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Self-organising life history selection from replicating molecules to large multicellular sexual organisms

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Abstract During their evolution from molecular replicators over asexual unicellular prokaryotes and protozoa to multicellular sexual reproducers, biological lifeforms increased in size with heritable gene replication increasingly embedded in more organised replicating units. Natural selection theory did not explain this evolutionary unfolding for 150 years, consolidating Darwinian evolution as a contingent diversifying, rather than force-driven directional, process. I review population ecological theory that predicts directional self-organising life history selection by a universal mechanism across all major lifeforms. It shows that the selection of net energy for replication is a primary force that drives the evolution of the major lifeforms forward through the gradually unfolding population dynamic feedback selection of intra-specific interactive competition. Speciation, inter-specific competition, and local adaptation are additional forces that expand and support evolutionary diversity. I begin by discussing predictability in the historical development of natural selection theory, covering the macro evolutionary pattern of the major lifeforms, before I describe the self-organising selection. I close with a discussion on the rise and fall of the contingent evolutionary paradigm, showing that the existing lifeforms cannot evolve by diversifying contingency due to their Malthusian fitness. The contingent assumptions of traditional life history theory are therefore not truly contingent, but placeholders for the self-organising selection that created the major lifeforms from the origin of replicating molecules.

Keywords: Natural selection, life history, allometry, major evolutionary transitions, self-organisation, eco-evo

1 Introduction

The last couple of decades have seen an increase in studies on the repeatability and predictability of biological evolution. Comparative studies have found that evolution in different taxa often converge on similar phenotypic solutions, illustrating the limited number of design options available (Conway-Morris 2003; McGhee 2013; Mazel et al. 2017). Combined with repeated parallel evolution in short-lived organisms during controlled experiments (e.g. Travisano et al. 1995; Cooper et al. 2003; Pelosi et al. 2006; Ratcliff et al. 2012; Simões et al. 2019), it is evident that evolution is predictable in many cases. If not in genetic detail, then on short timescales for fitness related life history traits and phenotypic adaptations, reflecting statistical extrapolations and natural selection predictions based on empirically estimated fitness landscapes (reviews by Lobkovsky and Koonin 2012; de Visser and Krug 2014; Lässig et al. 2017; Nosil et al. 2020).

These studies show that evolution by natural selection is predictable, but they do not develop a predictive theory of evolution. This is because it is first of all our ability to predict natural selection that questions our ability to predict evolution, instead of our ability to predict evolution from empirically estimated selection. That phenotypic selection generates phenotypic evolution is one of the best documented principles of the Darwinian hypothesis, let selection be artificial or natural. Traditional natural selection theory, on the other hand, is unprepared for the task because it lacks the necessary organising principle (Witting 2008; Conway Morris 2010).

Mainstream biology seems blissfully unaware of this major flaw in natural selection theory (Conway Morris 2010), which relates to life history evolution, and not so much to phenotypic adaptation. It is e.g. straightforward to expect the adaptation of eyes when mobile multicellular organisms evolve in illuminated environments. But why do large multicellular organisms exist in the first place? If we cannot deduce a self-organising selection that explains the evolutionary succession of the major lifeforms, evolutionary biology will continue its contingent endeavour based on neutral diversifying selection. The evolution of large multicellular sexually reproducing organisms will remain obscure, "explained" only as a random consequence of a long sequence of improbable events, instead of evolving inevitably from the natural selection laws of a predictive science.

While natural selection is the force of evolution, the evolutionary working hypothesis of mainstream biology has not developed beyond an overall diversifying non-

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directional/neutral natural selection. This reflects a continued strong influence from the contingent evolutionary paradigm that developed during the 19th and 20th century to describe a natural selection that lacked an identified organising principle (Witting 2008). It sees natural selection as "a strictly *a posterior* process" that is "not controlled by any law" (Mayr 1988), a process that can be understood only from its historical development once it has actually occurred (Gould 1989, 2002).

The development of traditional life history theory (reviewed by Roff 1992; Stearns 1992; Charlesworth 1994) consolidated the contingent paradigm formally by using the demographic trade-offs and constraints that have evolved in the species of today as the essential assumptions behind natural selection predictions. By analysing natural selection in this top-down backward way from the current endpoints of evolution, biology obtained a theory with no overall organising principle, a theory with life histories granted by the actual evolution of the past, instead of analysing for the natural selection principles that created them (see Section 1.1).

This form of contingent selection analysis remains, in one form or another, the most widely used framework in the evolutionary literature. But, based on population ecological theory developed over the last three decades (Witting 1995, 1997, 2008, 2017a,b), I argue that to identify the organising principles of natural selection and establish a predictive theory of evolution we need to analyse contingence-free natural selection in the opposite direction, i.e., bottom-up forwardly from the origin of replicating molecules.

To argue my case, I focus on the macro-evolutionary pattern of mobile lifeforms where virus, prokaryotes, protozoa, and ectotherm and endotherm animals arrange as an increasing function of size with limited overlap (Fig. 1, top). This reflects a selected increase in the biotic energy used to produce an individual, with the body mass scaling of life histories changing with this energy across lifeforms. A trait like mass-specific metabolism is non-existing in virus that depend on the metabolism of their hosts and, as illustrated in the bottom plot of Fig. 1, mass-specific metabolism increases almost proportionally with mass in prokaryotes (DeLong et al. 2010), is invariant or first increasing and then declining in protozoa (DeLong et al. 2010; Witting 2017a), before it approaches a negative 1/4-power scaling in animals (Kleiber 1932), while at the same time it is largely invariant of mass across lifeforms larger than virus (Makarieva et al. 2008; Kiørboe and Hirst 2014).

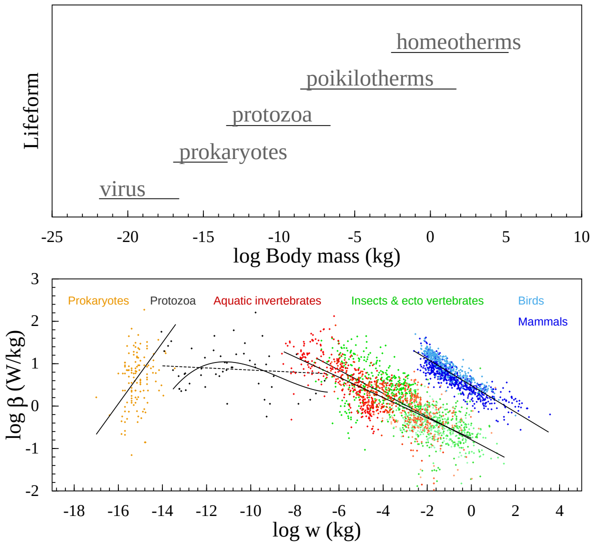

Figure 1: **Macro evolutionary relationships. Top:** The body mass range of mobile lifeforms (horizontal lines), illustrating lifeforms as a function of size. **Bottom:** The relationship between mass (w) and mass-specific metabolism (β) among mobile organisms. Data from Makarieva et al. (2008), plot from Witting (2017b).

