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a Malthusian Relativity paper

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Predicting the evolutionary unfolding from virus to multicellular sexually reproducing organisms

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Abstract Evolution on Earth produced larger and larger lifeforms with across-generation gene replication increasingly embedded in more and more organised replicating units. Natural selection theory did not explain this evolutionary unfolding for almost 150 years, consolidating Darwinian evolution as a contingent diversifying, rather than force-driven directional, process. I review recent selection theory that predicts the evolutionary unfolding of the major lifeforms, and the allometric scaling of their life histories, from the population dynamic force of the density-frequency-dependent interactive competition that unfolds from a continued selection increase in the net energy that organisms use for replication. This argues for a radical change in evolutionary biology, and I begin by discussing the macro evolutionary pattern of lifeforms in relation to the historical development of natural selection theory. I then describe the unfolding selection and discuss its evolutionary implications, focussing on the importance of population dynamic feedback processes in natural selection.

Keywords: Natural selection, eco-evo, life history, allometry, evolutionary transitions, fitness landscape

1 Introduction

For more than 150 years, biologists have seen evolution by natural selection as a contingent diversifying, rather than force-driven directional, process. This contrasts to earlier evolutionary interpretations, including Lamarckism where internal alchemy drives simple lifeforms towards higher levels of complexity (Lamarck 1809). Superimposed on this primary force of evolution, Lamarck had a secondary force of acquired characters that diversified life by adaptations to different environmental conditions.

I argue for a similar primary and secondary structure of natural selection based on population ecological theory developed over the last three decades (Witting 1997, 2008, 2017a,b). It shows that the natural selection of net energy for replication is a primary force that drives the selection of major lifeforms forward through population dynamic eco-evolutionary feedback processes, with the more traditional evolutionary ecology of speciation, inter-specific competition, and local adaptation being secondary forces that expand and support evolutionary diversity.

The major mobile lifeforms—from virus over prokaryotes and protozoa to ectotherm and endotherm animals—arrange as an increasing function of size with limited overlap (Fig. 1, top). This reflects an increase in the biotic energy used to produce an individual, with the body mass scaling of life histories changing with this energy across lifeforms. A trait like mass-specific metabolism (Fig. 1, bottom) is non-existing in virus that depend on the metabolism of their hosts, while 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;

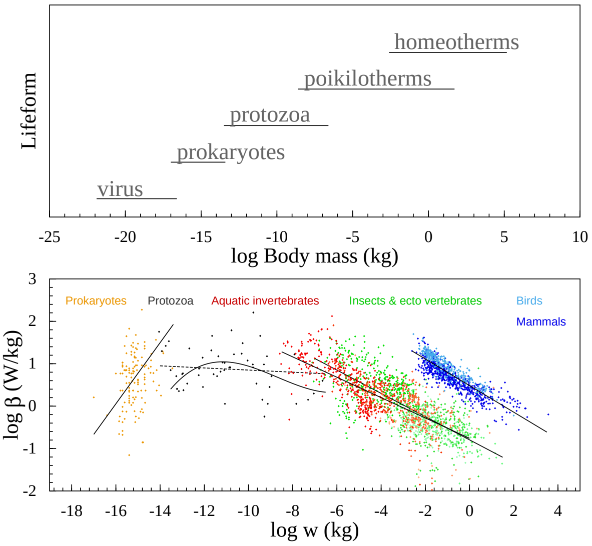

Figure 1: **Macro evolutionary relationships. Top:** The body mass range of mobile lifeforms (horizontal lines), illustrating lifeforms as a function of size. **Bottom:** The relationship between mass (w) and mass-specific metabolism (β) among mobile organisms. Data from Makarieva et al. (2008), plot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

Witting 2017a), before it approaches a negative 1/4-power scaling in animals (Kleiber 1932), while at the same time it is invariant of mass across lifeforms larger than virus (Makarieva et al. 2008; Kiørboe and Hirst 2014). On top of this, there is the transition between virus and prokaryotes from cell-less replicators to unicellular self-replicators, and the transition to multicellular sexually reproducing organisms at the boundary between protozoa and animals. The eco-evolutionary selection of the population dynamic feedback of interactive competition is now explaining this macro evolutionary pattern as a force-driven unfolding of a continued selection increase in the net energy that organisms use for replication (Witting 1997, 2017a,b).

