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Self-organising natural selection from replicating molecules to multicellular sexually reproducing organisms

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Abstract During their evolution from molecular replicators over unicellular prokaryotes and eukaryotes to multicellular sexually reproducing organisms, biological lifeforms increased in size with heritable codes increasingly embedded in more organised slower replicating units. This evolutionary unfolding is traditionally seen as a remarkable unpredictable coincidence of a directionless natural selection following long sequences of improbable diversifying events. I describe how this contingent paradigm of unpredictable evolution was consolidated somewhat counterintuitively by the life history theory of the population genetic synthesis that was developed to explain life history evolution.

The prediction of unpredictable evolution follows from an applied selection increase in average fitness towards contingently defined fitness peaks; a selection that is structurally insufficient to explain the Darwinian hypothesis that the life histories of species are naturally selected from the life history of their common ancestor. This major evolutionary paradox, where the life histories of the attracting fitness peaks follow from unknown contingencies instead of the identified natural selection itself, is solved in the scientific literature by integrating intra-specific interactive competition into the demographic selection of life histories.

This provides a population ecological synthesis that includes and expands beyond the traditional theory, generating a deterministic natural selection force that self-organises from mass, energy, and replication at the origin of replicating molecules. This selects—not an increase in average fitness but—a self-organising net energy driven change in relative fitness and natural selection itself, a selection change that is necessary and sufficient to select the evolutionary succession of the major lifeforms from a common ancestor.

I review how this selection of net energy for replication generates population growth that generates a density-frequency-dependent interactive competition that reallocation-selects the increase in replication-energy into larger, more cooperatively organised slower replicating units. This predicts an essentially inevitable evolution of the major lifeforms, including large multicellular organisms with inter-specific body mass allometries and sexual reproduction by a diploid genome with fair meiosis.

Keywords: Natural selection, life history, population ecology, allometry, major transitions, sexual reproduction

Contents

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 phenotypic evolution in different taxa often converge on similar solutions, illustrating the limited alternatives of design (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. That phenotypic selection generates phenotypic evolution is one of the best documented principles of the Darwinian hypothesis, let selection be artificial or natural. But despite of its many successes, traditional natural selection theory remains unprepared and incomplete as a predictive science because it lacks an explicit selection that predicts the evolutionary succession of the major lifeforms (Witting 2008).

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 sexually reproducing organisms exists in the first place? Their evolution seems obscure with no specific cause, explained traditionally as a remarkable coincidence of a long sequence of improbable events, instead of evolving inevitably from the natural selection force of a predictive science.

Where physicists have discovered universal forces of mass and energy that organise the non-living world into elements, space, stars, galaxies and more, most biologists agree that there is no universal natural selection force that organises the living world into virus, prokaryotes, unicellular eukaryotes and multicellular sexually reproducing organisms, assuming natural selection organised the evolution of the major lifeforms forceless by trial and error alone. This absence of an identified organising force developed into the contingent evolutionary paradigm during the 19th and 20th century (Witting 2008). It treats 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).

Being consolidated by the selection theory of the population genetic synthesis (Fisher 1930; Wright 1931; Haldane 1932; see Section 2), the contingent paradigm represents a persistent thought pattern in the evolutionary literature (e.g. Stanley 1973; Mayr 1988; Salthe 1989; Williams 1992; Maynard Smith and Szathmáry 1995; Michod 1999; Gould 2002; Brandon and McShea 2011; Lynch 2025). It sees the selection/fitness component of the three conditions [traits variation, heredity, and differential/relative fitness] necessary for evolution by natural selection as a multidimensional geno/phenotypic fitness landscape (Wright 1932) where species, contingent on their evolutionary past, are selected by an increase in average fitness (Fisher 1930) towards the life histories of the fitness peaks in the landscape.

This selection concept developed into a mathematical theory that describes the life history evolution of species on the fitness landscape (e.g. Lande 1982; Partridge and Harvey 1988; Caswell 1989; Roff 1992; Stearns 1992; Charlesworth 1994). This is done contingently in a somewhat circular manner where the demographic trade-offs and constraints that have evolved in the species of today define the peaks of the fitness landscape. By analysing life history selection in this top-down backward way contingent on the current state of evolution, biology obtained a theory with no overall organising force, having the life histories of fitness peaks granted by the actual evolution of the past, instead of analysing for the natural selection principles that created them (Witting 1997, 2008; Section 2).

The unpredictable evolution reflects not only the contingently defined fitness peaks of the applied selection, but also that this selection is structurally insufficient to select the Darwinian paradigm where the naturally selected life histories of species are naturally selected from the life history of their common ancestor (see Section 2). This major evolutionary paradox reflects a natural selection that is defined in such a way that life history evolution is controlled primarily by the contingencies of unknown origin rather than by the identified natural selection itself. To resolve this paradox, we need to identify a predictive theory of evolution where the

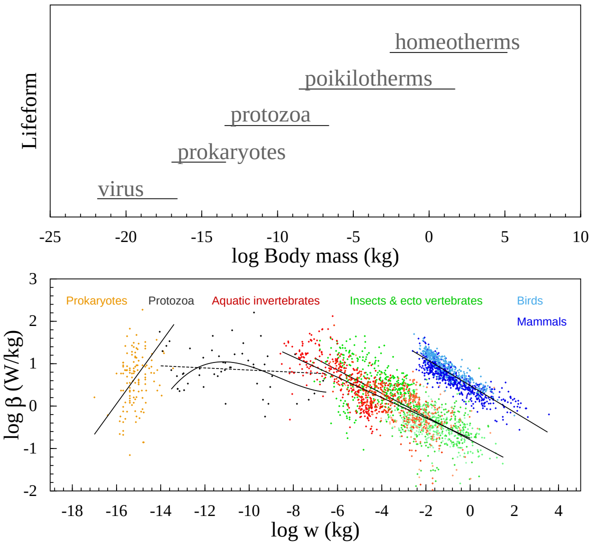

Figure 1: **Macro evolutionary relationships. Top:** The body mass range of mobile lifeforms (horizontal lines), illustrating lifeforms as a function of size. **Bottom:** Relationships between mass (w) and mass-specific metabolism (β) among mobile organisms. Data from Makarieva et al. (2008), plot from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

life histories of the major lifeforms are naturally selected from the life history of a common ancestor by the natural selection of the theory itself. The present review follow Witting's (1995, 1997, 2008, 2017a,b) attempt to identify such a selection by analysing for the self-organising powers of a contingence-free natural selection that unfolds bottom-up from first principles of mass, energy, and replication at the origin of replicating molecules.

To illustrate the evolutionary necessity of self-organising selection, I cover 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 pattern reflects an increase in the energy used to produce an individual, with the body mass allometries describing how the life history evolves with the selection increase in energy and mass, including an evolutionary change in the allometric scaling 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, it 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).

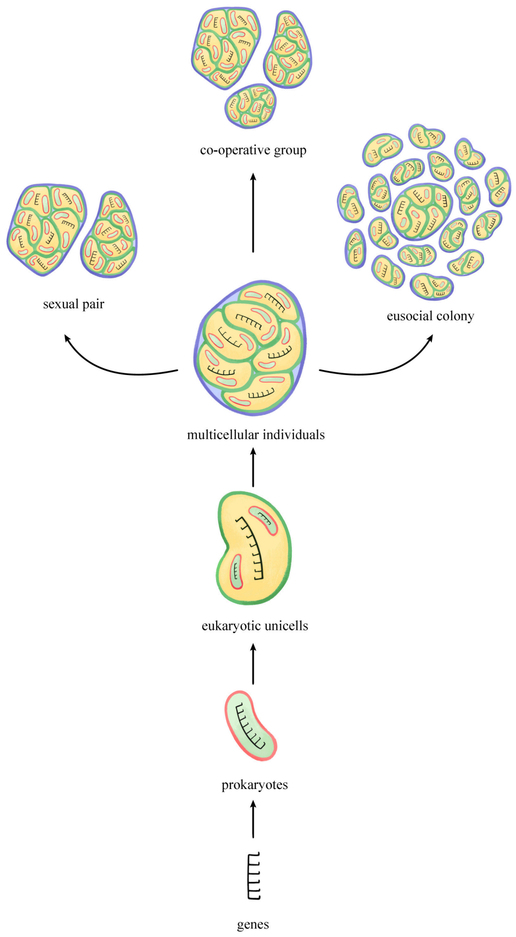

Figure 2: **The major evolutionary transitions** where genes, metabolising prokaryotes, eukaryotic unicells, and multicellular organisms that were "capable of independent replication before the transition can replicate only as part of a larger whole after it" (Maynard Smith & Szathmáry, 1995).

The major evolutionary transitions (Maynard Smith and Szathmáry 1995) sits on top of the life history continuum of the body mass allometries, with the heritable code increasingly embedded in more-and-more organised replicating units (Fig. 2). These transitions carried living organism from an initial molecular cell-less replicator, over the metabolising unicellular self-replicators of prokaryotes, and more advanced unicellular eucaryotes like protozoa, to multicellular sexually reproducing organism, including transitions from pair-wise sexual, over cooperative, to eusocially reproducing units.

The population energetics of interactive competition is now explaining this macro evolutionary pattern by a natural selection that self-organises from mass, energy, and replication at the origin of replicating molecules (Witting 1997, 2008, 2017a,b): The selection of net energy for replication generates population dynamic growth that generates a density-frequency-dependent interactive competition that reallocation-selects the increase in replication-energy into increasingly larger organisms with slower rates of replication, including successive selection transitions to more organised replicating units where lower-level entities cooperate in interactive competition.

This self-organising selection is described by the theory of Malthusian relativity (Witting 1997, 2008, 2017a,b) that identifies a deterministic energy driven population ecological force in natural selection, allowing for contingencies in other areas of evolutionary biology. The self-organising selection evolves by itself as the selected net energy generates a gradually unfolding population dynamic feedback selection from the interactive competition among the replicating units in the population, selecting metabolism, mass, life history allometries, and major evolutionary transitions forwardly (Witting 1995, 1997, 2002, 2007, 2017a,b). This is done by a self-organising selection attractor that evolves as a function of the selected net energy and mass, allowing the life history diversity of the major lifeforms to be selected directly from the life history of a common ancestor. Speciation, inter-specific competition, and local adaptation are additional factors that generate and maintain the inter-specific diversity of net energies, body masses, and life histories. This provides a universal mechanism that combines an energy driven self-organising natural selection with the Darwinian principle of inter-specific diversification through branching phylogenies.

To predict the natural selection of the major lifeforms, Malthusian relativity quantifies the flow of energy in the evolving population—from net energy assimilated by metabolising individuals over population dynamic growth and abundance to the interactive competition that distributes the ecologically available energy among the individuals—when calculating life history evolution from the demographic selection of the intra-population distribution in energy and fitness; with fitness calculated from the demographic traits as the Malthusian parameter of exponential increase (r) that "measures fitness by the objective fact of representation in future generations" (Fisher 1958; also Lande 1982; Partridge and Harvey 1988; Caswell 1989a; Charlesworth 1994 and others).

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; Lane 2015, 2019; Brown et al. 2024; Arcas 2025b; Vermeij et al. 2025). These studies are not based on demographic natural selection 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 natural selection, I do not discuss most these studies further.

I review and describe 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, 1932; Haldane 1932), its definition of fitness as the Malthusian parameter, and the subsequent development of selection theory on life history evolution (Lande 1982; Partridge and Harvey 1988; Caswell 1989; Roff 1992; Stearns 1992; Charlesworth 1994) and major evolutionary transitions (Buss 1987; Maynard Smith and Szathmáry 1995; Michod 1999).

2 Contingent selection

The contingent life history theory of the population genetic synthesis treats the trade-offs and constraints among the demographic traits as the first-order principle trait space that limits the potential covariance among traits and selects the balanced life histories of species (Roff 1992; Stearns 1992; Charlesworth 1994). This is done by a selection increase in average fitness (Fisher 1930) that selects the variant with the largest relative fitness as measured by the population growth of the Malthusian parameter, with e.g. the trade-off between reproduction and survival selecting optimal growth for a limited reproductive rate (Lack 1947). It is hereby assumed that the life histories of species are naturally selected primarily by the constraints and trade-offs among the demographic traits.