On top of this allometric pattern there is the transition from cell-less replicators to unicellular self-replicators between virus and prokaryotes, and the transition to multicellular sexually reproducing organisms at the boundary between protozoa and animals. This macro evolutionary pattern is now explained forwardly from the population dynamic feedback selection of intra-specific interactive competition, as it unfolds gradually from a continued selection increase in the net energy that organisms use for replication (Witting 1997, 2017a,b). Speciation, inter-specific competition, and local adaptation are additional forces that expand and support the evolution of biological diversity. This provides a single organising principle across all major lifeforms, combining a universal self-organising life history selection with the Darwinian principle of inter-specific diversification through branching phylogenies.

A rule in this work is to follow the flow of energy—from net energy assimilated by metabolising individuals over population dynamic growth to the interactive competition that distributes the ecologically available energy among the individuals—when calculating the relative Malthusian fitness of the individuals in the population. During the historical development of evolutionary thoughts there have been several other proposals on the importance of energy in biological evolution (e.g. Boltzmann 1886; Lotka 1922; Schrödinger 1944; Odum and Pinkerton 1955; Van Valen 1976; Wicken 1985; Brown et al. 2024). None of these use the agreed demographic definition of natural selection fitness as the Malthusian parameter r (Fisher 1930; Lande 1982; Partridge and Harvey 1988; Caswell 1989a; Charlesworth 1994), and there has thus been considerable confusion in understanding and applying these concepts (Hall and McWhirter 2023).

Due to their vaguely defined connection to demographic fitness and natural selection, I do not discuss these studies further. I review the bottom-up forward self-organising selection, and discuss and evaluate it as an extension of the mainstream evolutionary biology that developed from the population genetic synthesis (Fisher 1930; Wright 1931; Haldane 1932), its definition of fitness as the Malthusian parameter, and the subsequent development of traditional life history theory (Lande 1982; Partridge and Harvey 1988; Caswell 1989; Roff 1992; Stearns 1992; Charlesworth 1994).

1.1 Natural selection theory

Contingency underlies, to a smaller or larger explicitly or implicitly degree, almost all evolutionary work from Darwin up. This includes predicted adaptations that depend on the existence of the relevant lifeform, recent studies of evolutionary predictability that depend on empirically estimated fitness landscapes, and traditional life history theory that tangle in a contingent circularity of cause and effect. The latter reflects a theory that constructs life history models from the trade-offs and constraints that have evolved in the species of today (Roff 1992; Stearns 1992; Charlesworth 1994), implying that it uses the actual evolution of the past to measure, rather than first principle predict, the evolutionary outcome of natural selection (Witting 1997, 2008).

It is these measurements of the current endpoints of past evolution that define the success of traditional life history theory, but they are also a restriction that prevents us from analysing the deeper organising powers of natural selection. By measuring the evolved demographic trade-offs and constraints the traditional models have successfully documented selection that involves almost all life history traits, showing that the life history and demographic trade-offs of a species evolve in a mutual selection balance. But is this balance the actual selection of the life history or is it just a secondary optimisation that occurs in response to a life history that evolves by deeper underlying selection processes? The uncertainty remains because the selection models use of the measurements as contingent placeholders for the unknown selection that created the trade-offs and thus their associated life histories. By providing the life histories to the selection theory in this way, the theory is not identifying the unknown selection that organised the evolution of the life histories, and nor is it addressing the fundamental question of why the living world evolved the existing diversity of lifeforms, species, and life histories in the first place.

To better understand this absence of analyses directed towards the organising processes that control natural selection, it may help to think of traditional life history theory as an attempt to understand a suspension bridge by measuring the tension on the steel cables that hold the bridge deck and the compression on the towers that anchor the cables. By measuring the tension and compression it is possible to calculate that the cables and towers have the right dimensions to hold the bridge. This tells us that the bridge is well build, but it does not tell us why people decided to build that particular bridge and nor how they organised the building of it. In the same way, by measuring the evolved trade-offs and constraints of a species, we can calculate that the life history has the right demography for the species to exists with optimal fitness. This tells us that natural selection is doing its job, but it does not tell us why natural selection selected that particular life history and nor how it organised the selection of it.

In the end we have to accept that if we want to understand the organising powers and principles of biological evolution, we have to study them directly. This is e.g. done by studying a contingence-free natural selection bottom-up from the origin of replicating molecules and predict the observed evolution forwardly from a minimum of biological assumptions. This is the approach taken in the current review, based on models that do not include the evolved trade-offs and constraints as structural assumptions, not only because of the circular reasoning it involves, but also because these components are part of the trait-space that we aim to explain.

Before we turn to the bottom-up unfolding selection, let us briefly look at other forward studies in evolutionary biology. Studies of the fossil record is the traditional forward-looking approach, with Cope's (1887) rule documenting a widespread increase in size. Other studies include experiments that analyse ongoing evolution in short-lived organisms, identifying parallel and converging evolution (Travisano et al. 1995; Cooper et al. 2003; Pelosi et al. 2006; Ratcliff et al. 2012; Simões et al. 2019), in line with comparative studies of natural species (Conway-Morris 2003; McGhee 2013; Mazel et al. 2017). These findings confirm the presence of repeatable *a priory* given selection pressures, but they do not identify an overall organising principle (Powell and Mariscal 2015).

On the theoretical side we have neutral forward-looking hypotheses that propose a statistical view, where random diversifying drift, rather than natural selection, explains the observed trend towards increased size and organised life histories (Stanley 1973; Gould 1988; Brandon and McShea 2011; McShea et al. 2019). But where the drift of random mutations can account for the accumulation of neutral genetic variation (Kimura 1983), it does not account for life history evolution. Random demographic mutations are not neutral because they generate intra-population variation in the Malthusian parameter of exponential increase and, thus, natural selection by default. These studies aside, there was a vacuum with no forward-looking life history theory when I introduced Malthusian relativity in the mid-1990s, aiming to construct a strictly deductive population dynamic theory for the natural selection of living organisms (Witting 1995, 1997, 2008).