When Darwin (1859) introduced natural selection, he did not construct a mathematical theory that predicted the macro evolutionary unfolding. He developed population thinking instead, combining the struggle for existence with the probabilistic events of chance and history, to explain the origin of species from branching phylogenies. This started a top-down backward study where the evolution of the past was inferred from the present, consolidating the 20th century contingent paradigm (Witting 2008) that sees natural selection as “a strictly *a posterior* process” that is “not controlled by any law” (Mayr 1988), a process that can be understood only from its historical development once it has actually occurred (Gould 2002).

Even life history theory—that aims to predict the outcome of natural selection—was trapped in a contingent circularity that used the actual evolution of the past to explain evolved traits in current species, as inferred from the evolved present that it aimed to explain (Witting 1997, 2008). This framework produced life history models from the fitness trade-offs and constraints that have evolved in the species of today (Roff 1992; Stearns 1992; Charlesworth 1994); a method that used the evolution of the past to implicitly measure, rather than predict, the outcome of natural selection.

The contingent structure of traditional life history theory allows us to study the differentiation in fitness in natural species, but it does not directly address the more fundamental question of why the living world has evolved its diversity of lifeforms, species, and life histories in the first place. To deal with this ultimate evolutionary question, we need to study natural selection bottom-up and predict the observed evolution forwardly from a minimum of biological assumptions. This means that we should not include the evolved trade-offs and constraints in the structural assumptions of our models, 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.

Studies of the fossil record is the traditional forward-looking approach, with Cope’s (1887) rule documenting a widespread increase in size. Other forward studies are experiments that analyse ongoing evolution in short-lived organisms, identifying parallel and converging evolution (Travisano et al. 1995; Cooper et al. 2003; Pelosi et al. 2006; Ratcliff et al. 2012; Simões et al. 2019), in line with observations from natural species (Conway-Morris 2003; McGhee 2013). These findings reflect the presence of local repeatable *a priory* given selection pressures, but they do not document an overall natural selection direction (Powell and Mariscal 2015).

A deductive forward-looking theory of natural selection was however missing, and this led to neutral evolutionary hypotheses (Stanley 1973; Gould 1988; Brandon and McShea 2011). These proposed a statistical, rather than natural selection, trend towards increased size and complexity by the diversifying drift of neutral contingency. While random drift accounts for the accumulation of neutral genetic variation (Kimura 1983), it does not account for life history evolution where random variation generates fitness variation, and thus natural selection, by default as the Euler-Lotka equation defines the Malthusian parameter, i.e. fitness as the exponential rate of increase (r, Fisher 1930), from the age-structured demography of the life history. It was in this vacuum with no forward-looking life history theory that I introduced Malthusian relativity in the mid-1990s, aiming to construct a strictly deductive population dynamic theory for the natural selection of living organisms (Witting 1997, 2008).

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

The ultimate cause of the studied population ecological feedback selection is natural selection imposed by the non-evolving structure of the life history demography. Apart from the demographic traits, this structure involves energetic trade-offs and replication constraints like the proportional decline in fitness by the quality-quantity trade-off (Smith and Fretwell 1974; Stearns 1992), and the two-fold cost of males (Maynard Smith 1971) and meiosis (Williams 1975), but not the diversity of evolved trait-relations that we aim to explain (like species specific trade-offs between reproductive effort and survival). The population dynamic growth of the demography—and the resulting density-frequency-dependent interactive competition of the foraging ecology—provide the eco-evolutionary feedback with natural selection defined by the relative intra-population differentiation in the Malthusian parameter (hence the name Malthusian relativity).

The development of Malthusian relativity occurred during a period with a growing recognition of density-frequency-dependent interactions in natural selection (e.g. Abrams and Matsuda 1994; Mylius and Diekmann 1995; Day and Taylor 1996; Metz et al. 1996; Heino et al. 1998; Dercole et al. 2002). Yet, the concept of a population dynamic force-driven life history theory that unfolded from the non-evolving components of the replication structure was new, with the different structural components selecting the different traits. The selection increase in net energy for replication e.g. reflects an underlying selection increase in resource handling (i.e. the skills, traits, and physiology that organisms use to subtract net energy from the environment) multiplied by a selection increase in the pace of handling, with pace selected as mass-specific metabolism (Witting 2017a).