But life history evolution is more entangled and complex because most of the demographic trade-offs have an evolved and non-evolved component that can and cannot evolve by natural selection respectively, with the evolved component being part of the evolved life history itself. The possibility of allocating energy to either reproduction or survival is a structural constraint that cannot evolve as it follows from the conservation of energy, but the amount of energy allocated to individual survival is naturally selected to be substantially larger in elephants than mice. It is only the non-evolving components of the trade-off structure that are universally fixed first-order principles of natural selection, and by factoring in also the evolved trade-off components—as structural assumptions measured for each species—the contingent life history theory does not explicitly consider the natural selection of the difference between elephants and mice.

The inclusion of the complete trade-offs in the model structure has some unforeseen consequences when it comes to our interpretation of the evolutionary implications of the prosed selection (Witting 1997, 2008). This is because the evolutionary entanglement between life history traits and trade-offs has the side effect that the factoring in of complete trade-offs factor out the selection of some of the most influential trade-off components that cannot evolve by selection. These components include *i)* the quality-quantity trade-off where many small or a few large offspring can be produced from the same amount of energy (Smith and Fretwell 1974; Stearns 1992), *ii)* the two-fold cost of a male that does not contribute energetically to replication (Maynard Smith 1971), and *iii)* the two-fold cost of meiosis that reduces the probability of a gene being copied to an offspring from 1 to 0.5 (Williams 1975). These trade-offs are universal, and by factoring them out of the selection equation the contingent life history theory obtains a neutral selection background. This prevents the life histories in the selection models from collapsing to the Darwinian demon singularity with asexual replication, zero mass, and infinite fitness (Witting 1997, 2008).

Examples of this include models on the natural selection of body mass and size (Roff 1986; Stearns and Koella 1986) that factor out the selection against mass by the quality-quantity trade-off by assuming a proportional correlation between quality (mass) and quantity (reproductive rate). This intra-population correlation has evolved in many species with an observed selection of mass (Peters 1983; Kingsolver and Pfennig 2004), providing an evolved contingency that is incorporated as the unexplained structural assumption that makes it possible to model the selection of mass.

Another example is sex ratio theory, where the reproductive fitness that males and females obtain through the sexual mating structure predicts the observed sex ratios of a diversity of species (Fisher 1930; Hamilton 1967; Trivers and Hare 1976). Here it is the assumed/measured mating structure that factors out the costs of sex. But if the mating structure is allowed to evolve, the costs of sex would select for more-and-more local mating with a more-and-more female biased sex ratio, selecting the male and associated sexual reproduction out of the equation (Witting 1997).

Lack's clutch size is a third example that predicts the observed clutch sizes of different species from the currently evolved trade-offs between the reproductive effort and future survival of parents and offspring (Lack 1947; Schaffer 1983; Godfray et al. 1991). Here it is the assumed/measured amount of energy/effort that is allocated in the reproduction/survival trade-off that factors out the selection of the quality-quantity trade-off. But if trade-off evolution is allowed, the quality-quantity trade-off selects reproduction at the cost of mass selecting smaller individuals that require less energy to survive (Witting 1997, 2008).

These examples illustrate how the assumed presence of the evolved demographic trade-offs and constraints factor out the selection of the quality-quantity trade-off and costs of sex making it possible to calculate local fitness peaks for the evolved life histories. The evolved inter-specific life history diversity is in this way explained from a set of measured outcomes of the evolutionary history of the past, with the selection models explaining local selection towards the measured fitness peaks of the different species. But the quality-quantity trade-off and costs of sex remain in the background, and this selects for the Darwinian demon through changes in the evolved components of the demographic trade-offs, indicating that something is missing in the theory of natural selection.

Things that are missing include a selection that explains the evolved components of the demographic trade-offs and constraints. They define the life history positions of the peaks in the fitness landscape, and there is therefore no selection to explain why the fitness landscape peaks at the evolved life histories, instead of peaking at other life histories.

With the identified selection selecting different species towards different locally isolated fitness peaks, nor does the contingent selection explain evolution from one life history fitness peak to another. Evolution among fitness peaks is needed to explain the perhaps most central premise of the Darwinian hypothesis i.e. that the life histories of the major lifeforms are naturally selected from the life history of their common ancestor. But instead of being explained by natural selection per se, evolution from one fitness peak to another is conceptualised by fitness landscapes that change by other factors than the identified selection, by narrow unidentified fitness ridges that connect the peaks of the fitness landscape, or by historical events where adapted lineages at fitness peaks evolve downhill directly against natural selection (e.g. by drift) and through the valleys of the fitness landscape to evolve from one naturally selected life history to another. This need to use other explanatory factors than natural selection itself reflects an explicitly identified selection that is structurally incompatible with the Darwinian concept of species with naturally selected life histories that are naturally selected from the naturally selected life histories of their ancestors.

A related and equally essential paradox is that the contingent selection operates by a continued selection increase in the average Malthusian parameter fitness of the population (Fisher 1930), while larger species on Earth typically evolved from smaller species by a decline in the Malthusian parameter (Fenchel 1974; Damuth 1981, 1987). Evidence is that evolution occurred in an overall direction diametrically opposite to the direction predicted by a selection increase in average fitness, as concluded also by the quality-quantity trade-off and costs of sex that select for the infinite fitness of the Darwinian demon by changes in the evolved demographic trade-offs and constraints.

Theories on the major life history transitions in evolution (e.g. Buss 1987; Maynard Smith and Szathmáry 1995; Michod 1999; Lane 2015, 2019; Arcas 2025a,b) have somewhat similar issues. They describe how the major transitions follow from lower-level replicators that evolve into a next higher-level replicator by lower-level individuals that cooperate and trade-off their lower-level fitness for fitness at the next higher-level of selection.

Transition theory identifies the selected levels of cooperation necessary for the evolutionary unfolding of the major lifeforms, and the theory is directional as it starts from the molecular replicator working its way up. It usually applies either *i*) an opportunistic diversifying selection that identifies potential candidates for the type of lower-level cooperation that may select the transitions forwardly (e.g. Buss 1987; Maynard Smith and Szathmáry 1995; Michod 1999), or *ii*) it proposes directional evolution driven by an increase in organism energy by a symbiogenesis where evolved gene sequences form larger more efficient cooperating wholes (e.g. Lane 2015, 2019; Arcas 2025a,b), as in the apparent engulfing of one prokaryote by another during the transition from prokaryotes to unicellular eukaryotes (Sagan 1967; Lane 2017; Martin 2017). An increase in net energy is a necessary precondition for the evolution of larger higher-level reproducing units, but the transition theories of lower-level cooperation do not explicitly identify a selection that neutralises the selection against mass and sexual reproduction by the quality-quantity trade-off and costs of sex (see Sections 7 to 9 for details).

It is the entangled factoring out of the downward pull of the quality-quantity trade-off and costs of sex by the factoring in of a chosen subset of the evolved trade-offs, constraints and other conditions, that define the success of the contingent selection theory. Yet it implies a theory that uses the actual evolution of the past to measure, rather than first principle predict, the evolutionary outcome of natural selection, neglecting a formal analysis on the deeper organising selection (Witting 1997, 2008).

To see the blind angle in our understanding of evolution that follows from this absence of analysis on the organising force of natural selection, it may help to think of contingent selection theory as an attempt to understand the construction of 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 the bridge, and nor how they organised the building of the particular form of bridge, with its measurable compression and tension. In the same way, by measuring the evolved demographic trade-offs and constraints of a species, we can calculate that the species has the right life history demography 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 the lifeform of the species, and nor how it organised the selection of its life history, including the measured trade-offs and constraints.

3 Self-organising selection

As neither the contingent life history theory or transition theory solve the problem of selecting mass and sexual reproduction against the selection of the quality-quantity trade-off and costs of sex, let us try to resolve the issue by studying the self-organising force of natural selection. This is e.g. done by removing the contingency of the evolved entanglement of life history traits and trade-offs from our demographic selection model to factor in the quality-quantity trade-off and costs of sex and study natural selection bottom-up from the origin of replicating molecules predicting the observed evolution forwardly from a minimum of biological assumptions. This is the approach taken in the present paper where I follow Witting (1997, 2008, 2017b) and focus on the deterministic natural selection consequences of mass, energy, and replication. This involves models that do not include evolved trade-off components, constraints, and traits 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 self-organising 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). These findings confirm the presence of repeatable *a priory* given selection pressures, but they do not identify the organising principle (Powell and Mariscal 2015).

In addition to transition theory, on the theoretical side we have neutral forward-looking hypotheses that propose a statistical view, where random diversifying drift, rather than natural selection per se, 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 and major transitions. Random demographic mutations are not fitness 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 no forward-looking self-organising natural selection theory when the population ecological selection of Malthusian relativity was introduced in the mid-1990s to study the part of natural selection that self-organises deterministically from the origin of replicating molecules (Witting 1995, 1997, 2008).

To understand the intrinsic structure of self-organising selection, let us start from the contingent life history theory that studies natural selection mainly by the heredity of genetic alleles with frequency-independent constant relative fitnesses. This corresponds to a type of evolution where the fitness landscape and natural selection remain the same while the different species are selected towards different fitness peaks in the landscape, with each peak acting as a local attractor of natural selection. These landscapes are sometimes seen as seascapes with fitness waves created by changing environments (Mustonen and Lässig 2009); yet baseline seascapes are also not evolving directly from their own selection. The stable landscape is the sufficient metaphor for the present study where the essential arguments are independent of environmental changes.

The density-frequency-dependent selection of the interactive competition among the replicating units in the population, however, selects changes directly in the fitness landscape—and thus also in natural selection itself—as the relative fitness of a variant depends in this case not only on the interactive quality of the variant itself but also on the quality of the other variants in the population, and on the number of competitive encounters among individuals. While intra-specific interactive competition is observed commonly across lifeforms (Hardy and Briffa 2013), neither the contingent life history theory, and nor transition theory, incorporates interactive competition as a dominant component of natural selection. Yet, the fitness landscapes of natural populations are predicted to constantly self-organise their own evolution as they select the average life history and the associated intra-population density-frequency-dependent interactive competition from the selection of net energy for replication (Witting 1997, 2008, 2017b). This mechanism selects not an increase in average fitness but a change in relative fitness due to the constantly evolving fitness landscape. This implies a constantly evolving selection attractor that has the potential to evolve across essentially the complete life history space of the major lifeforms, selecting their life history diversity directly from the life history of their common ancestor. Following the analysis of Malthusian relativity, the deeper self-organising selection of the fitness landscape appears as an intrinsic part of all populations; a part that unfolds from mass, energy, and replication at the origin of replicating molecules, and provides a universal natural selection force that selects the changes in the relative fitnesses of natural selection that are necessary and sufficient to select the metabolism, body masses, life history allometries, and replicating units of the major lifeforms.

The population ecological self-organisation implies a natural selection that is much more than the trial and error of genetic variation entangled in the heredity of asexual and sexual reproduction. This *more* is the universal population ecological processes that follow *a priori* from the origin and actively selects—in a manner somewhat like artificial selection—the evolutionary success of the trial and error of genetic variation. These processes self-organise and alter the selection of the fitness landscape in a predictable way as the life history evolves, with the resulting evolution of the life history attractor explaining the life history diversity of the major lifeforms. As we will see, this selection explicitly predicts the successive co-evolution of the central life history traits of the different lifeforms, predicting an essentially inevitable evolution of large multicellular organisms (Sections 8) with inter-specific allometries (Sections 10) and sexual reproduction by the heredity of a diploid genome with fair meiosis (Sections 9; Witting 1997, 2002, 2008, 2017a,b).

The non-evolving constraints of mass, energy, and replication at the origin of replicating molecules are the initial first principle conditions that make the self-organising selection unfold (Sections 4 & 5). This generates an initial frequency-independent selection of prokaryote-like self-replicating unicells, when the selection of an internal metabolism generates sufficient net energy for replication to outbalance the selection against mass by the quality-quantity trade-off (Sections 6).