Malthusian relativity studies the part of natural selection that self-organises deterministically from the origin of replicating molecules, with the overall goal being to predict the existing life history variation from a minimum of biological assumptions. Of the three conditions [traits variation, heredity, and differential fitness] that define evolution by natural selection, Malthusian relativity deals primarily with the differentiation of fitness from eco-evolutionary feedback, assuming that a lack of heritable variation is rarely limiting long-term evolution. Where many of today's eco-evolutionary feedback studies deal with inter-specific interactions, community structure, and dynamics in changing and spatial environments (e.g. Hendry 2017; Brunner et al. 2019; Jarne and Pinay 2023; Fouqueau and Polechova 2024), the core of Malthusian relativity is the basic population dynamic feedback selection of the population itself; a process that responds to environmental change and inter-specific interactions through resource availability and survival effects.

The ultimate cause of the self-organising population dynamic feedback is natural selection imposed by the non-evolving structure of the life history demography of replication. This structure includes the metabolic energetics of resource assimilation and replication (Witting 2017a,b), trade-offs like the proportional decline in replication by the quality-quantity trade-off (Smith and Fretwell 1974; Stearns 1992), the two-fold cost of males (Maynard Smith 1971) and meiosis (Williams 1975), and the age-structured demography itself. The structural assumptions do not include evolving components like the absolute scaling of energetic trade-offs (by e.g. the mass of the organism) and, to keep the model relatively simple, nor do I include minor less straightforwardly quantified trade-offs. The population dynamic growth of the demography, and the resulting interactive competition of the foraging ecology, is then providing the eco-evolutionary feedback with natural selection defined by the relative intra-population density-frequency-dependent differentiation of the Malthusian parameter (hence the name Malthusian relativity).

The development of Malthusian relativity occurred during a period with a growing recognition of density-frequency-dependent interactions in natural selection (e.g. Abrams and Matsuda 1994; Mylius and Diekmann 1995; Day and Taylor 1996; Metz et al. 1996; Heino et al. 1998; Dercole et al. 2002). Yet, there was surprisingly low interest in integrating these interactions into a general life history theory (Day and Taylor 1996), with the concept of a bottom-up unfolding selection that self-organises deterministically from the non-evolving components of the replication structure being entirely new, with the different structural components selecting for different traits. The selection increase in net energy for replication e.g. reflects an underlying selection increase in resource handling (i.e. the adapted traits, skills, and physiology that organisms use to subtract net energy from the environment) multiplied by a selection increase in the pace (speed) of handling, with pace selected as mass-specific metabolism (Witting 2017a).

Other traits like body mass, multicellularity, the number of individuals in replicating units, non-replicating interacting individuals like males and offspring workers, and the parental sharing of offspring genomes through sexual reproduction (genomic ploidy-level) are inversely related to replication and thus proposed selected by other means. Given sufficient population dynamic pressure for interactive competition these traits are all selected as the interactive quality that enhances resource monopolisation during frequency-dependent interactive competition (Witting 1997, 2002). Life history selection overall is then a net energy driven density-frequency-dependent trade-off-balance between population dynamic growth and interactive quality. This balance does not restrict the involved traits from evolving other functions as well, but these are not necessary for the predicted evolutionary unfolding.

2 Self-organising selection of lifeforms

The formal deduction of lifeforms from first principles of replication follows from a detailed mathematically formulated energy-based population dynamic selection model (Witting 1997, 2008, 2017a,b). It ranges from the metabolism and energetically age-structured life history demography, over the resulting population dynamic growth, to the spatial foraging of individuals where the density-frequency-dependent interactive competition distributes the available resources across the individuals in the population. The biased resource distribution is then influencing the individually differentiated energetic demography that determines the distribution of Malthusian parameters that defines natural selection, with evolution converging on Continuously Stable Strategy (CSS, Eshel 1983) attractors. The original work describes the formal formulation of the selection model (Witting 1997, 2000, 2017a,b), the mathematical deductions of allometric scaling (Witting 1995, 2017a, 2018), major evolutionary transitions (Witting 2002, 2007, 2017b), body mass trajectories (Witting 2018, 2020), and more elaborate discussions relating to the scientific literature. Here, I summarise the underlying concepts, mechanisms, and processes verbally to outline the self-organising selection of the sequential evolution of lifeforms.

It is important that you free your mind from the logic of traditional life history theory in order to follow the logic of self-organising selection. Traditional theory explains the organised life histories of e.g. animals from the trade-offs and constraints that evolved in the demographic structure during the evolution of the life history. The self-organising selection unfolds instead from the non-evolving components of this structure, with the resulting selection selecting several of the evolved components of the traditional life history trade-offs and constraints. Most of the latter selection is not necessary for the deduction of the major lifeforms, with the last section of the review covering the relationship between the two life history approaches.

Another clarification relates to the distinction between r and k selection, which is often unclear because of a lack of consensus between the verbal (MacArthur and Wilson 1967; Stearns 1977; Parry 1981) and mathematical (Anderson 1971; Roughgarden 1971) version. I follow the mathematical life history selection definition where the two forms of selection are identical (Caswell 1989), with both r- and k-selection being r-selection at zero abundance and at population dynamic equilibrium receptively. I deal with populations in population dynamic equilibrium, where r-selection is the frequency-independent selection that generates an increase in the Malthusian parameter r, in contrast to frequency-dependent selection that can select also for a decline in r (Witting 2000).

2.1 Major evolutionary transitions

With these things in mind let us consider selection in replicating molecules at the origin of life, where we expect no resource monopolisation from interactive competition and thus no ecological frequency-dependence. This implies a frequency-independent r-selection where the quality-quantity trade-off selects the minimum mass possible, and the two-fold costs of sexual reproduction selects asexual replication.

But biological evolution is not stuck at this minimum-sized asexual replicator because the selection increase in net energy for self-replication generates increased population dynamic growth with an increased abundance and more interference between individuals. This interference selects for competitive interactions and a resource gradient in favour of the larger-than-average individuals, and when the gradient—due to the selection increase in net energy, population growth, abundance, and competitive ability—becomes stronger than a proportional increase with mass, it outbalances the downward selection of the quality-quantity trade-off and selects mass at the cost of the otherwise continued increase in the growth, abundance, and interference competition of the population (Witting 1997, 2008, 2017b). As illustrated by the outer loop in Fig. 2, the end-result is a density-frequency-dependent population dynamic feedback selection with an emergent selection attractor of interactive competition that reallocation-selects the primary selected net energy from replication to mass. This attractor selects a competitive interaction fix-point where the resource gradient of intra-specific interference balances the quality-quantity trade-off, with the selected interference being invariant across a range of species selected for inter-specific variation in net energy and mass (Witting 1997).

