measured empirically and interpreted theoretically:

- Cohort production rate, P_{coh} : Cohort production W , is the total quantity of biomass of offspring produced by two parents in one generation, G . It has units of energy, j , or mass, g . It can be calculated from a metabolic life table giving the number and energy content or body mass of surviving offspring as a function of their age, x

$$W = \sum_{x=0}^{x=G} N_d m_d \quad (2)$$

where m_d is the mass and N_d is the number of offspring when they died (including the two that died after replacing their parents). P_{coh} is the mass-specific rate of cohort production, obtained by dividing W by the masses of the female and male parents, $m_{A\varphi}$ and $M_{A\delta}$, and the generation time, G .

$$P_{\text{coh}} = \frac{W}{(m_{A\varphi} + m_{A\delta})G} = \frac{\sum_{x=0}^{x=G} N_d m_d}{(m_{A\varphi} + m_{A\delta})G} \quad (3)$$

P_{coh} has units of power (i.e., energy per time: J/s (watts) or kJ/y; or mass per time: g/s or kg/y). It can be calculated from a metabolic life table giving the number and energy content or body mass of offspring as a function of their age (Brett 1983; Burger et al. 2020; Van Valen 1975; Appendix S2).

- Generation time, G : is the duration of a complete life cycle. It can be calculated from a demographic life table as

$$G = \frac{\sum x l_x f_x}{\sum l_x f_x} \quad (4)$$

where x is age, l_x is survival (proportion of cohort still alive at age x) and f_x is fecundity (number of independent offspring produced by a parent of age x). Generation time, the most fundamental biological time, starts with fertilisation of the zygote, runs to maturity with varying speed depending on ontogeny and environment, and stops at death. Despite an enormous literature on biological time, there is little consensus on its biophysical basis (Winfree 1980).

- Efficiency of reproduction, F : is the unitless fraction of cohort production that is passed to surviving offspring in the next generation. For a sexual population at steady state this can be estimated as the sum of the masses of the parents divided by the total mass of the entire cohort:

$$F = \frac{m_{A\varphi} + M_{A\delta}}{W} \quad (5)$$

- Energy density of biomass, Q : is the energy density of the biomass incorporated into a cohort of offspring via growth

and parental investment. As indicated below, Q appears to be nearly constant, both over ontogeny within a cohort and across species: $Q \approx 22.4$ kJ/g dry weight (Brown, Hall, and Sibly 2018; Cummins and Wuychek 1967; Peters 1983; Popovic 2019). This allows us to rewrite Equation (1) as

$$M = P_{\text{coh}} GF = 1 \quad (6)$$

and evaluate the theory using the available data sets based on body mass as we do henceforth.

4 | What Does Nature Select? Comparison With Existing Theory

4.1 | Direct and Indirect Selection

At steady state, when parents are replaced by an equal mass, energy content and number of offspring—that is, when $M = P_{\text{coh}} GF = 1$ (Equation 6)—there is no directional selection. Selection occurs during departures from steady state when parents leave more or fewer surviving offspring than replacement ($M \neq 1$). Selection favours a trait when $M > 1$, and disfavours the trait when $M < 1$. Figure 3 and Equations (1) and (6) make explicit that selection acts directly only on the three parameters P_{coh} , G , or F .

So how does selection affect the evolution of other heritable traits? Earlier efforts to account for adaptive changes in various anatomical, physiological, ecological and behavioural traits recognised that selection operates through indirect pathways that link these traits to survival and reproduction (Arnold 1992; Bonnet et al. 2022; Ginther et al. 2024; Kingsolver and Huey 2003; Pelletier et al. 2007; Ricklefs and Wikelski 2002). Models of the pathways often focus on phenotypic or genetic trade-offs as expressed in statistical correlations (Figure 3). The EFP elucidates the mechanistic linkages. For natural selection to affect its evolution, a trait must be not only correlated statistically, but also tied mechanistically to one or more of the parameters of the basic equations (Equations (1) and (6)). For example, selection can cause an increase in body size, but only if larger parents leave more surviving offspring because $M > 1$ due to some combination of higher production rate (P_{coh}), longer generation time (G), or reduced mortality (higher F). More generally, disentangling pathways of cause and effect in the context of the EFP can provide new perspectives on longstanding phenomena, such as evolution of insular populations, domesticated plants and animals, and prehistoric and contemporary humans. For example, animal and plant breeders select for desirable traits by restricting breeding to individuals with appropriate combinations of P_{coh} , G , F and Q .

4.2 | Constraints Due to Energetic Trade-Offs

Many studies have suggested that selection inherently favours certain characteristics, such as faster life histories (and concomitant higher rates of individual production, more rapid ontogenetic and population growth and shorter generation times), greater metabolic power, or higher resource use efficiency. If this were true, large, slow, metabolically powerful