To select larger eukaryote-like unicells, natural selection itself must evolve (Sections 7). This happens as the emerging selection of the interactive competition among the replicating units in the population generates an evolving density-frequency-dependent relativity in the intra-population differentiation of the Malthusian parameter (hence the theory-name Malthusian relativity). This selection of eukaryotic-like unicells continues with an increasingly stronger impact from interactive competition, until the selection of metabolism is fully developed and the intra-population resource bias of interactive competition is strong enough to counterbalance the quality-quantity trade-off and select mass on its own.

This generates a new transition where the selection of interactive competition develops into a population dynamic feedback selection that maintains a competitive interaction fixpoint with a stable level of interactive competition, selecting lower-level traits like cells, females, males, offspring workers, and the sexual reproduction sharing of offspring genomes as cooperating entities that enhance the interactive quality of the replicating unit as a whole (Witting 1997, 2002). This process reallocation-selects the selection increase in net energy from replication to multicellular mass (Sections 8), with the selected level of interactive competition selecting sexual reproduction between a female and male (Sections 9), with eusocial colonies selected as a special case when there is no reallocation-selection of net energy from replication to mass. The overall selection of life histories beyond prokaryotes becomes in this way a net energy driven density-frequency-dependent trade-off-balance between population dynamic growth and interactive quality.

The competitive interaction part of Malthusian relativity was developed during a period with a growing recognition of intra-population 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). There was however surprisingly little interest in integrating these interactions into life history theory (Day and Taylor 1996), so I formulated a mathematical density-frequency-dependent population ecological life history theory from the bottom-up unfolding interactions that self-organise from the non-evolving components of the demographic replication structure (Witting 1997). The natural selection of metabolism was incorporated later (Witting 2017a,b) covering transitions from replicating molecules over unicellular prokaryotes to unicellular and multicellular eukaryotes.

Malthusian relativity has so far used the same demographic population ecological model structure across all lifeforms maintaining a consistent mechanistic framework. Natural selection is evidently more diverse and complex than this assumed theoretical baseline, but the baseline captures the essential structural constraints of self-organising selection, constraints that may vary somewhat dependent on the specific conditions of different species. No matter how simple the approach might seem, it is sufficient to predict the macro evolutionary pattern of the major lifeforms independently of trade-off components that are not considered explicitly.

As the major lifeforms are explained independently of the contingent life history theory, Malthusian relativity treats the traditional theoretical backbone—i.e. the evolved demographic trade-offs and constraints—as part of a broader selection that runs implicitly in the background optimising the life history physiology and ecology as a whole by the joint action of the frequency-independent selection of the physiology and the density-frequency-dependent selection of the ecology. Part of this process is included explicitly in Section 13 where I, among others, superimpose contingent life history models on top of the self-organising selection to analyse for the selection of the evolved trade-offs and constraints (Witting 1997, 2008).

The present review follows the mathematical demography where frequency-independent r- and k-selection are the same (Caswell 1989), with both being r-selection at zero abundance and population dynamic equilibrium receptively (where r_{max} and k are ecological estimates of r). I deal with selection at population dynamic equilibrium and refer to r-selection as the frequency-independent selection increase in the Malthusian parameter r, as described by Fisher (1930) when he formulated the fundamental theorem of natural selection (Witting 2000a). This sub-component of natural selection usually operates in combination with the selection of interactive competition. The latter generates a density-frequency-dependent resource distribution across variants that selects for increased interactive quality with a trade-off-imposed decline in r (Witting 2000a). Whether natural selection overall selects an increase, or decline, in r depends on the relative strengths of the two counteracting selection processes.

The formal mathematical deduction of lifeforms from the first principle selection of the demographic replication ecology is described in the original work, with predictions following from the Continuously Stable Strategy (Eshel 1983) selection attractor of an energy-driven density-regulated population dynamic life history model with density-frequency-dependent interactive competition (Witting 1997, 2000a, 2017a,b). This involves theoretical deductions of life history allometries (Witting 1995, 2017a, 2018), major evolutionary transitions (Witting 2002, 2007, 2017b), evolutionary trajectories in the fossil record (Witting 1997, 2018, 2020), and natural selection regulated population dynamics (Witting 1997, 2000b, 2025).

The present paper provides the first verbal review of the entire self-organising selection of the major lifeforms, analysing and discussing the underlying concepts, mechanisms, and processes in relation to traditional hypotheses on the natural selection of life histories and major transitions. This includes extended analyses on the natural selection of molecular replicators (Sections 4 & 5), small asexual unicells (Sections 6 & 7), large multicellular (Sections 8) sexually reproducing (Sections 9) organisms, allometric transitions (Section 10), and fitness (Section 11), including a discussion on the evolutionary maintenance of biological diversity (Section 12) and the historical development of contingent selection theory and its integration with self-organising selection (Section 13).

4 Molecular replicators at the origin

As I review the energetic cause of natural selection, I am not considering issues like the threshold of overcoming a high error rate in molecular replication (Eigen and Schuster 1977). Nor am I describing specific molecular successions for the evolutionary emergence of cooperating genes and phenotypes during the natural selection of a self-replicating cell (for this see e.g. Michod 1983, 1999; Maynard Smith and Szathmáry 1995).

I describe the self-organising natural selection of energy, mass, and life histories from the point of origin of demographic molecules with a positive net rate of replication, i.e. where the gross replication rate exceeds the mortality rate of spontaneous decomposition. For this let molecular replicators at the origin of life use energy (SI unit J)—obtained from organic or inorganic molecules or photons or other sources—for an anabolic replication where smaller organic or inorganic molecules are combined to form a copy of the organic replicator, with the mass (SI unit J) of the replicator being the amount of energy released by a complete decomposition of the replicator to inorganic molecules.

Let total metabolism (SI unit J/s) measure the energy that drives the chemical processes of the replicator per unit time, with mass-specific metabolism (SI unit J/Js = 1/s) measuring the rate/pace of these processes. Metabolism is extrinsic when run by the environment (as for virus) and intrinsic when performed by the replicator (as in prokaryotes), with the term self-replicator referring to the latter.

Let net energy be energy used for replication (SI unit J/s; covering both the anabolic building and metabolism of offspring), with net energy obtained as a product between net resource handling (SI unit J; the adapted traits, skills, physiology, and chemistry that organisms use to subtract net energy from the environment) and the speed of handling defined by metabolic pace (1/s; Witting 2017a). This handling could in-principle create a new replicate in a single handling cycle if it could obtain all necessary building blocks and sufficient energy to add all blocks in parallel at the same time (which would make resource handling proportional to mass). Yet, as this is unrealistic for resources distributed in space and/or time, I assume that the construction of a new replicate requires several resource items obtained independently of one another in a serial resource handling process (which is more like known RNA and DNA replication), assuming pre-evolution invariance between resource handling and mass.

Then, following Michod (1983, 1999) and Maynard Smith and Szathmáry (1995) let there be analogue inheritance initially, where the replicator as a whole is the heritable code that ensures identical copies in replication. Assuming that analogue inheritance can code for very simple replicators only, there is a necessary transition to a digital code (genotype) that codes for a separate life history (phenotype) of enzymes, proteins, metabolic pathways, and more should the replicator evolve into a self-replicating cell. Relating to the energetic cause of such a selection let us first, in line with what we will find, consider a selection that operates on the organised replicator as a whole. As I assume no resource monopolisation from interactive competition at the origin, we have a frequency-independent r-selection that selects the organised self-replicator-level-mutant that replicates fastest. This selects against defecting genes that replicate independently and faster than the organised replicator, as extra energy spent on these mutant genes leads to a decline in organised replication. Operating on the organised replicator as a whole, this selects for complete cooperation among genes allowing for the evolution of a fully linked genome.

This selection of cooperating genes provides the best starting point for the evolution of self-replicating cells like prokaryotes, but gene cooperation is not sufficient. The main issue is the energetic quality-quantity trade-off that selects against the extra mass of an increasingly organised self-replicator. The selection of the unicellular self-replicator depends first-of-all on a necessary replication enhancing factor that outweighs the replication cost of the quality-quantity trade-off, with mass-specific metabolism selected as the pace of replication solving the problem (Witting 2017b).

It is costly to burn energy in metabolism, and an internal metabolism is selected only if it increases the pace of replication by enhancing the amount of net energy available for replication per unit mass. With no resource handling or internal metabolism at the origin, we expect an initial selection of a metabolic pace that operates on local resources obtained passively through diffusion or a flowing medium (with the selection of organised resource handling behaviour coming later). This initial selection of metabolic pace comes with the joint mass of the selected cooperating metabolic pathways, enzymes, proteins, structures, and genes necessary to sustain the selected self-replicator, and this makes the potentially selected rate of metabolic replication functionally dependent on the mass of the replicator.

To analyse for a common functional form of the mass dependence of the replication selected metabolism we note—as Witting (2017b) and illustrated in Fig 3—that for a given metabolic pace the quality-quantity trade-off selects the smallest mass that can sustain that metabolism, and for a given replicator mass the increased replication of increased pace selects the fastest metabolic pace that can potentially be sustained by that mass. This joint selection provides a metabolic pathway specific boundary curve that describes the upper metabolic surface of the potentially selected trait space of mass-specific metabolism and mass, with evolution by natural selection expected to occur in either direction along this boundary, dependent on the overall selection (Fig. 3).

Although the boundary curve depends on the selected metabolic pathways and type of free energy utilised, we can expect a general functional form as the boundary reflects the optimal design of a potentially metabolising self-replicating entity. Initially for the smallest replicator at the origin, we expect a rather steep return in the maximum potentially obtained mass-specific metabolism per unit increase in mass, reflecting an optimising selection that targets the most rewarding metabolic solutions per unit mass involving, among others, enzymes that catalyse and speed up the replication process greatly. With increased size we expect a diminishing return as the best catalysing enzymes are already in place, the structure of the replicator increases in organisation and energy demand, and the replicator uses resources—supplied over the surface area—by volume and mass. This provides a boundary curve where the allometric exponent of mass-specific metabolism (i.e., the local slope of the boundary curve on double-logarithmic scale) declines from some positive value towards zero, and likely continuing to negative values, for an increasingly larger self-replicator.

Having described the expected functional relationship between mass and the return in internal metabolism of a potentially selected self-replicator, we may examine the conditions required for the natural selection of self-replicating cells. But let us first analyse the outcome for metabolic pathways where the potential metabolic return per unit mass is insufficient for the natural selection of metabolism and mass.

5 Zero-energy replicators, like virus

If the initial metabolic return from mass along the boundary curve is weaker than proportional to mass, the increased net energy of increased metabolism cannot counterbalance the proportional downward selection of the quality-quantity trade-off, as imposed by the mass of the replicator. This means selection against intrinsic metabolism (Fig. 3, left plot, right half), with replicator selection for exposed non-cellular genes that copy as fast as possible by the extrinsic metabolism of the environment. As these replicators have no internal metabolism, they are essentially zero-energy replicators with no phenotype.