The interference selected by the selection of mass is then selecting a more organised replicating unit from the potentially increased interactive quality of larger units where reproducing individuals (females) can attract interacting individuals (males) by the sharing of offspring genomes through sexual reproduction. When inserted into the selection equations of the reproducing unit, the predicted interference of a body mass in evolutionary equilibrium balances the two-fold costs precisely, selecting pairwise sexual reproduction between a female and male, with diploid inheritance selected as the sexually mediated glue that maintains the cooperative integrity of the interacting replicating unit (Witting 1997, 2002). The ecological selection of interactive competition is in this way solving the paradox of sex, where genomic recombination may provide

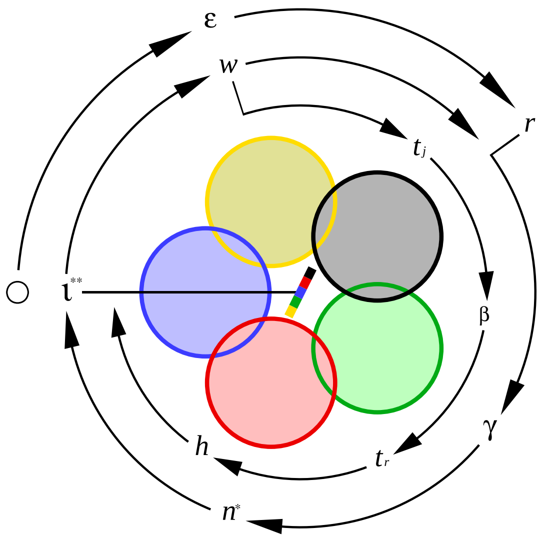

Figure 2: **Feedback selection diagram.** The small circle to the left represents the origin of self-replication, with selection for an exponential increase in net energy (ϵ) that maintains population growth (r) and a continued feedback selection of mass (outer feedback loop, see Section 2), with a steady state attractor ($**$) that determines the level of interactive competition (ι) among individuals in overlapping home ranges (coloured circles) where winners (dominating colour) monopolize resources. The competition generates a body mass biased resource access (slope of the multicoloured bar in centrum) that reallocation-selects net energy from replication to mass. This selection of mass induces a mass-rescaling selection of the life history (inner loop, see Section 2.2) that selects the exponents of the body mass allometries from the eco-physiological constraints between the pace of foraging and the spatial packing of home ranges (see Fig. 3 for allometric deduction). Outer loop: r:population growth → γ:density regulation → n^*:population abundance → ι:interference level → w:selection of body mass → r:population growth. Inner loop: w:mass change → t_j:juvenile period → β:metabolic rate → t_r:reproductive period → h:home range → ι:interference. From Witting (2017b).

a long-term advantages but no straightforward immediate selection that balances the two-fold cost of males and meiosis (e.g. Muller 1964; Hill and Robertson 1966; Hamilton 1980; Kondrashov 1994; Otto 2003; Hadany and Feldman 2005).

Dependent upon the selected feedback attractor of mass, the selected interactive competition may select larger replicating units also. An unconstrained selection of net energy, e.g., stabilises at a steady state attractor with a higher level of interference that selects co-operative reproduction and a body mass that increases exponentially over time (Witting 1997, 2002). This continuum selects eusocial reproduction as the extreme interacting unit, but this requires a special case where the selection increase in net energy does not reselect into an increase in mass, generating extreme intraspecific interference.

The selection of co-operatively and eusocially reproducing units allow for an in-principle selection of higher-level sexual reproduction with several males per female, and each individual transferring only a small amount of their genome to each offspring (Witting 2002, 2008). Yet, because sexual reproduction transfers some of the interactive quality of males to their offspring, there is a diminishing return in the extra interactive quality a female can obtain by adding an extra sexual male, compared to adding a non-reproducing offspring worker, to the interacting unit. This return is only sufficiently strong for the first added male (Witting 2002), selecting pairwise sexual reproduction and sexually-produced non-reproducing offspring workers where the inclusive fitness of the underlying relatedness (Hamilton 1964) maintains the co-operative integrity of the interacting unit.

The evolutionary dichotomy—between r-selected low-energy asexual self-replicators with minimum body masses on one side, and high-energy organisms with feedback selected body masses and sexual reproduction on the other—does not explicitly predict unicells like prokaryotes and protozoa. To predict these lifeforms, and virus-like replicators also, we need to take a closer look at resource handling and metabolic pace, the two subcomponents of net energy.

Initially at the origin there is no resource handling and metabolic pace, with the initial selection of pace acting on local resources obtained passively through e.g. diffusion or a flowing medium. This initial metabolic selection of pace comes with the mass of the selected metabolic pathways, including an expected diminishing return in the mass-specific metabolic efficiency of increasingly larger pathways (Witting 2017b). If the initial return of metabolism from mass is weaker than proportional to mass, the increased net energy of increased metabolism does not outbalance the proportional downward selection of the quality-quantity trade-off, as imposed by the mass of the metabolic pathways. This means selection against intrinsic metabolism, with replicator selection for exposed non-cellular gene codes that copy as fast as possible by the extrinsic metabolism of the environment (like virus).

When the initial metabolic return of the potential replicator is stronger than proportional, there is instead selection for self-replicators with intrinsic metabolism (Witting 2017b). And—as an advanced intrinsic metabolism depends on a cell-like structure for the concentration of metabolic pathways and other metabolites (e.g., Oparin 1957; Miller and Orgel 1974; Maynard Smith and Szathmáry 1995)—the diminishing metabolic return from the mass of the complete self-replicator selects for a cellular metabolic compartment with an embedded heritable gene code (assuming that analogue inheritance cannot produce cellular self-replicators). This selection stops when the diminishing metabolic return declines to the proportional return that balances the quality-quantity trade-off of the cell, selecting self-replicating cells with incomplete pathways that do not explore the full metabolic potential. This r-selection of metabolism, mass, and self-replicating cells does not select multicellular organisms because the quality-quantity trade-off halves the rate of replication with the addition of an extra similar cell, while the net energy of metabolism declines if the cell divides into smaller metabolic units.