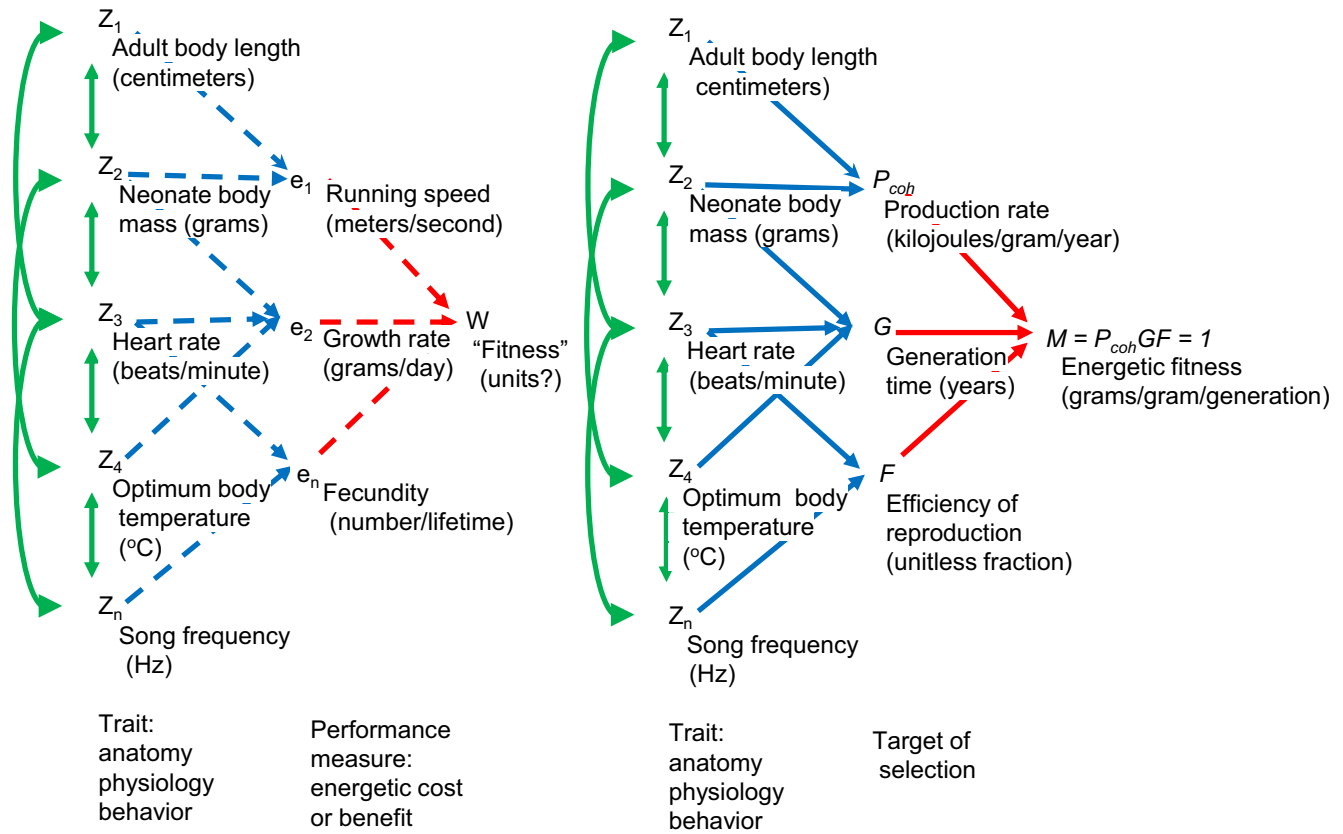


FIGURE 3 | Two scenarios for how nature selects on traits to affect fitness. On the left, the morphologyphysiology-fitness model (MPF; Lande and Arnold 1983; Arnold 1992; Kingsolver and Huey 2008) depicts relationships between phenotypic traits (green arrows), performance metrics (dashed blue arrows) and fitness metrics (dashed red arrows) as correlations in a path analysis. The traits shown here are examples of many that have been studied. On the right, the equal fitness paradigm (EFP) depicts the biophysical mechanisms whereby structural, functional and behavioural traits (green arrows) affect the parameters of the EFP (blue arrows), which are subject to the trade-off (red arrows) so that at steady state energetic fitness, $M = P_{coh}GF = 1$.

mammals would never have evolved. A corollary of the EFP is that for directional selection to cause lasting change in some trait, there must eventually be compensatory change in one or more other traits. The parameters, P_{coh} , G and F are interdependent, and Equations (1) and (6) specify the trade-off. For example, advantages of higher rates of growth (increased P_{coh}) are counterbalanced by disadvantages of shorter lifespans and/or higher mortality rates (decreased G and/or F). Insects weighing approximately 2 g differ in generation times and growth rates by more than two orders of magnitude, from migratory locusts with 4 or 5 generations per year to cicadas with 17-year life cycles (Brown et al. 2022).

Moreover, despite longstanding claims to the contrary (Hall 2004; Lotka 1922; Odum 1971; Vermeij 2023), selection does not inherently maximise either respiratory power or metabolic efficiency. Energy balance requires a trade-off in the allocation of assimilated energy between production and respiration (Appendix S1). So increased efficiency of production $K = \frac{P_{coh}}{A_{coh}} = \frac{P_{coh}}{P_{coh} + R_{coh}}$, requires some combination of increased assimilation or decreased respiration. A hypothetical species that expended all assimilation on respiration and survival would have none left over to produce offspring, and vice versa. But within these bounds, wide variation is possible theoretically and observed empirically (Brown et al. 2022; Burton et al. 2011;

Dammhahn et al. 2018; Ginther et al. 2024; Glazier 2014, 2022; Ricklefs and Wikelski 2002; White et al. 2022). Among birds, for example, some swifts and terns spend most their lives flying and their energy budgets on respiration, whereas flightless rails on islands efficiently allocate much more of their assimilated energy to reproduction (McNab 2002).

4.3 | Energy Efficiency

Frequently voiced in the literature of physiology and ecology is the misconception that selection tends to maximise 'energy efficiency.' Energy metabolism is subject to two efficiencies:

- Efficiency of production, K : is the fraction of energy assimilated from the environment that is passed to offspring in the next generation:

$$K = \frac{\text{useful output}}{\text{resource input}} = \frac{P_{coh}}{A_{coh}} = \frac{P_{coh}}{R_{coh} + P_{coh}} \quad (7)$$

It is equivalent to the trophic or Lindemann efficiency in ecosystems (Lindeman 1942; Kozlovsky 1968; Odum 1968). Importantly, it is not a direct component of fitness.

- Efficiency of reproduction, F : is the fraction of production that is incorporated into biomass of surviving offspring, $F = \frac{m_{A0} + m_{A1}}{W}$ (Equation 5). As shown in Brown et al. (2022), Burger et al. (2023, preprint.), and Figure 4, F varies widely among animals. It is not closely correlated with either adult or offspring body mass, but varies negatively with fecundity, N_O , and positively with the relative size of offspring (Figure 4A,B). This is logical, because F reflects survival. Survival to maturity is high and mortality is inevitably low when parents produce only a few offspring per lifetime. When parents produce enormous numbers of offspring, the vast majority die, leaving only the two survivors that replace their parents. Elsewhere we present an analytical theory that accounts for these patterns (Burger et al. 2023, preprint). A corollary is the parameter, $C = 1 - F$, which can be viewed as a tax of dead offspring and other biomass that a cohort of parents pays to the ecosystem to leave surviving offspring.

More generally, selection does not inherently favour higher metabolic power, ontogenetic or population growth rate, fecundity, or longevity, or greater efficiency of resource use, production (K), or reproduction (F). The diversities of life histories reflect multiple alternative stable strategies that confer equal fitness (Harman 2011). We present the following scenario for evolutionary constraints and energetic trade-offs that affect the evolution of F in animals (Figure 4C):

- Asexual fission: The ancestral condition, still found in prokaryotes and some eukaryotes, is a single-celled organism that reproduces asexually by mitotic fission. In one generation, a parent produces two offspring; one dies before reproducing; the other doubles in size and divides. So $F = \frac{m_A}{2m_A} = 0.5$.

As eukaryotic protists and algae evolved sexual reproduction and their descendants increased in body size and complexity, life history traits diversified to occupy the trait space between two alternative strategies:

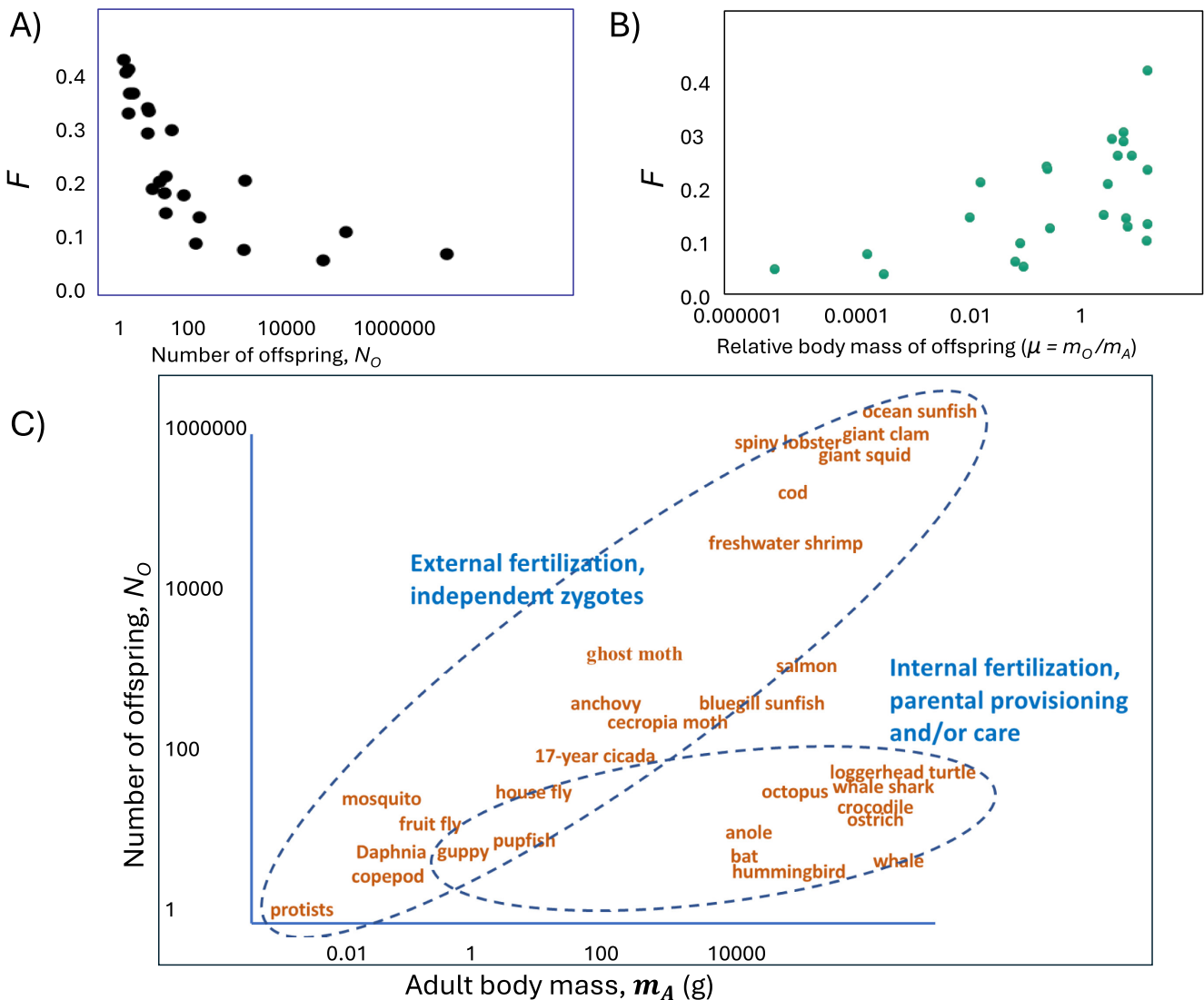


FIGURE 4 | Variation in parameter $F = \frac{m_{A0} + m_{A1}}{W}$, the efficiency of reproduction. (A) F is correlated negatively with lifetime fecundity, N_O . (B) F is correlated positively with relative body size of offspring, m_O/m_A . (C) The allocations between number and relative size of offspring reflect a wide range of parental investments in gametes and care; these are alternative stable strategies that confer equal fitness. From data in Brown et al. (2022).

- Many minute offspring: Most invertebrates (including marine annelids, molluscs and arthropods, and parasitic trematodes and cestodes) and large teleost fish produce large numbers of very small offspring, $m_O \ll m_A$, and have low values of F . Their minute externally fertilised zygotes contain just enough biomass of energy, materials, infrastructure, genes and clock to develop and survive to independence without feeding. Ontogenetic growth is fuelled by offspring assimilation, and mortality is high, especially early in ontogeny when the offspring are smallest and most vulnerable.
- Few large offspring: Some large animals, including sharks, reptiles, birds and mammals, produce just a few, relatively large offspring and have high values of F . Internal fertilisation allows zygotes to develop to relatively large size before birth, so post-embryonic growth, time to maturity, and mortality are relatively low. In mammals, birds and some reptiles, additional investments in post-natal care (e.g., incubation, lactation, feeding and protection from predators) allow production of even fewer and larger offspring. In the extreme cases of bats and altricial birds, offspring become independent at near-adult size, $m_O \approx m_A$, there is little or no subsequent growth, time to maturity is relatively short and mortality is very low.

4.4 | Limitations Due to the Red Queen

The EFP can be viewed as tautological in the sense that the maintenance of biodiversity over large scales of space and time implies a steady state of equal fitness across species. Otherwise, those with the highest values of E or M would monopolise energy resources and drive other species to extinction.

Departures from steady state occur when directional selection causes adaptive change. But such episodes tend to be small and temporary because of negative density dependence, resource limitation, ‘ecological compensation’ (Sæther and Engen 2015; Sibly and Calow 1987) and interspecific interactions (Van Valen 1973, 1977, 1980). The supply of usable biomass energy is finite—set by the input of solar energy and NPP of the ecosystem (Boltzmann 1886). The consequence is what Van Valen called ‘Red Queen’ and ‘zero-sum’ ecological and evolutionary dynamics. As coexisting species respond to selection to increase their share of biomass energy by evolving traits that enhance resource uptake, competitive ability, predator avoidance, disease resistance and so on, they continually interact and coevolve with other species. Some adapt and increase, or at least persist temporarily. Those that fail to do so lose out in the zero-sum game and ultimately go extinct. There is much room to explore in depth how the ecological and evolutionary interactions of the Red Queen affect the allocation of energy and materials to enforce equal fitness and regulate species richness.

4.5 | Rethinking Current Dogma

Many studies of ‘performance traits’ have perpetuated misconceptions about the nature of fitness and the process of evolution. They often violate—or at least fail to consider—the physics that underlies the biology. As emphasised above and elsewhere

(Brown et al. 2022), the EFP indicates why there is no inherent selective advantage to any particular morphological, physiological, behavioural or ecological trait, including body size, metabolic (respiration) rate, thermal performance curve (TPC), ontogenetic or population growth rate, fecundity, longevity, or resource use efficiency. Such performance traits are relative, determined by trade-offs between metabolic costs and fitness payoffs. Without going into additional detail here, it is sufficient to point out that selection can and does affect the adaptive evolution of such traits, but only indirectly, to the extent that they mechanistically (biophysically) affect P_{coh} , G , or F (Figure 3). Selection can favour a larger body, higher respiratory rate, or greater fecundity, but only in the restricted context of everything else being equal. As Van Valen (1980) noted, ‘Natural selection maximises many quantities if all else is equal ..., but only expansive energy (the E of the EFP: Equation 1) is maximised unconditionally’. And because of the Red Queen, such departures from steady state rarely last very long—otherwise biodiversity would not persist.

5 | Tests and Applications

After 6 years and four publications, response to the EFP has been both modest and contradictory. A consistent criticism is that we have not made a compelling case for why the theory is novel and useful. Does it do more than just translate traditional biological language and mathematical equations into physical terms? What are the implications for re-examining old studies and initiating new ones? How can the framework be applied in practical terms to shed light on central questions related to energy, life history and biodiversity?