To understand where this evolution ends, we extend the selected boundary curve between mass and metabolism to include extrinsic metabolism (Fig. 3, left plot, left half), where the boundary can evolve no further than the metabolic potential of the environment. This relates to a replicator that is metabolically optimal in the sense of utilising the metabolism of the environment per unit replicator mass, and this refers to the place on the boundary curve where the allomet-

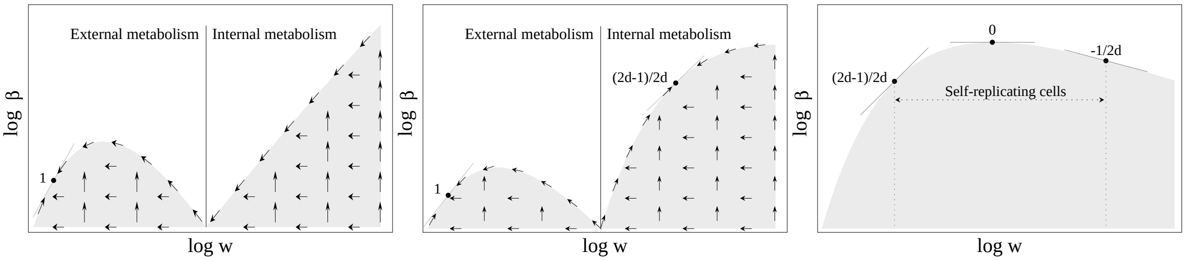

Figure 3: **The initial selection of mass-specific metabolism (β) and mass (w).** The grey area is the potential life history space, vertical and horizontal arrows the partial selection of increased metabolism for a given mass and minimum mass for a given metabolism, with the upper boundary curve being the selected mass dependent maximum mass-specific metabolism of the metabolic pathways under selection (Section 4). **Left:** A weaker than proportional initial return in internal metabolism along the boundary curve selects a molecular replicator with external metabolism (solid circle) that scales with an exponent around unity due to a selection balance between the quality-quantity trade-off and net energy generated by the extrinsic metabolic pace (Section 5). **Middle:** Given a stronger than proportional initial return, there is disruptive selection for replicators with external metabolism and prokaryote-like self-replicating cells with internal metabolism and a primary selected allometric exponent of unity (not shown, Section 6) that rescales to $(2d-1)/2d$ (shown) due to the mass-rescaling selection of Section 10 (d:spatial dimensionality of home range packing). **Right:** The gradually unfolding density-frequency-dependent interactive competition selects eukaryote-like self-replicating unicells, covering the size-range where the primary selected exponent of mass-specific metabolism declines from unity to zero (not shown, Section 7), having a mass-rescaling realised exponent from $(2d-1)/2d$ to $-1/2d$. Interpretated from Witting (2017b).

ric exponent is zero. For replicator masses below this point we expect an accelerating decline in the upper limit of mass-specific metabolism as mass declines towards the smallest molecules that are capable of replicating by extrinsic metabolism. This implies an allometric exponent that continues to increase with a decline in mass. For masses that are larger than the metabolic optimum, we expect a decline in the exponent as the total metabolic cost to the local environment around the replicator increases with an increase in mass. This gives the left boundary curve in the left plot in Fig. 3, where the quality-quantity trade-off selects for a decline in mass until the selection of the trade-off is neutralised by a proportional return in extrinsic mass-specific metabolism. The result is a replicator that selects both mass and extrinsic metabolism to smaller values than at the metabolic optimum of the external environment.

Where the left plot in Fig. 3 illustrates a case with directional selection towards extrinsic metabolism, the middle plot illustrates disruptive selection for internal and external metabolism dependent upon the initial position on the boundary curve. The mass space for internal and extrinsic metabolism has no overlap in these plots for illustrative purposes. Yet there may be cases with overlap and replicators that use both types of metabolism.

This selection of replicators with external metabolism depends on the existence of a sufficiently efficient external metabolism. If the external metabolism is insufficient, the generation of new replicates cannot outweigh the mortality of spontaneous decomposition. Absolute fitness is then always negative, and any spontaneously generated population goes extinct almost immediately. The apparent absence of well-established populations of inert molecular replicators apart from virus may indicate that the required physical/chemical conditions for these populations no longer exists, if they were ever available, on Earth. The exception is virus that are special zero-energy replicators selected by the efficient metabolism of cells.

6 Metabolising self-replicating unicells, like prokaryotes

When the initial return in mass-specific metabolism along the boundary curve is stronger than a proportional increase with mass, the increased pace of replication is stronger than the replication trade-off from mass, inducing selection for a self-replicator with intrinsic metabolism (Fig. 3, middle plot, right half; Witting 2017b). This metabolic selection of mass stops when the diminishing metabolic return has declined to the proportional return that is counterbalanced by the replication cost of mass.

While small self-replicators with low levels of internal metabolism might evolve independently of the development of a metabolic compartment like a cell, there is general agreement that a self-replicator with an advanced form of internal metabolism depends on a cell-like structure where the metabolic pathways, catalysing enzymes, and other metabolites concentrate (e.g., Oparin 1957; Miller and Orgel 1974; Maynard Smith and Szathmáry 1995; Michod 1999; Wächtershäuser 2000; Koch and Silver 2005). Following this logic, it is the replication selected increase in mass-specific metabolism and mass that organises the evolution of the self-replicating cell including not only the metabolic pathways themselves, but also the cell membrane and digital code of cooperating genes. The evolution of the cell and all its mass and structures becomes in this way naturally selected by a selection that operates at the level of organised metabolic replication during the whole transition from molecular replicators to self-replicating unicells.

Now recall that this evolution of a metabolising replicating compartment occurs along the boundary curve of a minimum mass that allows for the evolution of a given mass-specific metabolism, and the maximum selected mass-specific metabolism of a given mass. This dual selection implies self-replicators with the minimum mass necessary for the mechanistic functioning of the selected metabolic replication. Smaller cells cannot sustain the selected metabolism, and the quality-quantity trade-off selects larger mutant cells with the same mass-specific metabolism back to the metabolism-dependent minimum mass.

But is this prediction necessarily a unicellular self-replicator, as we may expect multicellularity when cooperation at the multicellular level trade-off fitness at the unicellular level (Buss 1987; Michod 1996, 1997, 1999; Michod and Roze 2001). Yet, if a selected unicell mutates to a completely cooperating double-cellular replicator it would double in mass and replication fitness consequently halves given the same availability of net energy. The unicell could though mutate to a double-cell with the same overall mass to avoid the cost of the quality-quantity trade-off. But with the metabolic compartment being the cell, the reduced cellular mass would then, due to the selected proportional metabolic return approximately halves metabolic pace, with the associated decline in replication selecting against the double-cellular self-replicator. So even with complete cooperation among cells and no defection, there is an initial two-fold cost to multicellularity that the metabolic selection cannot pass because the selected boundary curve links the metabolism and mass of the selected cell.

But how similar are the predicted life histories to those of prokaryotes? The predicted proportional relation between mass-specific metabolism and mass with an allometric exponents of unity, e.g., is not far from an empirically estimated exponent around 0.84 for heterotrophic prokaryotes (DeLong et al. 2010). The predicted exponent of unity, however, does not account for the metabolism of offspring mass that induces a mass-rescaling selection that adjusts the prediction down to a theoretical value of 0.83 (see Section 10 for details). Prokaryotes are also, in agreement with a frequency-independent r-selection, the only mobile cellular lifeform with a positive inter-specific correlation between body mass and the Malthusian parameter r (DeLong et al. 2010; Lynch and Marinov 2015). And the pure metabolic selection considered here involves passive resource handling, as seen in most prokaryotes where the rigid cell-wall makes active resource handling extremely difficult if not impossible.

We are thus predicting prokaryote-like self-replicating unicells as the selection attractors of pure metabolism-driven replication selection (Witting 2017b). This suggests that prokaryotes evolved as self-replicating metabolic compartments at the evolutionary endpoints of a frequency-independent selection with no resource bias from interactive competition. Their evolutionary diversity should then primarily reflect the exploitation of a wide range of resources by a variety of metabolic pathways.

7 Interacting self-replicating unicells, like unicellular eukaryotes

Having a selected proportional metabolic return per unit mass, we expect from the mass dependent boundary curve that prokaryotes are so small that it should be biochemically possible to artificially select larger unicells with an increased metabolic efficiency per unit mass. Our model does currently not support this evolution for natural selection, but is it possible for natural selection to select a change in the selection pressure and select maximum metabolic efficiency by selecting a unicellular self-replicator that is so large that the primary selected metabolic return per unit selected mass along the boundary curve is zero? With eukaryotic cells being about $15,000$ times larger than prokaryotes on average (Lane 2017), might unicellular eukaryotes have evolved to explore this extra metabolic space?

This possibility seems at first to agree with the symbiogenesis-driven prokaryote-eukaryote transition hypothesis that suggests that it is a surplus of energy generated by the mitochondria that explains the evolution of the larger, more complex eukaryotic cell (Lane and Martin 2010; Lane 2015, 2017, 2019; Arcas 2025a,b). A main evolutionary feature of the prokaryote-eukaryote transition is the evolutionary embedding of a prokaryote-like compartment as the metabolising mitochondria of the self-replicating unicellular eukaryote. Compared with prokaryotes, the mitochondria are more metabolically specialised in ATP synthesis from assimilated resources, reflecting an energetic optimisation with a restricted number of specialised genes maintained in the mitochondria, allowing energy to be allocated from gene replication to the evolution of larger, more complex cells (Lane 2017).

These mitochondria supply far more energy to the unicellular eukaryote than the cell-membrane embedded APT synthesis of prokaryotes (Lane 2017). But when corrected for the replication cost of mass, the observed mitochondria-driven rate of eukaryotic replication declines with an increase in mass (DeLong et al. 2010; Lynch and Marinov 2015, 2017). This contradicts the symbiogenesis transition hypothesis that requires the mitochondria to generate so much extra energy that they outbalance the replication cost of mass selecting larger and faster self-replicating eukaryotic cells. The empirical result, however, aligns with our theoretical prediction from the boundary curve, where we need a change in the mechanism of selection because metabolism driven net-energy replication cannot by itself select the mass and metabolism of unicells further than our predicted prokaryote-like self-replicator.

To identify this selection of a change in selection we recall that metabolic pace is one of two subcomponents needed for the generation of net energy, and we have so far ignored the other resource handling subcomponent (by assuming passive handling) because it requires a more advanced evolution of behaviour at the cellular level. The continued replication selection for more net energy, however, continues to select for active resource handling. This selects against the rigid cell-wall of protozoa to allow for behavioural changes in cell shape, assisted by e.g. the selection of some sort of internal stabilising skeleton that enables energy driven behaviour. The cytoskeleton and engulfing of resource particles by the phagocytosis of eukaryotic unicells is an obvious phenotypic solution to the selection of active resource handling. And with resources appearing internally in the cell, instead of diffusing through the cell-wall, and the cell membrane being the boundary to the environment that performs behaviour, the movement of ATP synthesis from the cell membrane to optimised internal metabolic compartments like mitochondria seems to be another obvious phenotypic solution, let the metabolic compartments originate either from the engulfing of a metabolising prokaryote (Sagan 1967; Martin 2017), and/or from a gradual selection of metabolic processes from the cell membrane to the interior.

While this selection restructuring of the unicellular phenotype to cope with active resource handling generates extra net energy, the observed decline in replication with increased mass (DeLong et al. 2010; Lynch and Marinov 2015, 2017) shows that it does not generate sufficient extra energy on top of the energy generated by metabolism to select the evolved mass against the replication cost of mass. Yet, given sustained natural selection, the selection of extra mass with a decline in the rate of replication is eventually expected from the selected net energy driven population dynamic growth and resulting increase in abundance and number of encounters between the individuals in the population.

This population dynamic pressure makes interactive competition an emerging process that changes the selection pressure on mass, as intra-specific interference selects behaviour and mass as interactive quality, generating a resource gradient in favour of the competitively superior larger-than-average individuals (Witting 2017b). These monopolise resources during competitive encounters, and this seems to hold even for passive behaviour where larger cells have more kinetic inertia than smaller cells and thus a larger probability of winning a competitive encounter. These density-dependent interactions lead to a density-frequency-dependent interactive selection, where the relative fitness of a variant depends on the net energy driven density of individuals in the population and their interactive qualities relative to the quality of the variant.

The interactive competition is unable to counterbalance the replication cost of mass, and thus unable to select mass on its own, as long as the resource gradient of interactive competition across the variants in the population is weaker than a proportional increase with mass. But, in combination with the remaining proportional metabolic return along the boundary curve, the initial resource gradient of interactive competition needs only to marginally exceed zero to select extra mass partially as mass-of-additional-metabolism and partially as interactive quality (Witting 2017b).

As this joint selection of extra mass depends on a selection increase in net energy, and as the relative importance of the primary selected increase in metabolic pace for the selection of net energy declines with the diminishing return along the boundary curve, there is a gradual transition where the selection of resource handling and interactive competition becomes increasingly important for the selection of net energy and larger interacting unicells. This selection continues until the selection of resource handling selects all new net energy, and there is no additional metabolic return because the metabolic pathways are selected maximally efficient per unit mass (Fig. 3, right). As this gradual selection transition depends on the metabolic return along the boundary curve, it selects the minimum mass necessary for the mechanistic functioning of the unicellular self-replicating metabolic compartment, and this selects actively against multicellular organisms as discussed in Section 6.