Beyond these r-selected self-replicating cells, the selection of extra net energy by active resource handling leads to the gradual unfolding of interactive competition. As long as the associated resource gradient is weaker than a proportional increase with mass, the feedback is incomplete and cannot select mass on its own. But, in combination with the remaining metabolic return, it selects another class of unicells with extra mass selected partially as mass-of-additional-metabolism and partially as interactive quality (Witting 2017b). This implies a genome increasingly embedded in larger more structurally organised unicells, where parts of the interior perform metabolic tasks while the boundary to the surrounding environment deals with active resource handling and interactive behaviour. The selection of these interacting unicells continues with an increasing behavioural component until the metabolic pathways become fully developed (i.e. with zero metabolic return from increased mass). This happens at the point where the resource gradient of interactive competition becomes a proportional increase with mass and the population dynamic feedback starts to select mass on its own. The complete feedback is thereafter selecting multicellular organisms from the net energy of increased resource handling, with extra metabolising cells and sexual reproduction selected as the interactive quality that monopolises resources and enhances the reproduction of larger cooperating units relative to that of smaller non-cooperating units.

The mate choice of the predicted interacting males in mobile sexual organisms selects against asexual female replication, isolating the across-generation replication of genes in a germ-line while the non-replicating soma performs the ecological tasks of the organism, exposing the individual to the selection of senescence (Williams 1957; Hamilton 1966). The co-operating interactive quality, where males compete for resources for females, vanishes with the evolution of sessile organisms that compete for positions in a flowing medium of resources, making co-operate interactive behaviour essentially impossible. This selects against interactively co-operating sessile units inducing selection for hermaphrodites that avoid the two-fold cost of males and meiosis, with the associated absence of a male mate choice allowing for the evolution of asexual replication in sexual sessile organisms (Witting 1997, 2002).

The selection of net energy for replication predicts in this way the observed evolutionary unfolding of increasingly larger lifeforms with an increasingly embedded across-generation replication of genes. This embedding reflects a series of hierarchically structured natural selection transitions (Hull 1980; Buss 1987; Brandon 1988; Michod 1999) where "entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it" (Maynard Smith and Szathmáry 1995). The next essential question is whether the population ecological structure selects also the observed allometric scaling on the continuum from prokaryotes to animals.

2.2 Allometric scaling

The natural selection of mass rescales the life history because the increased total metabolism of larger offspring reduces the rate of replication below the rate imposed by the increase in size alone (Witting 2017a). This selects a metabolic decline that maintains the size determined rate of replication during the selection of mass. The downscaling of metabolism, however, reduces the pace of foraging and thus the assimilated net energy in physical time. This selects a co-occurring inverse scaling between metabolism and life periods that maintains the foraging pace and resulting net energy on the per-generation timescale of natural selection.

This mass-rescaling (Fig. 2, inner loop) selects the numerical values of the allometric exponents from its influence on the spatial packing of home ranges (Witting 1995). The metabolic pace of interactive competition selects for small home ranges that minimize the cost of competition, but small home ranges have increased local exploitation. This tension determines the spatial packing of home ranges, creating a log-linear selection balance between metabolic pace, home range, and mass

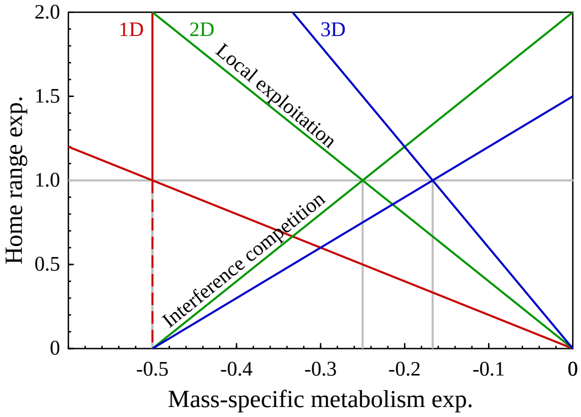

Figure 3: **Deduction of mass-rescaling allometries.** The selection of mass (w, Fig. 2) selects a mass-rescaling decline in mass-specific metabolism (β) that reduces the pace of foraging, affecting the ecological trade-off between the cost of local exploitation and interference competition. This influences the spatial packing of home ranges (h) where $\log h \propto -2d \log \beta$ describes the allometric constraints on local exploitation and $\log h \propto d(\log w + 2 \log \beta)/(d-1)$ the constraints on the cost of interference (Witting, 1995, 2023; $d \in \{1, 2, 3\}$: spatial dimension of home range packing). The plot solves the resulting equations [$\hat{h} = -2d\hat{\beta}$ and $\hat{h} = d(1 + 2\hat{\beta})/(d-1)$ with $\beta \propto w^{\hat{\beta}}$ and $h \propto w^{\hat{h}}$] for the allometric exponents $\hat{h}$ and $\hat{\beta}$ predicting a proportional scaling between home range and mass [$\hat{h} = 1$], and an allometric exponent for mass-specific metabolism [$\hat{\beta} = -1/2d$] that depends on the ecological dimensionality. From Witting (2023).

(see Witting 2017a, 2023 for details). When the equations of the selection balance are solved (Fig. 3), they predict a proportional scaling between home range and mass, and a negative 1/2-, 1/4-, or 1/6-power scaling of mass-specific metabolism dependent on a one-, two-, or three-dimensional packing of home ranges, with the predicted exponents supported by the allometries of animals (Witting 1995, 2017a).

Several other hypotheses have been proposed to explain the scaling of animal metabolism (e.g. Rubner 1883; Kozlowski and Weiner 1997; West et al. 1997; Banavar et al. 2002; Glazier 2010), but Malthusian relativity provides the only theoretical deduction of the body mass allometries from first principles of the natural selection of metabolism and mass; focussing not only on metabolism but on a simultaneous deduction of the scaling of the life history as a whole, involving eight traits of the life history and its associated ecology (Witting 1995, 2017a). These mass-rescaling allometries apply when it is variation in resource handling that generates the variation in net energy and mass, as in the predicted animals with completely developed metabolic pathways. Allometric scaling however depends more generally not only on the selected mass but also on the primary selected metabolism that generates net energy for the selection of mass (Witting 2017a).

Having net energy selected exclusively by metabolism, the predicted prokaryote-like unicells have a strong 5/6-power scaling of mass-specific metabolism (Witting 2017a,b) that resembles an average estimate of 0.84 across active and inactive prokaryotes (DeLong et al. 2010). The predicted protozoa-like unicells have a primary selected metabolism that span the range from prokaryotes to animals dependent of size, as supported by an allometric slope that declines from 0.61 among the smallest, over zero in intermediate, to -0.20 among the largest protozoa (Witting 2017a,b). The observed allometric range from prokaryotes to animals (Fig. 1, bottom) supports in this way the proposed self-organising natural selection of metabolism, mass, and lifeforms.