Our response is that the EFP is an integral part of a third and still incomplete evolutionary synthesis based on energy. Below we briefly highlight a few areas where the EFP offers new perspectives and suggests topics for theoretical and empirical investigation. Many of these have challenged evolutionary biologists since Darwin. All of them emphasise the importance of energy, not only in the process of evolution by natural selection, but also in the nature of life itself. For the sake of brevity and clarity and because we feel more confident about them, the examples are for animals with sexual reproduction. We emphasise, however, that the EFP should apply to all organisms: prokaryotes and unicellular eukaryotes, metazoan plants and animals, sexual and asexual organisms, wild, managed and domesticated populations.

5.1 | Constant Q ?

The EFP calls attention to the importance of parameter Q , the energy density of biomass, in the basic equation, $E = P_{\text{coh}}GFQ$ (Equation 1). In the 1960s and 1970s, when some ecologists turned to energetics for empirical investigation and theoretical unification, they measured energy content of tissues and whole organisms by direct calorimetry. Several authors noted that energy density of biomass of diverse species of animals, plants and microbes is approximately constant: ≈ 7 kJ/g wet weight and ≈ 20 kJ/g dry weight (e.g., Cummins and Wuychek 1967; Golley 1961; Slobodkin 1961, 1962). This potentially pervasive feature of life has been largely ignored

as other research topics became fashionable. But it has been confirmed by subsequent studies (e.g., Anthony, Roby, and Turco 2000; Kataki and Konwer 2002; Peters 1983; Popovic 2019; Van Pelt et al. 1997). It was incorporated into the EFP by Brown, Hall, and Sibly (2018); their Figure 4, who assumed $Q \approx 22.4$ kJ/g dry mass.

This begs the questions, to what extent is Q constant, and what accounts for its apparent invariance? We consider two non-mutually exclusive hypotheses:

- Constraints on composition of protoplasm.— Q reflects the biochemistry of protoplasm, which is composed of a mixture of carbohydrates and proteins (ca. 17 kJ/g) and lipids (ca. 37 kJ/g). Structural and functional constraints require a similar mixture of these compounds (e.g., carbohydrates or proteins for structure, nucleic acids for genetic information, lipids for membranes).
- Constraints due to the Red Queen.—The ecological and evolutionary dynamics of competition for usable energy result in trade-offs that enforce equal fitness across coexisting species (Burger et al. 2021). Selection tends to increase E and M , but ecological compensation and Red Queen coevolution prevent monopolisation of energy use. Any species that produces either cheaper or more expensive offspring (lower of higher E or M) will be outcompeted by species that produce biomass of optimal intermediate energy density ≈ 22.4 kJ/g.

The functional constraint hypothesis may have some merit, but available evidence suggests that the Red Queen hypothesis is necessary and sufficient to account for both the relative constancy and the observed variation in Q . There is variation (Brown, Hall, and Sibly 2018; Cummins and Wuychek 1967; Popovic 2019). Some organisms which might seem to be exceptions are composed of large quantities of non-living materials (e.g., cellulose in wood of trees, minerals in exoskeletons of molluscs, water in endoskeletons of coelenterates). The energy density of such organisms appears anomalously low if energy density is calculated as a function of a total body mass (Kataki and Konwer 2002). But Q is comparable to other organisms if only living protoplasm is included. Q can vary within individuals over ontogeny. For example, energy density of wild sockeye salmon is highest in eggs and in muscles of mature adults returning to fresh water to breed (Brett 1983). As adults expend stored energy to fuel upstream migration and competition on the spawning grounds, energy density decreases by 27%, from 24.3 kJ/g at the start of migration to 17.8 kJ/g in the carcasses of depleted spawners.

Additional insights into the relative constancy and absolute magnitude of Q may come from studies of artificial selection and bio-engineering. These have been applied to domestic animals and plants to produce food for human consumption (Gjedrem 1997; see salmon example below) and to microbes for high yields of energy in bioreactors (Peralta-Yahya et al. 2012). For example, oil content and energy density of seeds vary widely between wild plants and domesticated strains (Levin 1974). These cases suggest that the relatively constant values of Q reported for wild animals, plants and microbes reflect natural selection due to Red Queen interactions.

5.2 | Biogeographic Rules: Dwarf Elephants on Islands

Several well-known 'biogeographic rules' have been proposed: Bergmann's rule for body size as a function of latitude, elevation and environmental temperature; (ii) Foster's rule for body size as a function of isolation on islands; (iii) Lack's rule for clutch size as a function of climate (Gaston, Chown, and Evans 2008). Most of these are still controversial, often with both the patterns and evolutionary processes subject to debate. It should be informative to re-examine the empirical patterns and theoretical explanations in the light of the EFP.

The evolution of body size of elephants after isolation on islands provides an example of how the EFP can offer new perspectives on energetic processes of physiology, ecology and evolution that contradict earlier interpretations (Figure 5). At the end of the Pleistocene, rising sea levels created continental islands. On many of these (e.g., Cyprus, Malta, Crete, Rhodes, Sardinia and Sicily in the Mediterranean, the Channel Islands of California and Wrangel Island in the Arctic Ocean) surviving populations of elephants and mammoths rapidly evolved dwarf phenotypes, as much as an order-of-magnitude smaller body mass than ancestral mainland populations (Roth 1992). Because elephants often survived while coexisting species of large mammalian herbivores and carnivores went extinct, dwarfism was attributed to selection for faster life histories: that is, to higher rates of individual production and ontogenetic and population growth in response to increased food availability, reduced competition and predation, and lower mortality. For example, Raia and Meiri (2006): 'suggest dwarfism in large herbivores is an outcome of the fitness increase resulting from the acceleration of reproduction in low-mortality environments'. This interpretation is contested by recent studies of Köhler et al. (Köhler and Moyà-Solà 2009; Köhler et al. 2021). Their analysis of fossil remains of *Paleoloxodon* from Sicily provides convincing evidence that '*P. falconeri* did not shift towards the fast end of the life history continuum by truncation of the growth period, as widely claimed for insular dwarf elephants. ... (instead) dwarfing is associated to a decrease in growth rate and a concomitant delay in age at first reproduction combined with an increase in lifespan'. As depicted in Figure 5, the decrease in body size of elephants on islands was an indirect response to direct selection for decreased growth rate, P_{coh} , and increased longevity, G . Studies of body size evolution in domesticated dogs (Fan et al. 2016) and wild rodents (Bonnet et al. 2022) provide additional examples.

Other cases that might be re-examined in the light of the EFP include: 'reverse Bergmann's rules', 'Bergmann-like' patterns in ectotherms and flightless birds on islands (McNab 2002).

5.3 | Natural and Artificial Selection: Wild and Farmed Salmon

Wild and farmed salmon offer insights into how selection has shaped the evolution of metabolic and life history traits. Ancestral salmonids lived in streams and lakes (Quinn 2018).