This selection predicts eukaryotic-like unicells as a diverse group that covers a large life history spectrum across a selected continuum where the fractional importance of resource handling for the selection of net energy increases from zero to unity, as the resource gradient of interactive competition across the intra-population variation in mass increases from zero to unity, and the metabolic return of the selected mass declines from unity to zero, with a predicted decline in the allometric scaling of metabolism and replication (Witting 2017a) supported by the allometric correlations in protozoa (Section 10). This selection evolves into a new major restructuring at the point where the resource gradient of interactive competition exceeds unity, generating a major transition in the selection attractor that selects living organisms beyond eukaryote-like unicells.

8 Large multicellular organisms

When the resource gradient of interactive competition—due to the selection increase in net energy, population growth, density-dependent interactions, 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 on its own at the cost of an otherwise continued selection increase in the growth, abundance, and interference competition of the population (Witting 1997, 2008, 2017b). The outcome, illustrated by the outer loop in Fig. 4, is a density-frequency-dependent population dynamic feedback selection with an emergent selection attractor of invariant interactive competition that reallocation-selects the selected net energy from replication to mass.

The emerging selection attractor operates as a competitive interaction fix-point that selects the invariant level of intra-specific interference that is necessary to maintain the proportional resource gradient that counterbalances the quality-quantity trade-off, selecting body mass in proportion to net energy. This allows for a continued selection increase in mass from the selection increase in net energy, with the increase in mass following—not from the increase in energy itself but—from the frequency-dependent interactive competition that selects mass as interactive quality. The selection involves the quality-quantity trade-off that imposes a decline in the rate of replication as energy is reallocation-selected from replication to mass. Yet the selected decline in replication is counterbalanced by the underlying selection increase in net energy for replication, with the joint selection of energy and mass maintaining invariant replication on the per generation timescale of natural selection. The extra

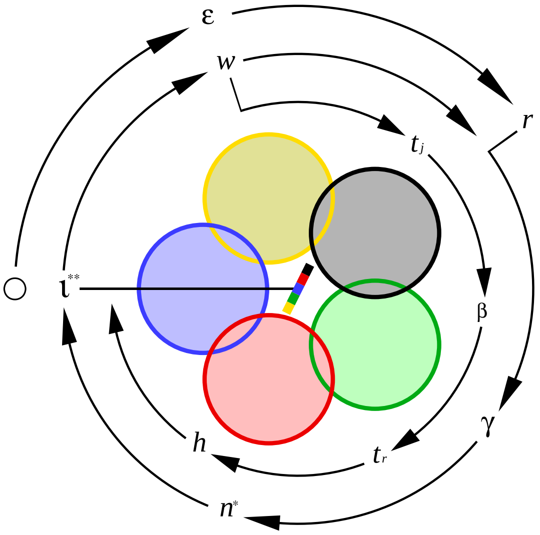

Figure 4: **Feedback selection diagram.** The small circle to the left represents replication selection for an exponential increase in net energy (ϵ) that maintains population growth (r) and a continued feedback selection of mass (outer feedback loop, see Section 8), with a steady state attractor ($**$) 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 multi-coloured 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 10) that selects the exponents of the body mass allometries from the ecophysiological constraints between the pace of foraging and the spatial packing of home ranges (see Fig. 6 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).

metabolism of the added offspring mass, however, generates an allometric mass-rescaling selection that dilates the timescale of natural selection to maintain the net energy driven replication during the selection of mass (Witting 2017a; inner loop in Fig. 4; see Section 10 for details), and this transforms the body mass invariant per-generation replication into a selected 1/4-power decline in the Malthusian parameter when measured in physical time, as reported empirically by Fenchel in 1974.

Dependent on the evolutionary ecology, the competitive interaction fix-point may select an equilibrium or steady state life history attractor (Fig. 5; Witting 1997, 2002, 2020). The equilibrium selects a stable body mass when the selection of net energy is temporarily constrained, e.g. by a resource handling that is selected to be fully optimised given the currently exploited resources of a species. The steady state follows instead from an unconstrained exponential selection of resource handling and net energy that generates the somewhat higher level of interactive competition that is necessary to constantly reallocation-select the exponential increase in net energy into an exponential increase in mass on the per-generation timescale of natural selection (Witting 1997, 2020). There is also a special case where the selection of mass is constrained and the increase in net energy is not reallocation-selected into an increase in mass, generating an extreme increase in abundance and interactive competition.

The competitive interaction fix-point may not only reallocation-select energy from replication to mass, but also temporarily from mass to replication, as the attractor buffers environmental changes and inter-specific interactions by adjusting the selected mass and life history to changes in the available resources and average survival of individuals, while selecting the invariant level of interference competition in the population (Witting 1997).

As the density-frequency-dependence of the population dynamic feedback selects mass beyond the boundary curve of Fig. 3, it is no longer possible to select an increase in metabolic pace, with interactive competition selecting mass independently of metabolism. This implies that there is no longer an unpassable two-fold cost of multicellularity imposed by the selection of the minimum mass needed for the mechanistic metabolic functioning of the unicellular replicator. This allows for the selection of multicellularity as a higher-level selection cooperative trait (Buss 1987; Maynard Smith and Szathmáry 1995; Michod 1999; Witting 2017b) that may not only be selected to obtain a more flexible and organised interactive resource handling behaviour but also to maintain the metabolic pace of the organism, as larger unicells may constrain metabolic efficiency.

9 Sexually reproducing organisms

A main feature of the lifeform transition from unicells to multicellular organisms is the additional transition from asexual to sexual reproduction. Explanations for the evolution of sex have traditionally been gene centric, with sex defined by the transfer of genes between individuals, including everything from the vertical gene transfer of sexual reproduction where a haploid copy of the diploid genome is transferred from both the mother and farther to the offspring, to the symbiogenesis of lateral transfer where e.g. a prokaryotic cell, independently of replication, incorporates genes that are either transferred from another prokaryotic cell or picked up from free genes in the environment. Defined in this way, there is no obvious sexual transition as all self-replicating lifeforms include one or several forms of sexual gene transfer that may not even have an obvious cost of sex. But when we focus on sexual reproduction there is a well-define transition where prokaryotes have asexual reproduction, most mobile multicellular eukaryotes have obligatory sexual reproduction, and eukaryotic unicells are in-between with sexual life-stages confirmed for about 20% of the studied species (Rizos et al. 2024).

While neither logically, or empirically (e.g. Raikov 1982; Verma and Ruttner 1983; Canning 1988), necessary for the sexual transfer of genes between individuals, associated with its evolution there has in nearly all species been the evolution of gene mixing by recombination and chromosomal segregation. The gene centric view uses this evolutionary cooccurrence to explain the evolution of sexual gene transfer by a positive symbiogenesis of gene mixing which may provide a long-term advantage when compared to lineages with no mixing. Recombinatory gene mixing may protect against the accumulation of deleterious mutations by Muller's ratchet (Fisher 1930; Muller 1932, 1964; Crow and Kimura 1965; Kondrashov 1982, 1993), either by segregation that breaks up genetic associations within a locus (Otto 2003; Dolgin and Otto 2003) or because it prevents deleterious mutations from hitchhiking the selection of rare beneficial mutants (Manning and Thompson 1984; Rice 1987). Recombination may also bring together gene sequences in a favourable symbiogenesis (Weismann 1889; Kodric-Brown and Brown 1987; Kondrashov and Kondrashov 2001), with the Red Queen hypothesis suggesting that the diploid genome may hide gene combinations that currently are bad, and expose them later by

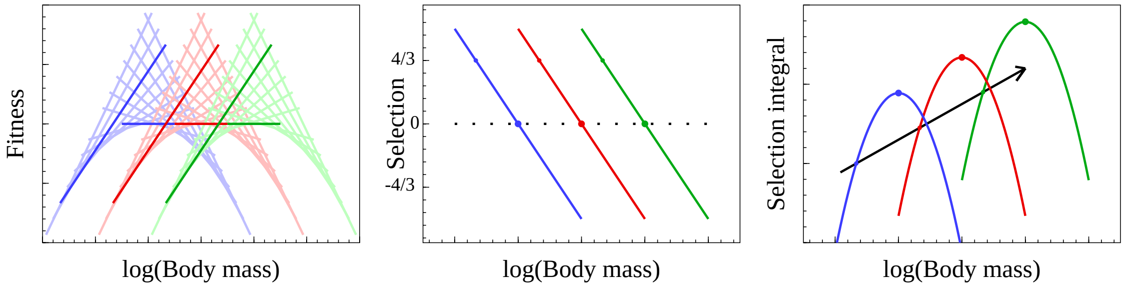

Figure 5: **Population dynamic feedback selection of mass.** To visualise the selection attractor of the density-frequency-dependent population dynamic feedback selection of mass we calculate the selection integral from the predicted evolution of the fitness landscape (Witting, 1997): **Left:** Each line is the intra-population variation in fitness (fitness landscape) for different average body masses, with the three colours (blue, red, green) representing different levels of net energy. Bold horizontal landscapes are for masses in evolutionary equilibrium (constant net energy), and bold increasing landscapes for time-specific steady state attractors with exponentially selected net energy and mass. **Middle:** Selection gradients are the local slope of the fitness landscape around the average mass of the population, shown here as a function of average mass across a potential range of populations. Zero dots are equilibrium attractors of stable net energy, and 4/3 dots the steady state attractors for a two-dimensional packing of home ranges. **Right:** Selection integrals are selection gradients integrated across the potential range of average body masses. Integral optima are equilibrium attractors, and the arrow is steady state evolution with its intercepts with the left part of the integrals being the time-specific steady state attractors. From Witting (2017b). See Sections 8 and 11 for details.

recombination when they become beneficial e.g. for protection against mutant parasites (Hamilton 1980; Bell and Maynard Smith 1987; Hamilton et al. 1990).

The common selection mechanism of these hypotheses is that gene mixing increases the future genetic variance among offspring allowing for a potentially faster adaptation to the environment. The increased future variance provides no immediate fitness advantage and no immediate selection, but it may nevertheless allow for a statistically faster future adaptation (e.g. Otto 2009, 2021; Roze 2012). This requires selection away from equilibrium (Feldman et al. 1997) on a subset of potentially negatively curved fitness surfaces (Charlesworth 1993; Otto and Barton 1997) and/or additional factors like environmental changes in space (Pylkov et al. 1998; Agrawal 2009) and time (Peters and Lively 1999; Gandon and Otto 2007), and/or individual variability (Redfield 1988; Hadany and Beker 2003), and/or genetic drift (Felsenstein and Yokoyama 1976; Martin et al. 2006; Roze and Barton 2006). Combinations of these factors can allow for the evolution of a low frequency of sex especially in the absence of a cost to sex (Otto 2009, 2021; Roze 2012), but they do not explain the evolution of frequent and obligatory sexual reproduction, and nor do they provide an immediate fitness advantage that outbalance the costs of sex.

Transition theory indicates that the immediate selective advantage of sexual reproduction comes from individuals that cooperate to trade-off the costs of sex at the gene and individual level against increased fitness for the sexually reproducing unit as a whole (Maynard Smith and Szathmáry 1995; Witting 1997, 2002; Michod 1999). From this life history centric point of view there is at minimum a two-fold cost to sexual reproduction between a female and male, with an apparent six-fold cost in at least many species of mammals and birds. The cost paid by a sexually reproducing male-female pair is up to six-fold because we may need to add the two-fold cost of sharing a common resource (cost of group size), with the two-fold cost of evolving a non-replicating individual (cost of male), and the two-fold cost of halving the probability that a gene is copied to an offspring (cost of meiosis).