There is however much more to the natural selection of allometries because the mass-rescaling of animals selects a metabolic decline that induces a primary net energy driven reselection of metabolism lost in mass-rescaling. This primary reselected metabolism contracts the per-generation timescale of natural selection relative to the dilation imposed by mass-rescaling (Witting 2020), and this allows for deeper evolutionary insights. It is e.g. the rate of primary selected metabolism relative to the selected rate of resource handling that determines the curvature of the evolutionary body mass trajectory when the exponential log-linear trajectory of steady-state selection on the per-generation timescale of natural selection scales into physical time. This implies that the accelerating upward bending body mass trajectory of browsing horses in the fossil record (MacFadden 1986) agrees with early habitat adaptation followed by almost no resource handling evolution thereafter, with primary selected metabolism being the estimated main reason for the size increase in browsing horses over 57 million years (Witting 2020).

Another example is the decelerating downward bending evolutionary trajectory of maximum mammalian mass following the Cretaceous-Paleogene extinction of dinosaurs (Fig. 4 left; Smith et al. 2010). It agrees with a resource handling selection that outruns metabolic selection on the scale of maximum evolutionary diversification (Witting 2020). This aligns with a present-day approximate 3/4-power inter-specific scaling of total metabolism (Fig. 4 middle) that confirms a fast radiation in resource handling for the majority of the mam-

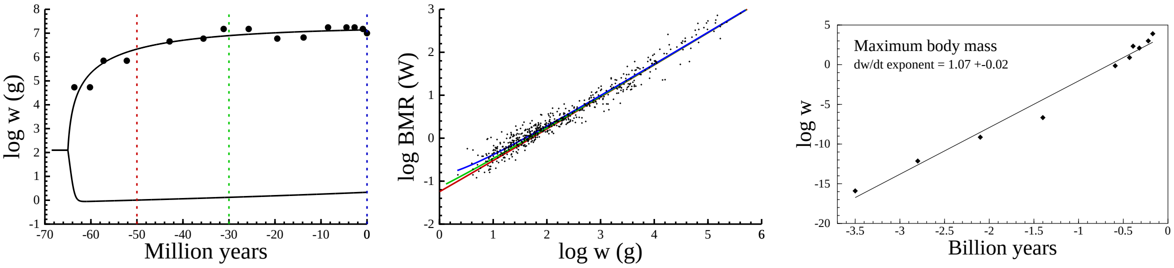

Figure 4: **Selection of mass and metabolism. Left:** The evolution of the body mass (w) distribution of placental mammals (boundary curve) over the last 65 million years, as simulated by a fast selection differentiation in resource handling and a small amount of primary selected metabolism [fit to global maximum mass estimates from Smith et al. (2010), and 2.2-gram current minimum]. The background selected metabolism is estimated from the curvature of the current inter-specific allometry [middle plot: basal metabolic rates (BMR) from McNab 2008. Linear regression exponent: overall:0.72; lower half:0.67; upper half:0.74], with dashed colour lines in the left plot and corresponding curves in the middle plot illustrating the selection of allometric curvature over time. From Witting (2018). **Right:** The maximum mass (length raised to third power) of mobile organisms during 3.5 billion years of evolution. The estimated $\mathrm{d}w/\mathrm{d}t$ exponent around unity (allometric regression on the rate of increase in mass in physical time) indicates a complete reselection of metabolism lost in mass-rescaling during the selection increase in mass. From Witting (2020), data from Bonner (1965) and Payne et al. (2009).

malian size expansion, with the inter-specific partitioning of resources and associated habitat adaptations supporting a diversity of mammalian sizes.

The slightly smaller (0.72; Fig. 4 middle) than expected (0.75) allometric exponent for total metabolism in present-day placentals is then most likely reflecting a small amount of primary selected metabolism (Witting 2018). Metabolic selection bends the metabolic allometry upward in the lower size range as evolution proceeds (Fig. 4 left & middle) because it accelerates most in smaller species due to their shorter generations. This explains the observed (Kolokotrones et al. 2010; MacKay 2011; Packard 2015) curvature in the metabolic allometry from a mass-specific metabolism that increases exponentially at a per generation rate of 9.3×10^{-9} (95% CI: 7.3×10^{-9} - 1.1×10^{-8}), on average. The estimated rate for marsupials is an order of magnitude smaller reflecting their almost perfect 3/4-power scaling (Witting 2018), agreeing with about 30% larger metabolism in today's placentals compared to marsupials of comparable size.

The majority of the mammalian adaptations in resource handling are likely to occur by minor adjustments to the overall mammalian Bauplan. The evolutionary building of a new Bauplan from one major taxon to another is a much more complicated and slower evolutionary process, which may involve new phenotypic solutions for the exploitation of previously unexploited resources. If this across-taxon selection of resource handling and mass is sufficiently slow, we predict a complete reselection of metabolism lost during the mass-rescaling selection of a new taxon. This explains (Witting 2017b) the observed (Makarieva et al. 2008; Kiørboe and Hirst 2014) across taxon invariance in mass-specific metabolism (Fig. 1, bottom), where the evolution of a larger animal taxon selects no change in the slope of the metabolic allometry, but an increase in the intercept as the taxon diversifies across ecological habitats. It agrees also with an observed log-linear trajectory of maximum mass evolution across all mobile organisms covering 3.5 billion years (Fig. 4 right), estimating a reselection of the metabolism lost in across-lifeform mass-rescaling during the deepest evolutionary time window on Earth (Witting 2020).

3 The rise and fall of contingent life history evolution

The outline above illustrates how the origin of replicating molecules initiates a directional self-organising selection of the major lifeforms, allowing evolutionary biology to develop beyond the diversifying contingency that has dominated natural selection theory since its introduction by Darwin and Wallace in 1858. While Darwin envisioned "progress towards perfection" from the "struggle for existence" that "inevitably follows from the high rate at which all organic beings tend to increase" (Darwin 1859), he never formulated the underlying mechanisms leaving natural selection to the unsolved diversifying contingency of particular circumstances, providing no overall organising principle (Witting 2008).