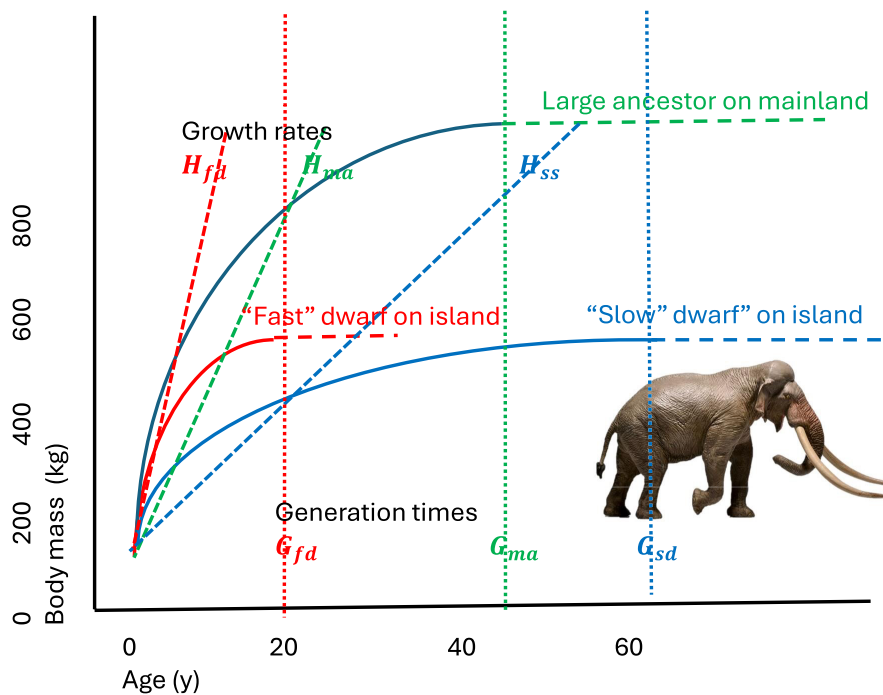


FIGURE 5 | Evolution of dwarf elephants on islands. Models of ontogenetic trajectories of body mass as a function of age for three populations: (i) green: the ancestor on the mainland; (ii) red: the hypothetical faster life history predicted for dwarfs based on allometric scaling, with a higher growth rate and shorter lifespan; and (iii) blue: the slower life history actually observed for dwarfs, with indirect selection for smaller body size due to direct selection for lower production rate and longer generation time. The fossil history is consistent with the EFP, but not with the explanation based on standard allometric scaling. Based on Köhler and Moyà-Solà (2009) and Köhler et al. (2021).

Multiple lineages in Pacific drainages evolved anadromous life histories: four-year life cycles in which juveniles migrate to sea, spend 2 years feeding on abundant plankton and return to fresh water to breed. Secondly, populations, isolated in lakes by Pleistocene geological events or recent human introductions, evolved a morpho-ecotype known as kokanee (USDA Forest Service 2015). Adapting to the lower productivity of freshwater habitats, kokanee rapidly and convergently evolved an alternative life history: smaller mature size, three-year life cycle (shorter G), higher production rate (P_{coh}) and reduced mortality (higher F). The net result is that Kokanee and sockeye represent alternative stable evolutionary strategies: different combinations of traits that trade off to confer equal fitness ($M = P_{\text{coh}}GF \approx 1$; Figure 6).

Still different combinations of traits have been created in salmon farmed for human consumption (Figure 6). Salmon aquaculture is big business: generating > 16 billion dollars, employing > 130,000 people and producing > 2.8 million tonnes of flesh annually. Farmed fish account for > 70% of the salmon consumed worldwide (https://en.wikipedia.org/wiki/Aquaculture_of_salmonids). Changes in just a few decades have been remarkable as growers have used energy from fossil fuels, high-tech husbandry, improved foods, antibiotics, artificial selection and genetic engineering to produce domesticated strains with desirable traits, including spectacular increases in production efficiency, $K = \frac{\text{biomass produced}}{\text{food consumed}}$. Selection for reduced activity and lower respiration rates, higher growth rates, shorter generation times and high-quality flesh have resulted in high rates of production of biomass rich in omega-3 fatty acids and carotenoid pigments (Aursand et al. 1994). For example, Aqua Bounty Farms markets a modified Atlantic

salmon that requires only 18 months and 10% less food to produce mature fish of nearly twice the size of wild populations (<https://aquabounty.com/>). There is much debate about the environmental and conservation implications of salmon farming, which uses enormous subsidies of fossil fuel energy and wild-caught fish for food.

5.4 | Sexual Selection and Exaggerated Traits: Peacock Tails and Deer Antlers

Darwin was challenged to explain the ornaments and weapons used by males to compete for mates. He complained in a letter to Asa Gray that ‘The sight of a feather in a peacock’s tail, whenever I gaze at it, makes me sick!’. In his book on ‘Selection in Relation to Sex’ (Darwin 1888), he recognised that evolution of these traits must depend ‘not on a struggle for existence, but on a struggle between the males for possession of the females’. Subsequently, evolutionary biologists have proposed explanations involving handicaps, good genes, truthful or deceptive advertisement, supernormal stimuli, perceptual bias, attractive sons, sexual conflict and runaway selection (Clutton-Brock 2017; Emlen 2008; Harman 2011; Kokko, Jennions, and Brooks 2006; Kuijper, Pen, and Weissing 2012; Smith 1991). Many of these refer to ‘metabolic costs’ and ‘fitness benefits’, but do not provide a complete energy budget for the physical mechanisms underlying the genetic and phenotypic correlations among physiological and life history traits.

Antlers of deer (mammalian family Cervidae) provide examples that are as challenging as peacocks’ tails (Figure 7). The EFP offers a synthetic theoretical framework based on energy