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

2 The natural selection of lifeforms

The formal deduction of lifeforms from first principles of replication depends on a detailed mathematical model (Witting 1997, 2008, 2017a,b). It ranges from the energetically structured life history demography, over the associated population dynamic growth, to the spatial foraging of individuals exposed to density-frequency-dependent interactive competition, to the resulting resource access, Malthusian parameters, and Continuously Stable Strategy (Eshel 1983) natural selection attractors. I summarise the underlying concepts, mechanisms, and processes to describe the overall evolution of lifeforms, with details and elaborate discussions given in the original work.

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

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

The interference selected by the selection of mass is then selecting a more organised replicating unit from the potentially increased interactive quality of larger units where reproducing individuals (females) can attract interacting individuals (males) by the sharing of offspring genomes through sexual reproduction. When inserted into the selection equations of the reproducing

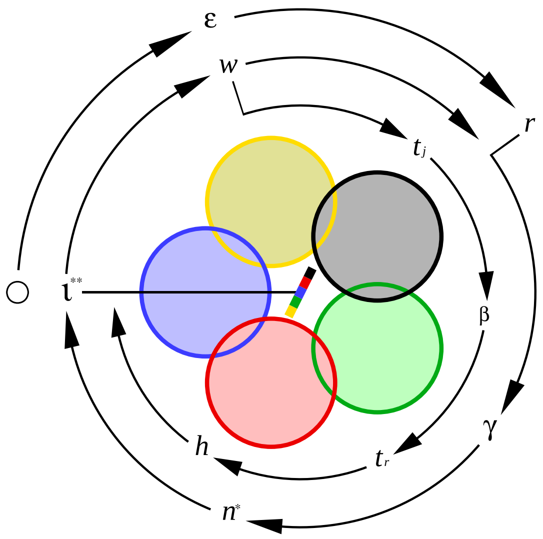

Figure 2: **Population dynamic feedback selection.** The small circle to the left represents the origin of self-replication, with selection for an exponential increase in net energy (ϵ) that maintains population growth (r) and a continued feedback selection of mass (outer feedback loop, see Section 2),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

unit, the predicted interference of a body mass in evolutionary equilibrium balances the two-fold costs precisely, selecting pairwise sexual reproduction between a female and male, with diploid inheritance selected as the sexually mediated glue that maintains the co-operative integrity of the interacting replicating unit (Witting 1997, 2002). The ecological selection of interactive competition is thus solving the paradox of sex, where genomic recombination may provide a long-term advantages but no straightforward immediate selection that balances the two-fold cost of males and meiosis (e.g. Muller 1964; Hill and Robertson 1966; Hamilton 1980; Kondrashov 1994; Otto 2003; Hadany and Feldman 2005).

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

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

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

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

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

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

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

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

3 Allometric scaling

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

This mass-rescaling (Fig. 2, inner loop) selects the numerical values of the allometric exponents from its influence on the spatial packing of home ranges (Witting 1995). The metabolic pace of interactive competition selects for small home ranges that minimize the cost

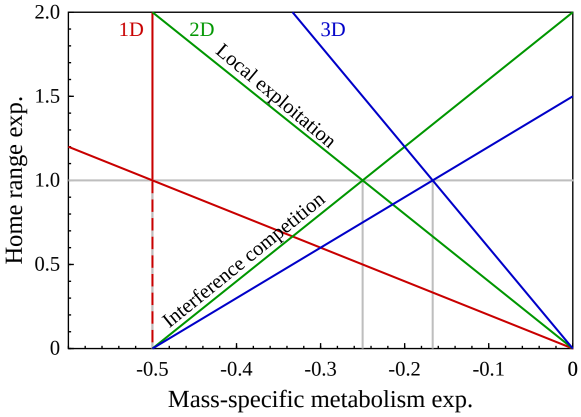

Figure 3: **Allometric deduction.** The selection of mass (w, Fig. 2) selects a mass-rescaling decline in mass-specific metabolism (β) that reduces the pace of foraging, affecting the ecological trade-off between the cost of local exploitation and interference competition. This influences the spatial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

of competition, but small home ranges have increased local exploitation. This tension determines the spatial packing of home ranges, creating a log-linear selection balance between metabolic pace, home range, and mass (see Witting 2017a, 2023 for details). When the equations of the selection balance are solved (Fig. 3), they predict a proportional scaling between home range and mass, and a negative 1/2-, 1/4-, or 1/6-power scaling of mass-specific metabolism dependent on a one-, two-, or three-dimensional packing of home ranges, with the predicted exponents supported by the allometries of animals (Witting 1995, 2017a).