This dichotomy—between envisions of an overall directional evolution (often towards increased perfection and phenotypic complexity) and no explicitly formulated supporting selection—remained for almost 150 years. While originally a pre-Darwinian concept of biological evolution (Lamarck 1809; Chambers 1844; Spencer 1855), the idea of an overall directional evolution remained widespread up through the modern synthesis in mid-20th century (McShea 1991). The popularity of the concept declined thereafter following the rise of traditional life history theory, but new hypotheses on a directional evolution of complexity and order continues to appear from time to time reflecting the ultimate unsolved paradox of evolutionary biology (e.g. Demetrius 1974; Saunders and Ho 1976; Brooks and Wiley 1986; Kauffman 1993; Brandon and McShea 2011; Brown et al. 2024). At least ten hypotheses propose to explain an evolutionary increase in complexity (McShea 1991), but most of these are not based on demographic natural selection. The proposed self-organising selection (Witting 1997, 2017b) is the only directional hypothesis available that explicitly predicts the natural selection succession of the major lifeforms, and it is also the only hypothesis based on contingence-free life history selection by the agreed demographic fitness of the Malthusian parameter.

The theoretical development of a self-organising selection falls as a logical extension of the traditional life history theory that emerged from the contingent paradigm. While argued as one of the most characteristic features of biological evolution (e.g. Mayr 1988; Gould 1989; Salthe 1989), the contingency of "chance and necessity" (Monod 1971) is a somewhat self-contradictory natural selection concept where the main force of evolution has no organising force. It is fairest to understand the contingent hypothesis in a historical perspective where the absence of an identified organising force was a successful working hypothesis. Not only did it allow plenty evolutionary hypotheses to flourish without the constraints of a dominating force, but it allowed also for an easy explanation of the diversity of life, providing convincing arguments against the widespread critique of biological evolution.

An influential development came when the focus of evolutionary theory shifted from Darwin's original proposal on ecological interactions to the mathematically more straightforward calculations of inheritance by Mendelian genetics. This provided a strong genetic theory that developed into the population genetic synthesis that consolidated the Malthusian parameter as the agreed measure of fitness (Fisher 1930; Wright 1931; Haldane 1932). As already discussed, the exponential Malthusian increase is a powerful force where the quality-quantity trade-off selects for the absence of mass and absence of multicellular organisms, and the two-fold costs of males and meiosis select for the absence of sexually reproducing organisms.

Given this formal definition of fitness, natural selection theory had eventually obtained an organising principle, but the predicted minimum-sized asexual replicator was not particularly useful as a bottom-line conclusion for evolutionary biology. This paradox sparked the development of contingent life history theory (Partridge and Harvey 1988; Caswell 1989) that aimed for a mechanistic understanding using natural selection models with no explicit frequency-dependent interactive competition (Roff 1992; Stearns 1992; Charlesworth 1994). It documented how the intra-specific trade-offs and constraints among the demographic traits generate fitness landscape peaks that resemble the observed life history strategies.

To evaluate the evolutionary implication of traditional life history theory we need to examine its predictive power and degree of contingency. For this we take a closer look at the demographic trade-offs and constraints that the selection models use to calculate the fitness peaks of the predicted life histories. Many of these are based on *a priory* arguments like energy allocated in the trade-off between reproductive effort and survival in Lack's (1947) clutch size, and constrained mating probabilities in sex ratio theory given specific mating systems (Hamilton 1967). The relations have evolved components also, like the body mass scaling of the amount of energy allocated in the reproduction/survival trade-off, and like the evolved degree of local mating. The theory then uses the trade-offs and constraints from studied species to show that the predicted life histories coincide with the life histories of those species, with deviations typically reflecting necessary refinements in the trade-off space of a model.

Traditional life history theory is thus essentially a set of models that show that the life history and demographic trade-offs of a species have evolved in a mutual selection balance, reflecting among others energy that cannot be allocated from one life history trait to another without fitness consequences. These models are contingent in the sense that they use the actual evolution of the trade-offs and constraints as the essential organising principle and thus they avoid addressing questions on the natural selection origin of the life histories. The predicted life histories follow instead from the assumed trade-offs and constraints with the additional implicit assumption that these evolved, if not by an unknown organising selection, then by a neutral contingency of a long sequence of improbable events.

This uncertainty on the natural selection origin of the existing life histories allows for multiple more or less equally valid evolutionary hypotheses. Examples of this include r versus k strategists (MacArthur and Wilson 1967; Stearns 1977; Parry 1981), differentiation along a fast–slow continuum (Sæther 1987; Promilsow and Harvey 1990; Bielby et al. 2007; Jeschke and Kokko 2009), size and lifestyle differentiation (Dobson 2007; Sibly and Brown 2007), and metabolic allocation (Burger et al. 2019), to name a few.

To check the contingent premiss behind these hypotheses we can examine if it is in fact possible at all to have a truly contingent selection theory that allows the existing life history diversity to evolve. This requires selectively neutral trade-offs and constraints that cover the diversity of the existing life history variation, and to check for this we let the underlying model selection operate on the life history as a whole. This activates the Malthusian force where the quality-quantity trade-off and the two-fold costs of sex select the minimum-sized asexual replicator and its inherent trade-offs (Witting 1997, 2008), revealing an insufficient natural selection theory that *i*) disrupts the diversifying contingency required for the existing life histories to exist under the contingent paradigm, and *ii*) nor offers an adequate organising principle as a suitable alternative.

These results show that the direct link between life history traits and Malthusian fitness leaves no room for selectively neutral life histories, and life history theory does therefore not belong under the contingent evolutionary paradigm with a multitude of equally probably sequences of improbable events. The fundament of life history theory is instead a predictive science based on an active natural selection with the necessary organising principles, with traditional theory incorporating the historical evolution that actually occurred as a contingent placeholder for the unidentified organising selection.

It is the displacement of this contingent placeholder by its underlying organising selection that brought us to the present review of Malthusian relativity, with the problems of traditional theory indicating that we need some sort of frequency-dependent selection to organise evolution in the opposite direction of the frequency-independent pull of Malthusian increase. The review shows how the ecological connection between population dynamic growth and intra-population interactive competition provides a self-organising natural selection of the major lifeforms from net energy selected for replication. These feedback processes react to inter-specific interactions as they adjust to the available resources and average survival of individuals.

The proposed transition from random diversifying contingency to deterministic directional self-organising selection changes the way we evaluate evolutionary hypotheses. As already discussed, the contingent paradigm allows for many hypotheses as there is supposed to be an almost infinite number of more or less equally probable sequences of evolutionary events that can take you from one phenotype to another. Valid evolutionary hypotheses under the self-organising selection paradigm, on the other hand, are those that sustain a balanced intra-population selection on the life history as a whole, also when we investigate the influence from external factors. This restricts the agreeable hypothesis-space enormously calling for a reexamination beyond the scope of the present paper.