Energy allocation in sea-run, landlocked and farmed salmon

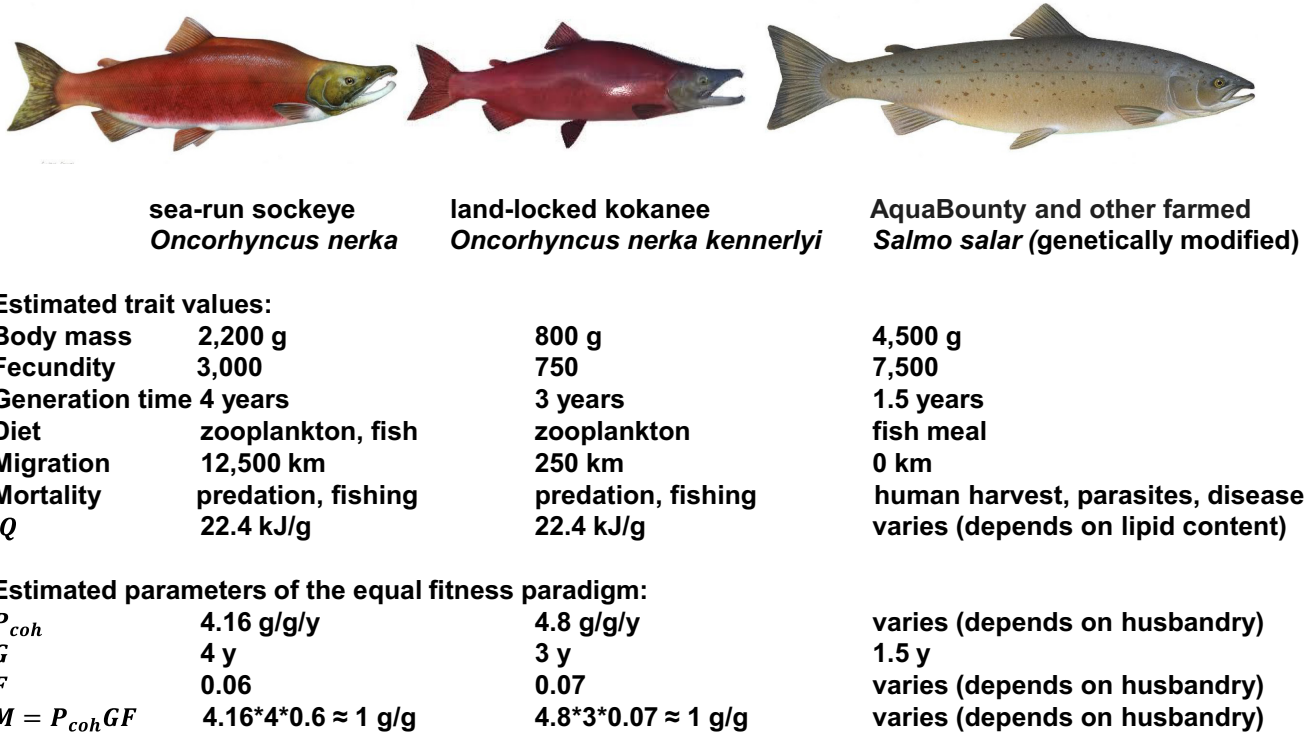


FIGURE 6 | Models of energetics and life history of three strains of salmon: (i) wild sea-run sockeye (*Oncorhynchus nerka*); (ii) wild landlocked sockeye (*Oncorhynchus nerka kennerlyi*); and (iii) artificially selected, genetically engineered, farmed salmon (e.g., AquaBounty's modified *Salmo salar*). Based on information in Brett (1983); USDA Forest Service (2015); <https://aquabounty.com/>.

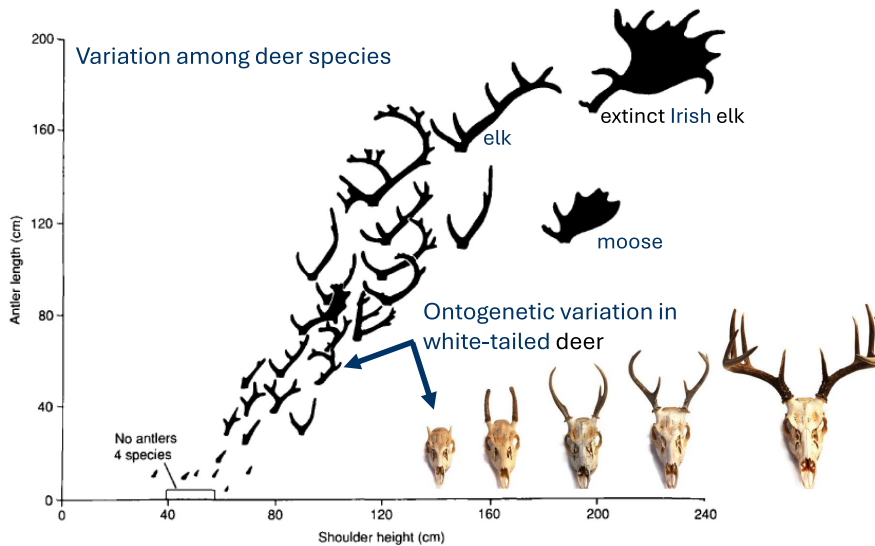


FIGURE 7 | Allometric variation in antler size of deer as a function of body size across species and over ontogeny in white-tailed deer (*Odocoileus virginianus*). Based on Lincoln (1992); https://animaldiversity.org/collections/mammal_anatomy/horns_and_antlers/.

that can address well-documented empirical patterns and still-unanswered questions:

- *Sexual dimorphism*: The sexes differ in morphology and life history, and the magnitude of dimorphism increases with increasing body size. In the smallest deer, *Pudu mephistophiles*

of South America, both sexes weigh about 5 kg and males have simple unforked antlers 6 cm long (<https://en.wikipedia.org/wiki/Pudu>). At other extreme, the extinct Irish elk, *Megaloceros giganteus*, weighed about 450 kg and sported antlers spanning more than 2 m and weighing more than 40 kg (Lincoln 1992).

- **Positive allometry:** Antler size increases disproportionately with increasing body size (exponent > 1), both within individuals over ontogeny and across species of deer (Figure 6). Despite several models (Kodric-Brown, Sibly, and Brown 2006; Kuijper, Pen, and Weissing 2012) this pervasive phenomenology raises still unanswered questions about the biophysical basis of fitness.
- **Metabolic life tables:** These questions could be addressed with data on metabolic ecology and demography. The red deer population on the isle of Rom provides a promising model system (Clutton-Brock, Guinness, and Albon 1982; Appendix S2). The sexes differ conspicuously in body mass (females ca. 250 kg vs. males ca. 450 kg), generation time (ca. 3 vs. ca. 6 years), and parental investment in offspring (two calves weighing ca. 50 kg at weaning vs. 2 sperm). Other populations of red deer vary substantially in morphological, physiological, ecological and behavioural traits, which presumably reflect direct and indirect selection in native and introduced, wild and managed populations. A combination of empirical data and theoretical models can potentially account for this variation in terms of parameters of the EFP and trade-offs among energy gains, metabolic expenditures and fitness benefits.
- **Biochemistry:** Several authors have pointed out mechanistic links between mineral and energy metabolism, stoichiometry and life history in the production of antlers by males and milk by females (Dryden 2016; Moen and Pastor 1998). Antlers are composed of bone; antler growth is fuelled by selective consumption of plants high in calcium and phosphorus. The biochemical and physiological processes carry over to affect mineral nutrition of lactating females and growth and survival of fawns.
- **Related patterns in other taxa:** The above phenomenology is quite common; similar traits have evolved convergently in antelopes (Bovidae), stag beetles and other animals (e.g., Kodric-Brown, Sibly, and Brown 2006; Emlen 2008). But there are also well-documented examples of ornaments and weapons that exhibit isometric or negative scaling with body size, and associated models that invoke traditional biological measures of performance and fitness (Eberhard et al. 2018). The EFP offers an alternative or complementary framework based on biophysics and energetics that can be applied to understand the observed diversity of form and function.

The more general phenomena of anisogamy and sexual selection beg still-unanswered questions about the evolution of sex and the fitness contributions of males and females (Barton and Charlesworth 1998; Harman 2011). Females typically supply most of the energy and materials invested in eggs and juveniles prior to independence. Males invest a smaller quantity of biomass to produce enormous numbers of miniscule sperm. There is competition among the more numerous sperm to fertilise the much smaller number of eggs: both among sperm of individual males during spermatogenesis and mating and between sperm of different individuals due to aggressive contests with rivals and courtship displays to attract females. The resulting differential selection on sperm and eggs—and on males and females—suggests that higher-quality genetic information (fitter genes)

contributed by fathers may compensate to some extent for their lower investment in biomass.

5.5 | Complex Life Histories: Parasitic Worms and Social Insects

Darwin (1859) faced another challenge: ‘I...will confine myself to one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect communities: for these neuters often differ widely in instinct and in structure from both the male and fertile females, and yet from being sterile they cannot propagate their kind’. Indeed, complex life cycles, not only of social insects, but also of mites, crustaceans, fish, and parasitic worms pose still unanswered challenges for existing theory. We briefly consider two cases.