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

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

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

Another example is the decelerating downward bending evolutionary trajectory of maximum mammalian mass following the Cretaceous-Paleogene extinction of dinosaurs (Smith et al. 2010), which agrees with a resource handling selection that outruns metabolic selection on the scale of maximum evolutionary diversification (Witting 2020). This agrees with a present-day negative 1/4-power inter-specific scaling of mass-specific metabolism that confirms a fast radiation in resource handling for the majority of the mammalian size expansion, with the inter-specific partitioning of resources and associated habitat adaptations supporting a diversity of mammalian sizes.

The inter-specific allometry of present-day mammals, however, contains a footprint from primary selected metabolism (Witting 2018). As metabolic selection accelerates most in smaller species due to their shorter generations, it bends the metabolic allometry upward in the lower size range as evolution proceeds. This predicts (Witting 2018) the observed (Kolokotrones et al. 2010; MacKay 2011; Packard 2015) curvature in the metabolic allometry of placentals from a mass-specific metabolism that increases exponentially at a per generation rate of 9.3×10^{-9} (95% CI: 7.3×10^{-9} - 1.1×10^{-8}), on average. The estimated rate for marsupials is an order of magnitude smaller, agreeing with about 30% larger metabolism in today's placentals compared to marsupials of comparable size.

The majority of the mammalian adaptations in resource handling are likely to occur by minor adjustments to the overall mammalian Bauplan. The evolutionary building of a new Bauplan from one major taxon to another is a much more complicated and slower evolutionary process, which may involve new phenotypic solutions for the exploitation of previously unexploited resources. If this across-taxon selection of resource handling is sufficiently slow, we predict a complete reselection of metabolism lost during the mass-rescaling selection of a new taxon. This explains (Witting 2017b) the observed (Makarieva et al. 2008; Kiørboe and Hirst 2014) across taxon invariance in mass-specific metabolism (Fig. 1, bottom), where the evolution of a larger animal taxon selects no change in the slope of the metabolic allometry, but an increase in the intercept as the taxon diversifies across ecological habitats. This agrees with an observed log-linear trajectory of maximum mass evolution across all mobile organisms covering 3.5 billion years (Bonner 1965; Payne et al. 2009), estimating a reselection of the metabolism lost in across-lifeform mass-rescaling during the deepest evolutionary time window on Earth (Witting 2020).

4 Discussion

Given the 20th century denial of a natural selection force for increased biotic organisation (Mayr 1988; Gould 1989; Salthe 1989; Williams 1992; Kauffman 1993; Maynard Smith and Szathmáry 1995), the identified net energy driven evolutionary unfolding of the major lifeforms is one of the more radical developments in evolutionary biology since Darwin and Wallace introduced natural selection in 1858.

This conceptual change aligns with a growing recognition of eco-evolutionary feedback processes (e.g. Thompson 1998; Hairston et al. 2005; Hendry 2017; Brunner et al. 2019; Jarne and Pinay 2023), extending beyond the evolutionary era of the population genetic synthesis (Fisher 1930; Wright 1931; Haldane 1932) that focussed on the intrinsic fitnesses of genes. These gene fitnesses consolidated the diversifying selection of the contingent paradigm by their absence of an overall natural selection force. The synthesis, however, did not account for the extrinsic eco-evolutionary feedback of the "struggle for existence" that "inevitably follows from the high rate at which all organic beings tend to increase" (Darwin 1859). It is first of all this ecological connection between population growth and interactive competition that drives the natural selection of lifeforms forward from net energy selected for replication.

The contingent life history theory (Roff 1992; Stearns 1992; Charlesworth 1994) is part of the population genetic era, and it neither includes the population dynamic feedback interactions explicitly. It does though include them implicitly through the intra-population correlations among the demographic traits of current species. But with no explicit feedback model the theory cannot predict the long-term/inter-specific natural selection changes in the demographic correlations and life histories. The contingent models are mainly snapshot-measures of the current fitness differentiation in natural populations, rather than complete selection models that predict the evolution of the species in question.