We saw above that traditional top-down theory fails to pass the evaluation on its own because it lacks a balanced selection on the life history as a whole. Yet, by superimposing traditional top-down models on top of the self-organising model it is possible to extend the self-organising selection. While the top-down models do not include the density-frequency-dependent population dynamic feedback interactions explicitly, their instant measures of intra-population correlations among the demographic traits include the fitness effects of the interactions implicitly. This allows the self-organising selection to meet top-down modelling at a common intermediate interface, generating a more inclusive analysis where the self-organising selection provides evolutionary stability to the otherwise unexplained and evolutionarily unstable trade-offs and constraints of the top-down models.

Several analyses have examined this interface between the two approaches, with the feedback selection of mass making the fitness landscape an instant measure that evolves with the selection of mass (Witting 2017b). Populations that climb the peaks of more or less stable fitness landscapes is therefore not a valid metaphor, but dependent on the situation, populations may climb the selection integral that integrates the selection gradient of the evolving fitness landscape across the potential evolution of a trait, looking along the evolving population instead of looking only within it at a given point in time. The biased resource access of this selection explains an intra-specific proportional correlation between reproduction and mass (Witting 1997, 2003) that is part of the structural constraints of the contingent models on the selection of size (e.g., Roff 1986; Stearns and Koella 1986), with a bottom-up predicted “Lack’s clutch size” scaling the trade-off between reproductive effort and survival (Witting 1997, 2008). Population dynamic feedback selection includes also traditional sex ratio theory (Fisher 1930; Hamilton 1967; Trivers and Hare 1976) as an essential component, allowing the mating system and sex ratio to adjust to the overall energetic selection pressure in the population (Witting 1997), and for eusocial species we find that the fitness components of the sexually reproducing males explain diploid termites with male and female workers, and haplodiploid ants with female workers only (Witting 1997, 2007). The two approaches not only have their own right, but their joint integration allows for deeper evolutionary insights, enhancing our abilities to predict and mitigate evolutionary impacts of anthropogenic disturbances including climate change.

With the contingent paradigm failing for life history evolution, and the assumptions of traditional life history theory being contingent placeholders of the underlying organising principle, I propose that Malthusian growth and the resulting struggle for existence—that catalysed Darwin's understanding of natural selection when he read Malthus (1798) on September 28, 1838 (Darwin 1887)—is the major self-organising force of life history evolution, given that "struggle" is interpretated not as the Malthusian "war of nature, from famine and death" (Darwin 1859), but as the density-frequency-dependent interactive competition that distributes resources among the individuals in the population.

It is important to keep in mind that the necessary incorporation of the interactive feedback ecology is not just a mathematical modelling issue. It is first of all an evolution in evolutionary thinking away from "chance and necessity" to energy flowing from metabolising reproducing units over their population dynamic growth to their interactive competition and back through the resulting differentiated availability of energy. I find that the ecological and evolutionary interactions between these processes sustain a dissipative self-organising selection that keeps the ever-evolving population in energetic balance.

4 Conclusions

(1) Malthusian fitness leaves no room for selectively neutral life histories, and life history theory does therefore not belong under the contingent evolutionary paradigm with a multitude of equally probably sequences of improbable events. Life history theory is instead a predictive science, where traditional theory incorporates the actual evolution of the past as a contingent placeholder for the organising selection that caused the life history to evolve. I reviewed population ecological theory that identifies these organising principles by studying a contingence-free natural selection bottom-up forward from the origin of replicating molecules.

(2) Resource handling for the generation of net energy for replication selects metabolism as the pace of handling, with the mass of the metabolic pathways constraining this selection at the origin of replicating molecules. If the initial metabolic return is weaker than a proportional increase with mass, the increased net energy of increased metabolism does not outbalance the proportional downward selection of the quality-quantity trade-off, generating selection for exposed non-cellular gene codes that copy as fast as possible by the extrinsic metabolism of the environment (like virus).

(3) When the initial metabolic return is stronger than a proportional increase, there is selection for self-replicators with intrinsic metabolism selecting for a cellular metabolic compartment with an embedded heritable gene code (like a prokaryote). This selects against multicellular organisms because the quality-quantity trade-off halves the rate of replication with the addition of an extra cell.

(4) Selection continues beyond these initial unicells by the build-up of interactive competition from the population growth of a selection increase in resource handling. This selects larger unicells like protozoa, with extra mass selected partially as mass-of-extra-metabolism and partially as interactive quality. This implies a genome increasingly embedded in larger more structurally organised unicells, where parts of the interior perform metabolic tasks while the boundary to the surrounding environment deals with active resource handling and interactive behaviour.

(5) The selection of interacting unicells from increased net energy continues until the metabolic pathways and population dynamic feedback selection become fully developed. The feedback is thereafter selecting mass from net energy on its own, with multicellular organisms and reproducing units with pairwise sexual reproduction selected as interactive quality. If the selected increase in net energy does not reselect into increased mass, it generates extreme intra-specific interference with eusocial colonies selected as the interacting reproducing unit.

(6) The allometric scaling of life histories with mass depends *i*) on the primary selected metabolism that generates net energy for the selection of mass, and *ii*) on a mass-rescaling selected change in metabolism, natural selection time, and spatial home range packing that is necessary to maintain net energy and reproduction during the selection of mass. This predicts *i*) the almost proportional scaling of mass-specific metabolism in prokaryotes from mass selected by metabolism, *ii*) the negative 1/4 exponent of animal taxa as a mass-rescaling exponent from net energy and mass selected by increased resource handling, and *iii*) the intermediate exponents of protozoa from their metabolism to resource handling transition in the selection of net energy and mass.

(7) The selection of new taxa occurs slowly because it depends on the selection of new resource handling solutions. A sufficiently slow evolution allows for a complete reselection of metabolism lost during the mass-rescaling selection of the new taxa, predicting the observed across-taxa invariance of mass-specific metabolism. This also predicts the log-linear trajectory of maximum mass evolution across all mobile organisms, with mass-rescaling lost metabolism reselected across lifeforms during 3.5 billion years of evolution on Earth.

(8) This identifies a directional self-organising selection that keeps the ever-evolving population in energetic balance across the major lifeforms, thanks to the population dynamic feedback selection of interactive competition that unfolds gradually from net energy selected for replication.

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