It is the combination of the replicating group size, its division in replicating and non-replicating individuals, and individual probability of transferring a gene to an offspring, that defines the reproducing unit, with the sexually reproducing pair being the only solution—out of an essentially infinite number of potential possibilities—with a two-fold cost associated with each of the three traits (Witting 1997, 2002). Cases with smaller costs include unicellular eucaryotes with infrequent sexual reproduction and multicellular species with female biased sex ratios, and cases with larger costs include cooperative breeding where a small number of offspring help the sexually reproducing pair, and eusocial colonies like ants, bees, and termites.

The three traits that define the replicating unit are all exposed to the selection pressure of interactive competition. Larger groups can be selected to dominate smaller groups, non-replicating individuals can be selected to use energy on interactive quality instead of replication, and a replicating individual can be selected to use the probability of sexual gene transfer to attract high-quality interacting individuals, mediating the risk of defection to maintain the cooperating integrity of the reproducing unit as a whole. The level to which each of these three traits evolve depends on the level of interactive competition, with higher levels of interference being able to counterbalance larger costs selecting for larger groups that contain more-and-more interacting individuals (Witting 1997, 2002).

The level of interference competition selected by the selection attractor for the evolution of mass is therefore determining the fitness differential for the natural selection of the reproducing unit. When inserted into the selection equations of the reproducing unit, the population dynamic feedback selected interference of a multicellular body mass in evolutionary equilibrium counterbalances the two-fold costs of each of the three traits precisely (Witting 1997, 2002), selecting pairwise sexual reproduction between a female and male, with diploid inheritance and fair meiosis selected as the phenotypic solution that maintains the cooperative integrity of the interacting replicating unit. On top of this we have the predicted absence of interactive resource handling in our predicted prokaryote-like unicells that selects for asexual reproduction, and the continuum of a gradually increasing level of interference competition in our predicted eukaryote-like unicells that selects for lower levels of sexual reproduction. And having explained the sexual reproduction transfer of genes between individuals, genetic recombination may evolve with almost no costs by speeding up the rate of adaptation.

Dependent upon the selected feedback attractor of mass, the selected interactive competition may select larger reproducing units also (Witting 1997, 2002): The unconstrained steady state attractor with an exponential selection of net energy, e.g., stabilises at a higher level of interference that selects cooperative reproduction and a body mass that increases exponentially over time. This continuum selects eusocial colonies as the extreme interacting unit, when the selection increase in net energy does not reallocation-select into an increase in mass, generating extreme intra-specific interference.

The selection of cooperatively and eusocially reproducing units allows 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. 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 sexually produced non-reproducing offspring worker, to the interacting unit. This return is only sufficiently strong to select the first added male, selecting pairwise sexual reproduction and sexually produced non-reproducing offspring workers (Witting 2002, 2008) where the inclusive fitness (Hamilton 1964) of the underlying relatedness maintains the cooperative integrity of the interacting replicating unit.

The ecological constraints on the interactive competition of these sexually reproducing units select other life history patterns as well. The predicted competitive cooperation in mobile sexual organisms—where males compete for resources for the replication of females—selects for a male choice against asexually replicating females. This isolates the across-generation replication of genes in a germ-line with the non-replicating soma performing the ecological tasks of the organism, exposing individuals to the selection of senescence (Williams 1957; Hamilton 1966).

The possibility for cooperative competition vanishes in sessile organisms that compete for positions in a flowing medium of resources, where cooperate interactive behaviour is essentially impossible as males that aim to compete for a female end up shading for her flow of resources (Witting 1997, 2002). This selects against replicating units of competitively cooperating sessile individuals inducing selection for hermaphrodites that avoid the two-fold cost of males and meiosis. The resulting absence of a male mate choice allows for the evolution of asexual replication in sexual sessile organisms weakening the selection of senescence. It is also intriguing that parthenogenesis in wild animals occurs only in poikilotherm taxa like insects and reptiles that, due to their restricted control of metabolic pace, are in less control of their population growth determined interactive ecology than homeotherm taxa like birds and mammals.

The selection of net energy for replication predicts in this way a self-organising natural selection of increasingly larger lifeforms with an increasingly embedded across-generation replication of genes (Fig. 2). This embedding reflects a series of hierarchically structured natural selection transitions (Hull 1980; Buss 1987; Brandon 1988; Michod 1999) where cooperating "entities"—like genes, cells, multicellular individuals, and offspring—"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). While it is the hereditary variation of lower-level mutants that generates the variation in the higher-level cooperating interactors, it is the self-organising selection of the ecological interactions in the population that selects among the available replicating units, determining the higher-level selection that selects the major evolutionary transitions forwardly.

Behind the predicted succession of the major transitions lies an evolutionary continuum where the selected variation in metabolism, net energy, and mass selects inter-specific life history variation. This continuum is described by the body mass allometries, with the next essential question being whether the self-organising selection predicts also the observed allometric scaling across lifeforms from prokaryotes to mammals.

10 Allometric scaling

The inter-specific body mass allometries describe the life history and other traits of organisms as linear functions of body mass on double logarithmic scale, with the slope of the lines being the exponent, or power, of the underlying power function on ordinary scale. The best known allometry is Kleiber (1932) scaling where a 3/4 exponent describes the relationship between total metabolism and mass in animals. Yet, there are empirical allometries for most life history traits, and the exponent of each trait tends to change with the scale of observation (e.g., Peters 1983; Calder 1984).

Following Rubner (1883), the body mass scaling of metabolism has traditionally been seen to follow from physiological trade-offs with a multitude of hypotheses being developed over the last 30 years (see e.g., Kozlowski and Weiner 1997; West et al. 1997; Banavar et al. 2002; Darveau et al. 2002; Demetrius 2003; Fujiwara 2003; Makarieva et al. 2003; Glazier 2010). Most of the physiological trade-offs have components that evolve by natural selection, and from an evolutionary point of view we expect that the scaling exponents of life history traits like metabolism follow from the natural selection of mass and the trait itself, with the natural selection of the whole life history adjusting the physiological trade-offs to match the naturally selected scaling (Witting 1998). The physiological scaling hypotheses however pay essentially no attention to how it is possible to naturally select metabolism and mass and consequently their observed inter-specific evolutionary relationship. While neglecting analyses on the demographic natural selection cause of allometric scaling, the physiological hypotheses document a large degree of coevolutionary adaptation between the physiology and the naturally selected scaling.

Two papers 22 years apart deduce the natural selection of the allometric scaling exponents from the self-organising natural selection of metabolism, net energy, and mass (Witting 1995, 2017a). Inter-specific allometries are usually studied across current species, yet allometric selection is first-of-all about the naturally selected changes in life histories within individual evolutionary lineages when the mass of a species evolves over time, with different lineages being selected to diversify from their common ancestor by the selection of inter-specific variation in net energy. The allometric selection describes how much extra mass that is naturally selected from a given selection increase in net energy, and how this selection selects changes in the other life history and ecological traits. Apart from being an approximation for the natural selection of the inter-specific life history diversity across current species (Witting 2017a, 2023), this selection analysis can be applied to body mass trajectories in the fossil record to estimate details of the underlying life history selection (Witting 2020), and used to simulate the diversification of evolutionary lineages over millions of years to estimate the underlying selection details of log-linear deviations in current inter-specific allometries (Witting 2018).

The self-organising selection of allometric scaling follows from the interplay between the non-evolving trade-off components of the demography and the spatial constraints on the ecological foraging of the individuals in the population. These constraints limit the trait space of possible life history solutions available to natural selection when it selects mass from net energy obtained in ecological foraging.

This natural selection of mass involves a mass-rescaling selection (Fig. 4, inner loop) that compensates for a reduced rate of replication that is imposed when natural selection attempts to select larger individuals with larger offspring that metabolise extra net energy that would otherwise be used for replication (Witting 2017a). This trade-off selects a metabolic decline that maintains the size determined rate of replication during the selection of mass. The selected downscaling of metabolism, however, reduces the pace of foraging and thus the assimilated net energy. This trade-off is then selecting a co-occurring inverse scaling between metabolic pace and life periods that maintains the foraging pace and resulting net energy driven replication on the per-generation timescale of natural selection. Mass-rescaling selection is in this way dilating the timescale of natural selection to maintain the selected life history, net energy, and replication during the selection of mass.

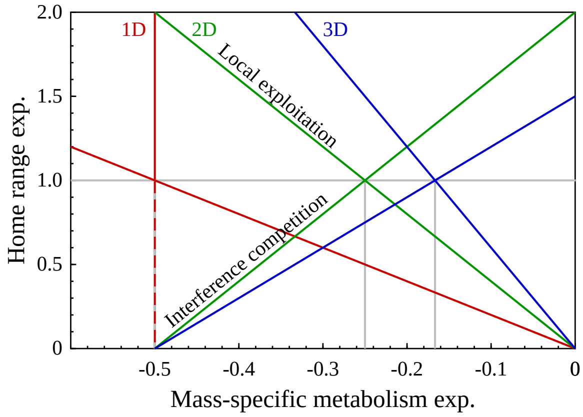

Figure 6: **Deduction of mass-rescaling allometries.** The selection of mass (w) selects a mass-rescaling decline in mass-specific metabolism (β) that dilates natural selection time to maintain net energy and replication during the selection of mass (Witting 2017a; Section 10). This reduces the pace of foraging affecting the ecological trade-off between the cost of local exploitation and interference competition, and this determines the spatial packing of home ranges (h) with $\log h \propto -2d \log \beta$ and $\log h \propto d(\log w + 2 \log \beta)/(d-1)$ describing the allometric constraints on local exploitation and the cost of interference (Witting, 1995, 2023; $d \in \{1, 2, 3\}$: spatial dimension of home range packing). The plot solves the corresponding $\hat{h} = -2d\hat{\beta}$ and $\hat{h} = d(1+2\hat{\beta})/(d-1)$ equations [with $\beta \propto w^{\hat{\beta}}$ & $h \propto w^{\hat{h}}$] 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 spatial packing of home ranges. From Witting (2023).

The trait-space imposed by these metabolic trade-offs of demographic replication is limited further as natural selection rescales the spatial packing of home ranges to maintain the amount of net energy obtained in foraging (Witting 1995). The metabolic pace of interactive competition selects for small home ranges with little overlap to minimize the cost of competition, but small home ranges have increased local exploitation, and this tension selects the spatial packing of home ranges. When formulated mathematically we can condense these joint constraints down to two equations that describe the allometric constraints between metabolic pace, home range, and mass at the lowest combined cost of local exploitation and interactive competition at the foraging optimum (see Witting 1995, 2017a, 2023 for details). When the two equations are solved (Fig. 6) they constrain the selected trait space to 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 (1D, 2D, 3D), with additional exponents predicted for life periods, abundance, and the Malthusian parameter (which are 1/4, −3/4, & −1/4 in 2D).

These predictions are generally supported by the inter-specific allometries of animals (Witting 1995, 2017a), providing consistency between the net energy driven self-organising density-frequency-dependent selection of mass and the observed negative scaling of the Malthusian parameter (Fenchel 1974) and abundance (Damuth 1981, 1987). The predicted spatial dimensionality transition from 1/4 to 1/6 between 2D and 3D is supported by e.g. an empirical lifespan exponent that changes from 0.25 ± 0.04 to 0.16 ± 0.02 between terrestrial and pelagic mammals (Witting 1995).

The obtained 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 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 theoretically 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 empirical exponent that declines from 0.61 among the smallest, over zero in intermediate, to -0.20 among the largest protozoa (Fig. 1, bottom; Witting 2017a,b).

To analyse the selection of allometries further let us turn to the selection of body mass over time where the selection attractor of the evolutionary steady state predicts an exponential increase in net energy and mass on the per generation timescale of natural selection, i.e. a linear trajectory when log mass is plotted as a function of time. If this log-linear trajectory is converted to physical time by a correction for the mass-rescaling dilation of natural selection time, it scales into a decelerating downward bending evolutionary trajectory as illustrated by the upper trajectory in the left plot in Fig. 7.