Schistosoma mansoni is a parasitic trematode that causes tens of thousands of human deaths each year, mostly in developing countries with limited public health systems. It has a complex life history that includes episodes of sexual and asexual reproduction in alternative mammal and snail hosts, migration between internal environments of hosts and free-living stages in fresh water, and paired lifetime association of an adult male and female (Figure 8). The EFP can go some way toward explaining this complexity in terms of energetic mechanisms, and consistent with other parasites and general theory (Grunberg and Anderson 2022).

The approach should focus on the fluxes and stocks of energy and materials at the level of the colony, or more precisely on the cohort of offspring produced by a pair of male and female parents. From this perspective, the episodes of sexual and asexual reproduction are components of a single life cycle of one generation, extending from fertilisation of eggs soon to be released into fresh water to death of the attached pair of reproducing male and female in a mammalian host. The asexual phase in the snail can be treated conceptually and analytically as analogous to the ontogenetic growth of an individual allocating assimilated biomass to produce a ‘body’ of many independent ‘cells’ that disperse and infect hosts. This framework could be implemented by compiling a metabolic life table giving the age-specific number and body mass of the cohort of descendants of a single pair of reproducing adults. A prediction from the EFP (Equations 1 and 6) is that *S. mansoni* and many other parasites must have high values of P_{coh} and perhaps of G , to offset very low values of F , because the lifestyle of infecting dispersed, immune-defended hosts necessarily entails extremely high mortality. Despite all the biomedical research on parasitic flukes, we are unaware of any complete cohort-based analysis for any species. We crudely estimate that the total potential fecundity of *S. mansoni* is on the order of 200 billion (ca. 200,000,000,000!) offspring per mated pair, giving an astronomically low efficiency of reproduction, F , and a correspondingly high ecosystem tax of dead offspring recycled in the ecosystem (Figure 8).

Similar theoretical and empirical considerations apply to eusocial insects in the orders Isoptera (termites) and Hymenoptera (wasps, bees and ants). For example, termites are among the largest consumers of biomass in many tropical ecosystems. They cause billions of dollars per year of damage to structures. They

Life cycle of *Shistosoma mansoni*

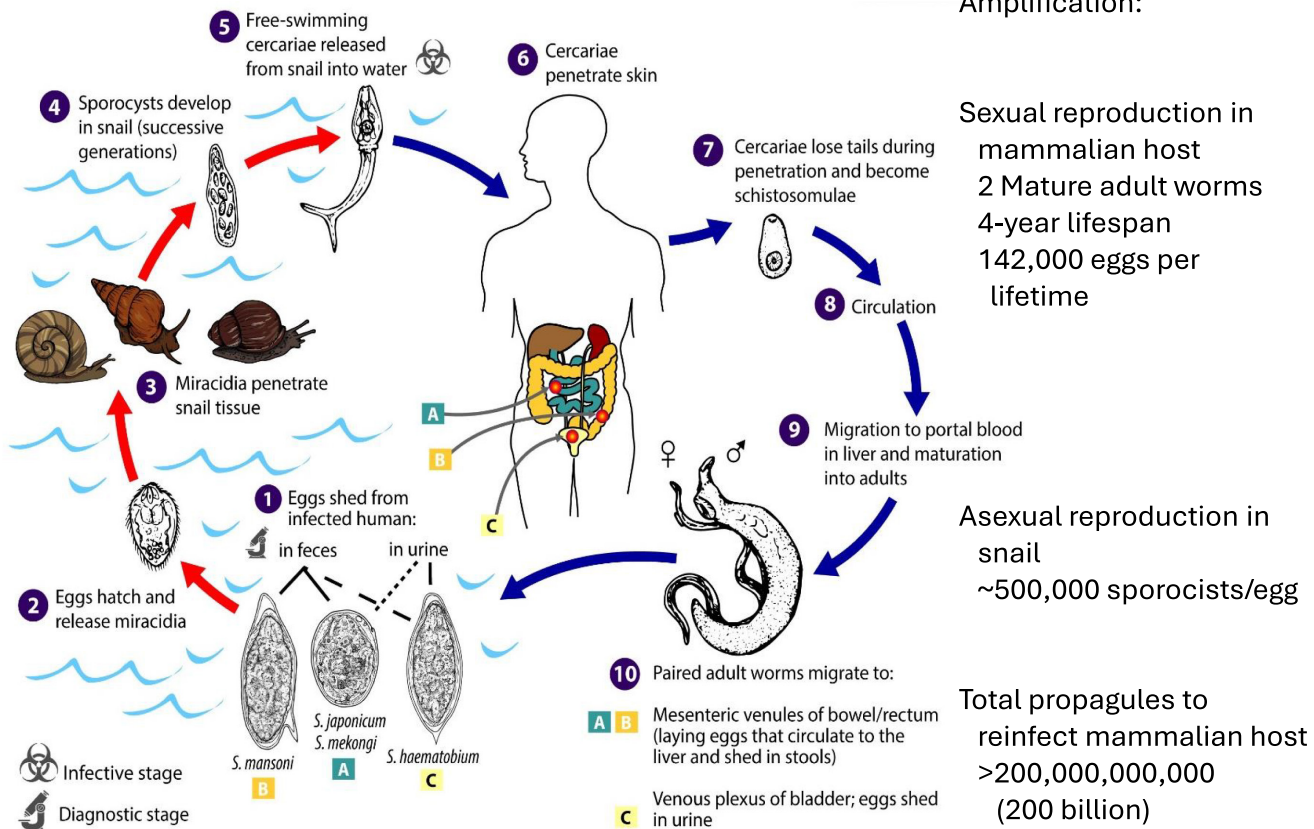


FIGURE 8 | Complex life cycle of the liver fluke (*Shistosoma mansoni*). Selection to disperse between and infect hosts has resulted in alternating cycles sexual reproduction in the mammal and asexual reproduction in the snail that potentially produce billions of offspring, with consequently a vanishingly small efficiency of reproduction, F , and a nearly astronomical ecosystem tax, $C = 1 - F$. Modified from https://www.google.com/search?q=schistosoma+mansoni+life+cycle&tbm=isch&prmd=ivsnmbtz&rlz=1C1GCEA_enUS950US950&hl=en&sa=X&ved=2ahUKewiB8pOZvs_eFAxWbPEQIHRI_AxsQrNwCKAB6BQkBEOkB&biw=1519&bih=703#imgsrc=mnJbvLDXEJGaiM; https://en.wikipedia.org/wiki/Schistosoma_mansoni.