The strongholds of the contingent life history models are their focus on specific species and ability to examine fitness interactions and trade-offs at finer scales than usually feasible in population dynamic force-driven selection models. The deterministic bottom-up study of natural selection may though eventually meet the contingent top-down study at a common intermediate interface. This is already happening in several cases, with feedback selection predicting an intra-specific proportional correlation between reproduction and mass (Witting 2003) that is part of the structural constraints of the contingent models on the evolution of size (e.g., Roff 1986; Stearns and Koella 1986). The common selection interface (Witting 2008) explains also the reproductive effort/survival trade-off of Lacks clutch size (Lack 1947), and population dynamic feedback selection includes traditional sex ratio theory (Fisher 1930; Hamilton 1967; Trivers and Hare 1976) as an essen-

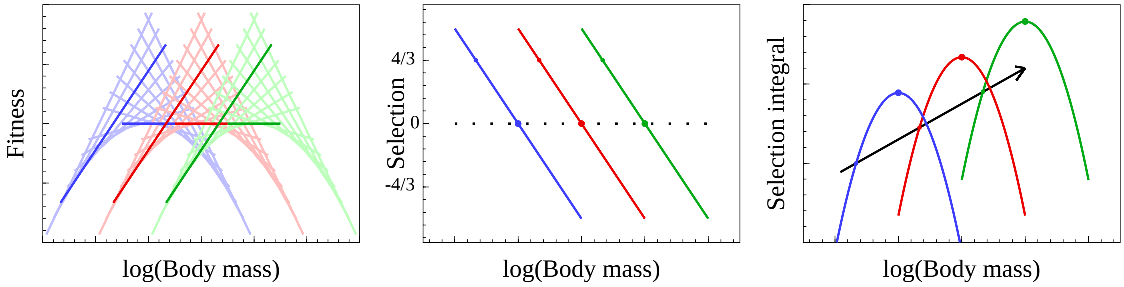

Figure 4: **The selection of body mass** illustrates the difference between fitness landscapes and selection integrals. **Left:** Each line is a fitness landscape (profile) of population dynamic feedback selection that describes the intra-population variation in fitness, covering a potential range of inter-population body mass variation (different lines) for three (blue, red, green) 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 increasing 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 left-intercepts between the arrow and integrals being the time-specific steady state attractors. From Witting (2017b).

tial component. Combined with different fitness components of the sexually reproducing males, the latter integration explains the differentiation of eusocial insects in diploid termites with male and female workers, and haplodiploid ants with female workers only (Witting 2007). The two approaches not only have their own right, but their joint integration allows for deeper evolutionary insights.

This integration separates the force of natural selection from the fitness landscape (including seascapes, Mustonen and Lässig 2009), providing informative information for the growing use of fitness landscapes in evolutionary interpretations (e.g. Gavrilets 2004; de Visser and Krug 2014; Fragata et al. 2019; Stroud et al. 2023). The fitness landscape (even in a stable environment) is only an instant measure of an ever-changing force, as illustrated by the feedback selection of interactive competition that controls and changes the fitness landscape during the evolution of mass (Fig. 4). As evolution by natural selection changes fitness landscapes constantly, populations cannot climb them by natural selection; but they often climb the stable selection integrals instead. These integrals integrate the selection differentials of the changing fitness landscape across the potential evolution of a trait, looking along the evolving population instead of looking only within it at a given point in time.

The selection integral and fitness landscape, however, have similar surfaces when the evolving population is not influencing the relative fitnesses of variants, but this refers to the frequency-independent case that applies only to virus and prokaryotes in the present study. So, to predict more generally life history selection beyond a couple of generations, we need to explicitly model the population ecological feedback interactions to account for the evolutionary changes in the fitness landscape. This should help us understand and predict evolution by natural selection, enhancing our abilities to mitigate evolutionary impacts of climate change and other anthropogenic disturbances.

The incorporation of the feedback ecology is not only a mathematical modelling issue. It is first of all a conceptual change where population dynamic feedback processes become necessary parts of population thinking. Life history selection is density-frequency-dependent it seems, making it impossible to understand by measuring and visualising fitness landscapes only. It all depends on the underlying population dynamic feedback interactions that form natural selection as a force-driven forward-looking process based on the Malthusian growth that catalysed Darwin's understanding of natural selection as a struggle for existence on September 28, 1838 (Darwin 1887).

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