But the natural selection of allometries is more entangled than this because the mass-rescaling decline in metabolism allows for a net energy driven reselection of metabolism lost in mass-rescaling, a process

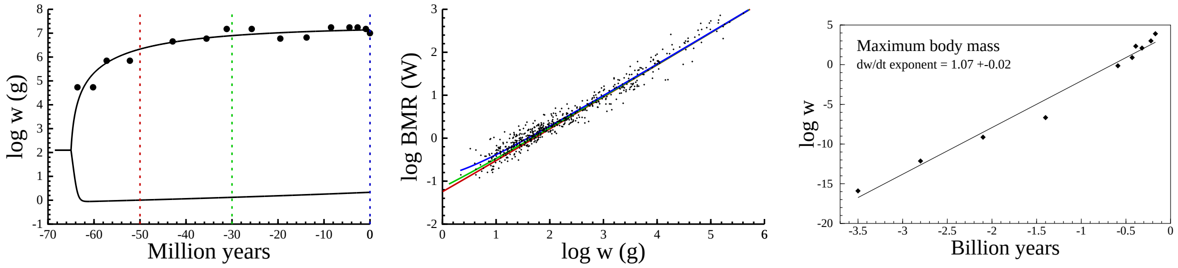

Figure 7: **Selection of mass and metabolism over time. Left:** The evolution of the body mass (w) distribution of placental mammals (maximum and minimum boundary curve) over the last 65 million years, as simulated by a fast selection differentiation in resource handling and a small amount of primary selected metabolism [fit to global maximum mass estimates from Smith et al. (2010), and 2.2-gram current minimum]. The underlying selection of metabolism is estimated from the curvature in 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). See Section 10 for details.

that contracts the timescale of natural selection relative to the dilation imposed by mass-rescaling (Witting 2020). This implies that it is the selected rate of increase in primary selected metabolism relative to the selected rate of increase in resource handling that determines the curvature of the evolutionary body mass trajectory when the predicted log-linear trajectory of steady-state selection on the per-generation timescale of natural selection scales into physical time. This explains (Witting 2020) the accelerating upward bending body mass trajectory of browsing horses in the fossil record (MacFadden 1986) by an early habitat adaptation followed by almost no resource handling evolution thereafter, with a selected increase in primary selected metabolism being the estimated main reason for the size increase in browsing horses over 57 million years of evolution.

At the other extreme we have the decelerating downward bending evolutionary trajectory of maximum mammalian mass following the Cretaceous-Paleogene extinction of dinosaurs (Fig. 7 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), in agreement with a present-day approximate 3/4-power inter-specific scaling of total metabolism (Fig. 7 middle) confirming a fast radiation in resource handling for most of the mammalian size expansion.

This dependence of the allometric exponents on the primary selected metabolism may also be used to obtain a better understanding of the natural selection difference between the fast evolutionary radiation within taxa like mammals and the much more slowly long-term across-taxa macro evolution of mass. Most of the mammalian adaptations in resource handling e.g. are likely to occur by minor adjustments to the overall mammalian Bauplan. The evolutionary building of a new Bauplan from one major taxonomic group to another is a much more complicated slower evolutionary process, that 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 the new taxon. This explains the observed (Makarieva et al. 2008; Kiørboe and Hirst 2014) across taxon invariance in mass-specific metabolism (Fig. 1, bottom), where the selection of a larger animal taxon tends to select an increase in the intercept of the allometry with no change in the negative 1/4 or 1/6 power scaling within the taxon (Witting 2017b). A slow macro evolution of resource handling agrees also with an observed log-linear trajectory of maximum mass evolution across all mobile organisms covering 3.5 billion years (Fig. 7 right; Witting 2020). This estimates an essentially complete reselection of metabolism lost in across-lifeform mass-rescaling during the deepest evolutionary time window on Earth.

We generally expect the selection of log-linear allometries owing to the multiplicative relationships between many life history and ecological traits. Yet for inter-specific allometries that describe the current endpoints of a large set of evolutionary trajectories that diversified from a common ancestor, this is expected only if there is no net energy driven primary selection of metabolic pace (Witting 2018). If instead as expected there is a somewhat common background selection of metabolic pace, the selected acceleration of metabolic pace occurs on different timescales across species as each lineage has its own natural selection of the per-generation timescale of natural selection. The selected metabolic acceleration is therefore faster in physical time in the smaller species due to their shorter generation time, and this bends the inter-specific metabolic allometry upward in the lower size range as evolution proceeds.

To analyse for this background selection of metabolism in mammals, Witting (2018) simulated the natural selection of net energy, metabolism, and allometries forward for 65 million years for a set of evolutionary lineages that cover the observed radiation in placental body mass evolution from a common ancestor. By fitting the inter-specific allometry across the simulated evolutionary lineages to the currently slightly curved (Kolokotrones et al. 2010; MacKay 2011; Packard 2015) metabolic allometry data of placentals (Fig. 7 left & middle), the analysis obtains a best curvature fit for a mass-specific metabolism that was selected to increase exponentially at a per generation rate of 9.3×10^{-9} (95% CI: 7.3×10^{-9} - 1.1×10^{-8}), on average. The corresponding estimate for marsupials is an order of magnitude smaller reflecting their almost perfect 3/4-power scaling, in agreement with an about 30% larger metabolism in today's placentals compared to marsupials of comparable size.

11 The natural selection of fitness

Having dealt with the natural selection of the life history diversity of the major lifeforms, let us consider the natural selection of fitness and thus potentially the natural selection of natural selection itself.

As the selection of traits occur through their link to fitness, the evolution of fitness was coined by Fisher (1930) as perhaps the most essential part of natural selection when he defined the fundamental theorem from the demographic fitness of the Malthusian parameter r (denoted m by Fisher). Having a gene centric point of view, Fisher applied a frequency-independent selection where the relative fitnesses of the alleles of genes are genetically inherent constants (Witting 2000). Having constant relative fitnesses this selection allows for no selection of natural selection itself, and this is the most widely applied selection of the contingent life history theory. Here it is the contingencies of the past that place each species near its current peak in the fitness landscape, with no selection to predict the life history positions of the fitness peaks. Lacking this predictability, maybe the only general prediction possible for frequency-independent selection is Fisher's fundamental theorem stating that natural selection selects an increase in average fitness, reflecting populations that climb the peaks of constant fitness landscapes and changing seascapes, while the relative fitnesses and natural selection among the potential variants remain the same.

By including the density-frequency-dependent interactive competition among the replicating units in natural populations (Witting 1997, 2008, 2017a,b), Malthusian relativity shows that life history evolution is explained better by a self-organising selection that selects—not an increase in average fitness but—a change in relative fitness and thus a change in natural selection itself, a change that is necessary and sufficient to select the life history diversity of the major lifeforms. As reviewed in the sections above, this implies a fitness landscape and natural selection that evolves by its own selection of net energy for replication, selecting a constantly evolving selection attractor that evolves across essentially the full range of life histories from the origin of a common ancestor. This forward selection of a continuously evolving naturally selected life history solves the paradox of the traditional metaphor where populations must evolve against natural selection—downhill from a fitness peak by a decline in average fitness and across the valleys of the fitness landscape—to evolve from one naturally selected life history to another.

The self-organising selection of relative demographic fitness limits the scope of relative fitness to a relative measure among the replicating units in the evolving natural population, making it meaningless to compare measures of average fitness across populations in time and space (Witting 1997, 2017b). There is consequently no selection of populations towards fitness peaks, but if we want to visualise the potential evolution of a population, we can calculate the selection gradient (Fig. 5, middle plot) from the within-population variation in the fitness landscape (left plot) and integrate the selection gradient across the potential evolution in the average trait value of the population to obtain the selection integral (right plot). The selection integral is a visualisation of the potential evolution of a population, with the peak of the integral being at the average trait value of the attracting evolutionary equilibrium if there is no steady state selection of net energy. The alternative selection attractor of the evolution steady state is situated on the left-side of the integral, selecting a steady change in the fitness landscape, selection gradient, and selection integral.

The frequency-independent selection of the contingent life history theory is a special case however, where the surfaces of the fitness landscape and selection integral are identical (Witting 2017b) and natural selection selects an increase in the population average of the Malthusian parameter r, as explained by Fisher in 1930. But, when r measures fitness it remains an intra-population comparison, with the natural selection changes in the population average of r measuring the average replication benefits or costs associated with a selection.

The predicted and often observed 1/4 power decline in r with a selection increase in the mass of multicellular animals e.g. measures the replication costs associated with the selection of mass by interactive competition. The lower-level replication cost of each major transition is in a similar way transferred to the next higher-level replicating unit, except that the frequency-independent replication benefits of metabolic pace outweigh the initial cost of mass in prokaryote-like unicells, selecting prokaryotes as the only major lifeform with a positive inter-specific correlation between replication and mass. For all subsequent transitions it is mainly the resource bias of interactive competition that outweighs the replication costs and selects a life history that preserves the costs in a frequency-dependent selection decline in the Malthusian parameter. These predicted and observed evolutionary declines in the population average of our measure of fitness illustrates quite clearly that natural selection does not select an increase in average fitness.

12 Biological diversity

While it seems to be impossible to use a selection increase in average fitness to select the observed inter-specific life history diversity from a common ancestor (Section 2), the present review has shown that a net energy driven selection change in the density-frequency-dependent relative fitness of interactive competition selects life history diversity from a common ancestor. The diversity of organisms on Earth is nevertheless sometimes seen as being incompatible with a universal force of selection that operates in the same way in all species (e.g. Lynch 2025). But this view ignores additional factors like speciation, inter-specific interactions, and local adaptation that generate and maintain a diversity of net energies across species preventing them from evolving identical life histories (Witting 1997, 2008).

Due to the relatively large phenotypic differences between species, inter-specific interactions are usually operating symmetrically on all the individuals in a population. Inter-specific interactions are therefore not necessarily inducing any direct intra-population differentiation in fitness that leads to demographic natural selection, but they are expected to rank species in a hierarchy of net energies across ecological resources. This ranking is expected to scale all the way from birds and mammals to unicellular eukaryotes and prokaryotes determining ecologically different backgrounds for the population dynamic feedback selection of each species.

Where dominant species may have an unconstrained exponential selection of net energy and mass, inter-specific interactions may prevent competitively inferior species from exploring rewarding resources, with resource handling adaptation to the available resources securing stable net energy and mass at a lower level, unless inter-specific interactions, or environmental changes, force inferior competitors, or species more generally, into sub-optimal habitats with an overall decline in net energy and the selected mass (Witting 1997, 2008).

There is also a division of taxa into locally adapted clusters that are spatially (e.g., terrestrial, benthic, pelagic), temporally (e.g. day vs. night), and adaptively (e.g. predator vs prey) separated, and likely also ecologically ranked by inter-specific interactions (e.g. homeotherm vs. poikilotherm). These interactions and factors appear sufficient to generate and maintain the wide distribution of net energies, adaptations, and extrinsically imposed mortalities necessary for a population dynamic feedback selected evolution of life history diversity.

This diversity includes the predicted variation in reproducing units. We saw in Section 9 how multicellular species with a locally optimised vs. unconstrained resource handling selection differentiate into pair-wise sexual vs. cooperative reproducers, while specially constrained cases where the selection of net energy does not reallocation-select into mass select eusocially reproducing species like ants, bees, and termites. We saw also that a clear-cut evolution of sexual units seems to depend on species like homeotherm birds and mammals that are in energetic control of their population dynamic processes, with sexual reproduction being less certain and more diverse in poikilotherm taxa like insects and reptiles due most likely to their restricted control of metabolic pace. Add to this the predicted absence of sexual reproduction in prokaryote-like replicators, the predicted partial sexual reproduction in unicellular eukaryotes, and predicted sessile multicellular hermaphrodites with partial asexual replication. While all these reproducing units were shown to evolve by the same self-organising selection, the outcome depends on the selected net energy and underlying resource handling ecology allowing for the natural selection of biological diversity.

Another diversifying factor is the adaptation of resource handling to a variety of resources. This not only generates diversity by itself, but it is also an essential component of the process that drives evolution forward; a process that may in some cases end up in evolutionary dead ends and/or optima that prevent further evolution. The diversity of prokaryotes e.g. is to a large degree reflecting the exploitation of a wide range of resources by a variety of metabolic pathways. Each evolved case is expected to represent a locally adapted optimum of metabolism-driven r-selected replication, with the local optima acting as evolutionary constraints that make transitions between metabolic pathways unlikely due to less efficient intermediate solutions.