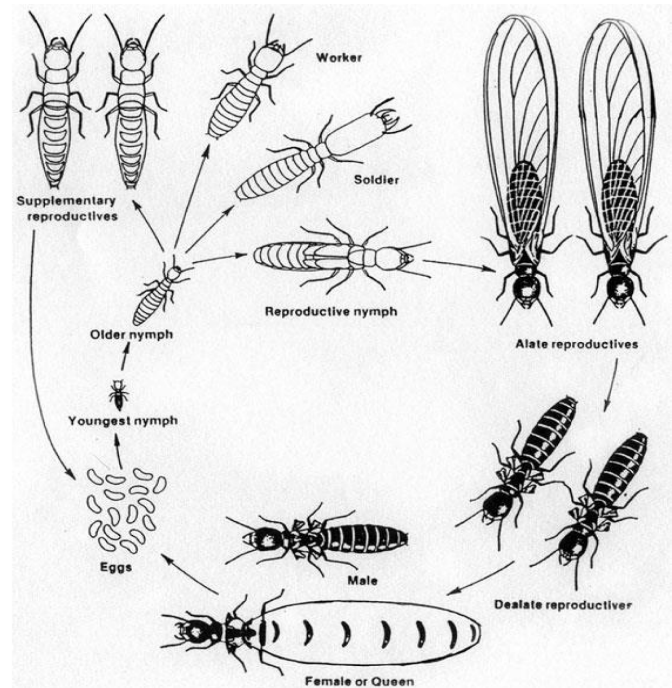
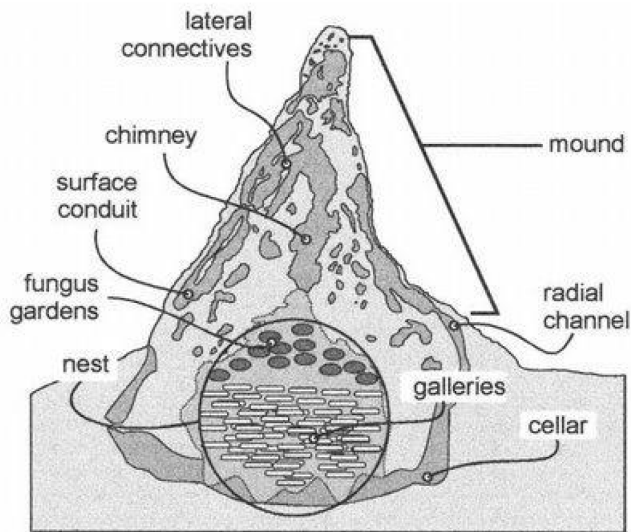
exhibit an enormous variety of taxa (ca. 3,000 species), colony size (hundreds to millions), life history (fecundity up to 40,000 eggs per day, lifespan up to 50 years) and ecology (diets of wood, grass and fungi; terrestrial, arboreal and subterranean habits) (<https://en.wikipedia.org/w/index.php?title=Termite&oldid=1214340005&action=edit>). The species with the most complex life histories have multiple specialised castes, which differ in structure, function and mode of development (Figure 9).

In applying the EFP to termites and other social insects, the unit of analysis should be a colony, the cohort of offspring of a pair of reproductives. The colony is the fundamental unit of demographic steady state, energy and mass balance, genetic inheritance, biological time and energetic fitness (Hou et al. 2010). The cohort typically includes a mature reproducing female (queen) and male (king), their sterile offspring of morphologically and functionally distinct workers and soldiers, and their fertile offspring of new reproductives. Ontogenetic development from newly hatched larva to mature adult can be complicated, with flexible allocation to different castes depending on social cues and environmental conditions. In addition to their complex life cycles, some kinds of termites are distinctive for expending large

quantities of metabolic energy and material resources to create elaborate nest architectures, regulate microclimate and culture symbiotic fungi (Bourke 1999, <https://en.wikipedia.org/wiki/Termite>; Figure 9).

It would be instructive to apply the theoretical perspective of the EFP and the empirical analysis of metabolic life tables to the energy budget of a termite colony. Mound-builders of the genus *Macrotermes* are keystone species in savannahs of Africa and Asia. They are dominant herbivores, comparable in quantitative consumption and keystone impacts to large grazing mammals. They are a significant source of food for animals, including humans. They construct elaborate mounds that provide a regulated microclimate for the termites and commensal inhabitants. They tend gardens of symbiotic fungi that metabolise plant biomass, breaking down cellulose to produce nutritious compounds. A termite mound is an ecosystem with its own economy: it houses a cohort of inhabitants with its own fitness. The energetic perspective of the EFP suggests attention to how a termite colony and a human society allocate 'gross domestic product' (gdp) to food supply, defence, infrastructure and reproduction, and how these expenditures

Metabolic ecology of termite nests and castes



Complex architecture of nest mound provides for climate control, fungus garden, and functional organization of castes and activities

Complex life cycle: genetic, physiological and environmental processes regulate production of reproductive and sterile castes

FIGURE 9 | Complex mound architecture and life cycle of mound-building termites (*Macrotermes* spp.). The colony uses energy and materials to construct a large mound with specialised galleries and chambers for climate control, fungus gardens and spatially segregated functions of the castes. The life cycle is comprised of a sexual queen and king, immature reproductives and enormous numbers of sterile workers and soldiers. A colony can contain billions of individuals and survive for decades, resulting in a very low efficiency of reproduction, F , and an astronomically high tax of dead biomass paid to the ecosystem, $C=1-F$. From (https://www.google.com/search?q=termite+mound+diagram&tbm=isch&prmd=ivsnmbtz&rlz=1C1GCEA_enUS950US950&hl=en&sa=X&ved=2ahUKewin1KD7xceFAxXZPUQIHYSFSDAgQrNwCKAB6BQgBEN4B&biw=1519&bih=703#imgrc=ulqG4hzkUs-eM) and (https://www.google.com/search?sca_esv=1a57d827cf09faae&rlz=1C1GCEA_enUS950US950&sxsrf=ACQVn08iMTfriDk1IlgKQQMgXSxjfwJwFg:1713298511374&q=termite+life+cycle&tbm=isch&source=lnmd=ivsnmbtz&sa=X&ved=2ahUKewisqKipxseFAxVMIEQIHTLPDhkQ0pQJegQIDxAB&biw=1536&bih=703&dpr=1.25#imgrc=IsZdAJH9N1nYYM&imgdii=jmIPaSBpLRuNeM).

respond to changes in the extrinsic environment and internal conditions.

5.6 | Coda

In a paper on ‘Life, Death and Energy of a Tree’, Leigh Van Valen (1975) compiled perhaps the first metabolic life table. He estimated that ‘the realized fitness of *E. globosa* (a tropical palm) is roughly comparable to that of *Homo sapiens*’. When we apply the EFP, account for trade-offs between rates of biomass production, generation times and mortality, and estimate the energetic fitness of amoebas, parasitic worms, deer and other animals, we confirm Van Valen’s result. This remarkable unifying feature of life has been under-appreciated for half a century; Van Valen’s paper has been cited only 116 times between 1975 and 2004.

There are still tangled banks along the roadsides and railways of rural England. The number, identities and relative abundances of the plants, birds, insects and worms may not be exactly the same as in Darwin’s time, but the ‘laws acting around us’ have not changed. One is that all species survive, produce offspring and persist for millennia by allocating energy to surviving offspring and recycling biomass in the ecosystem at the same rate: ca. 22.4kJ/g of energy and ca. 1g/g of biomass per generation. The third evolutionary synthesis is exploring the profound implications for the past history and current diversity of life.

Author Contributions

All co-authors contributed significantly to all parts of this study. All authors approved the final version of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data in this paper have been published and sources are cited.

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14517>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.