While the diversity of metabolic solutions in prokaryotes is predicted to represent current states of different evolutionary trajectories in the same overall life history direction, the predicted transition to a unicellular eukaryote-like lifeform depends on the possibility to select resource handling and net energy to a next level where the replication-driven interactive competition assists in the natural selection of mass. This selection might not be possible for most metabolic pathways, and the continued further selection across the predicted range of eukaryote-like unicells towards multicellular organisms might be somewhat similarly constrained.

Such limitations are indicated by the evolution of eukaryotic unicells about 2.0 to 1.8 billion years ago (Ga; Craig et al. 2023) shortly after the Great Oxidation Event (2.4 to 2.2 Ga). The subsequent eukaryotic diversification of multicellular organisms was likely catalysed by an increased concentration of oxygen that allowed the self-organising selection to unfold to higher energetic levels in aerobic lineages (Sagan 1967; Hedges et al. 2004; Bonner 2009; Martin 2017), with a more restricted evolutionary unfolding of anaerobic unicellular eukaryotes in anaerobic environments. This indicates that the selection of eukaryote-like unicells and multicells is if not limited to, then at least easier and faster for, a sub-set of the metabolic pathways available in prokaryotes.

13 Population ecological synthesis

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). But he never formulated the underlying mechanism leaving natural selection theory to the diversifying contingency of particular circumstances (Witting 2008).

This conceptual dichotomy—between envisions of an overall directional evolution (often towards increased perfection and phenotypic cooperative complexity) and no explicitly formulated supporting demographic natural 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 the mid-20th century (McShea 1991), with the popularity of the concept declining among evolutionists thereafter following the development of the contingent life history theory.

An increasing number of ideas on the evolution of biological complexity and order (e.g. Demetrius 1974; Saunders and Ho 1976; Brooks and Wiley 1986; Kauffman 1993; Pross 2003; Brandon and McShea 2011; Lane 2015, 2019; England 2020; Sharma et al. 2023; Wong et al. 2023; Brown et al. 2024; Arcas 2025a,b; Tlusty and Libchaber 2025) continues to remind us of the ultimate paradox of living organisms that evolved in an overall unpredicted direction. Many of these proposals are by outside physicists and chemists that aim to resolve biological evolution blindly without reference to the demographic natural selection that has been agreed and proven for almost a century as the central force of life history evolution (Lynch 2025). Natural selection follows from the demographic origin of self-replication and selects living organisms that originate from, and evolve beyond, the realm of physics and chemistry into the realm of biology.

Malthusian relativity stands out from the somewhat abstract theories above as it is developed from within the agreed framework of demographic natural selection by the relative fitness of the Malthusian parameter. And being based on the self-organising interactive selection of the density-frequency-dependent changes in relative fitness, it stands out from the widely applied frequency-independent selection of the population genetic synthesis that selects an increase in average fitness along the surface of non-evolving fitness landscapes contingent on the current state of evolution.

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 power to organise the selection attractors of the fitness landscape. Yet this absence of an identified organising principle was a successful working hypothesis historically. Not only did it allow plenty evolutionary hypotheses to flourish without the constraints of a dominating force, but it allowed for easy explanations of the diversity of life, providing convincing arguments against a widespread critique of biological evolution.

The detour of natural selection thinking away from Darwin's original proposal on ecological interactions started with the mathematical calculations of heredity by Mendelian genetics (Mendel 1865). 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). Given a formal definition of fitness, natural selection theory obtained an organising principle. But the demographic selection of Malthusian growth 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 cost of males and meiosis selects for the absence of sexually reproducing organisms. Not particularly useful as a bottom-line conclusion for evolutionary biology.

This predicted singularity of the Darwinian demon sparked the development of the contingent life history theory (Partridge and Harvey 1988; Caswell 1989) that aimed for a population genetic understanding based primarily on demographic trade-offs and a frequency-independent selection with constant relative fitnesses assigned to the alleles of genes. This theory aligned with the intuitively straightforward interpretation that populations climb the local peaks of fitness landscapes (Wright 1932), following Fisher's (1930) fundamental theorem of a selection increase in average fitness. This generated a diversity of selection models that used measurements of the demographic trade-offs and constraints in current species to calculate fitness landscape peaks at or near the observed life histories, illustrating the life history optimisation of natural selection (Roff 1992; Stearns 1992; Charlesworth 1994).

By defining the selection structure in this way, the contingent trade-offs and constraints factor out the selection of the quality-quantity trade-off and costs of sex providing the illusion of a neutral selection background that allows the life history to be naturally selected to the estimated optimum of fitness (see Section 2). But having no selection that counterbalances the quality-quantity trade-off and costs of sex, these trade-offs select in the background altering the evolved components of the demographic trade-offs and constraints while selecting the Darwinian demon with asexual replication, zero mass, and infinite fitness. This frequency-independent selection structure is so rigid that it cannot straightforwardly select the life histories of evolutionary descendants from the life history of an ancestor. With the life history diversity of species being described by the set of local fitness peaks, populations must evolve directly against natural selection—i.e. downhill from a fitness peak by a decline in average fitness and across the valleys of the fitness landscape—to evolve from one naturally selected life history to another.

We may argue for mechanisms and historical events that make this unlikely non-selection evolution possible, but this will not explain the predominant allometric pattern (Fenchel 1974; Damuth 1981, 1987) where larger species have been selected from smaller species—not by an increase in average fitness but—with a selection decline in the population average of the Malthusian parameter r that "measures fitness by the objective fact of representation in future generations" (Fisher 1958). The only realistic solution seems to be to include the commonly observed (Hardy and Briffa 2013) intra-population density-frequency-dependent interactive competition as an integral part of our natural selection theory. This *i*) maintains the Malthusian parameter as the measure of fitness, *ii*) provides a selection that outbalances the downward pull of the quality-quality trade-off and costs of sex, *iii*) limits the scope of relative fitness to within population comparisons allowing for no predictable change in average fitness, *iv*) is necessary to select the observed decline in the population average of the Malthusian parameter, and *v*) supports the Darwinian paradigm by being sufficient to naturally select the life history of a species straightforwardly from the naturally selected life history of its ancestor.

By including the density-frequency-dependent interactive competition, Malthusian relativity shows that the main organising power of natural selection emerges from the demographic population ecology rather than population genetics. The population ecology implies that natural selection contains a directional force that self-organises from mass, energy, and replication at the origin of replicating molecules, and selects a predictable net energy driven change in relative fitness and natural selection that is necessary and sufficient to select the evolutionary succession of the life history diversity of the major lifeforms. This provides not only the first first principle prediction of the joint natural selection of metabolism (Sections 4 to 7), mass (Sections 4 to 8), life history allometries (Section 10), and multicellular sexually reproducing organisms with diploid genomes and fair meiosis (Sections 8 & 9). But this is done by a fitness landscape and natural selection that evolves by its own selection of net energy for replication, selecting a constantly evolving selection attractor that evolves from one life history to another across essentially the full range of life histories from a common ancestor at the molecular level, with the diversity of net energies across current species explaining the life history diversity of the major lifeforms.

While the selection increase in net energy is a precondition necessary for this evolution, it does not by itself explain the evolutionary succession towards large multicellular sexually reproducing organisms. It is instead the net energy driven gradually unfolding population dynamic feedback of interactive competition that selects mass and the major transitions forwardly, allowing evolutionary biology to develop beyond the forceless contingency that has dominated natural selection thinking since Darwin and Wallace (1858).

The self-organising selection is best seen as a population ecological synthesis where the contingent fitness peaks of the population genetic synthesis are local time-specific approximations of selection attractors that evolve by population dynamic feedback selection. With an underlying diversity of net energies allowing for a feedback selected diversity of life histories, it is the natural selection of the whole life history that positions the evolved trade-offs and constraints relative to the selected life history, forming locally evolving peaks in the fitness landscape of contingent trade-offs. This allows the bottom-up self-organising selection to meet traditional 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 (Witting 1997, 2008).

Several analyses of animal life histories have examined this interface between the two approaches. The net energy driven density-frequency-dependent feedback selection selects mass and the amount of energy allocated in the reproduction-survival trade-off of Lack's clutch size (Witting 1997, 2008). It selects also a resource bias that explains the intra-specific proportional correlation between reproduction and mass (Witting 1997, 2003) that is used as the structural constraint in the contingent models on the selection of size (e.g., Roff 1986; Stearns and Koella 1986).

Moving to traditional sex ratio theory (Fisher 1930; Hamilton 1967; Trivers and Hare 1976), the self-organising selection allows the population dynamic feedback to selectively adjust the mating system to match the sex ratio of the energetic selection pressure in the population (Witting 1997). This integration extends to eusocial species where differences in the ecological role of the sexually reproducing male selects for diploid termites with male and female workers, and haplodiploid ants with female workers only (Witting 1997, 2007).

Where the two life history approaches study evolution from either end, their population ecological integration allows for deeper evolutionary insights. This involves population ecological processes that fundamentally change natural selection theory; from gene centric models with intrinsic fitnesses, non-selected fitness landscapes, and a selection increase in average fitness, to a population ecological self-organising selection of evolving fitness landscapes with no natural selection increase in average fitness. Demographic Malthusian fitness is concluded to be not only a phenotypic life history expression of the genotype and the frequency-independent environment, but primarily a relative measure that is formed by the selected population dynamic pressure of the evolving ecological interactions among the replicating units of the population.

This necessary incorporation of the intra-population population dynamic feedback interactions is not just a mathematical modelling issue. It is first of all an evolution in evolutionary thinking away from the trial and error of chance and necessity to an active selection that unfolds from energy that flows 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 these evolving ecological interactions sustain a dissipative self-organising selection where the ever-evolving fitness landscape buffers environmental changes and keeps populations in energetic balance as they evolve across the life history diversity of the major lifeforms.

14 Conclusion

i) The contingent selection of the life history theory of the population genetic synthesis—towards fitness peaks by an increase in average fitness—represents an unpredictable diversifying evolution where the life histories of the attracting fitness peaks follow from unexplained contingencies rather than being explained by the identified natural selection itself.

ii) This aligns with the contingent evolutionary paradigm of the 20th century, where evolution by natural selection is understood from its historical development once it has actually occurred. The contingent selection hypothesis, however, generates several evolutionary paradoxes. These include a selection that fails to align with the natural selection principles of Darwin and Wallace (1858) as it cannot straightforwardly naturally select the life histories of species from the life history of their common ancestor.

iii) Other issues include a selection that does not counterbalance the selection of the quality-quantity trade-off and cost of sex, with the singularity of the Darwinian demon—with asexual replication, zero mass, and infinite fitness—being predicted when selection operates on the life history as a whole.

iv) A third issue is the selection increase in average fitness that reflects an increase in the Malthusian parameter (r_{max} and/or k) of the population. This theoretical cornerstone of the fundamental theorem (Fisher 1930) is empirically contradicted by larger species that evolved from smaller species primarily by a decline in the Malthusian parameter.

v) These paradoxes, that follow from the widely applied frequency-independent selection of constant relative fitnesses, are resolved by the density-frequency-dependent selection of the interactive competition among the replicating units in the population. These interactions maintain the Malthusian parameter as the measure of fitness, generate a population ecological force that self-organises from mass, energy, and replication at the origin of replicating molecules, and select a predictable net energy driven change in relative fitness and natural selection that is necessary and sufficient to select the evolutionary succession of the life histories of the major lifeforms.

vi) The interactive selection counterbalances the quality-quality trade-off and costs of sex, limits the scope of relative fitness to within population comparisons allowing for no predictable change in average fitness, selects a change in relative fitness that explains the observed decline in the population average of the Malthusian parameter, and aligns with the Darwinian paradigm selecting the life history diversity of species straightforwardly from the life history of a common ancestor.

vii) The selection of the intra-population interactive competition provides a population ecological synthesis that includes and expands beyond the population genetic synthesis. This predicts an essentially inevitable evolution of the major lifeforms, including large multicellular organisms with inter-specific body mass allometries and sexual reproduction by a diploid genome with fair meiosis.

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