Why there are so many definitions of fitness in models

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Data availability

No new data were used in this study. Code is available at: https://github.com/DanielSmithEcology/Fitness_Definitions_Code

Conflicts of interest

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Abstract

"Fitness" quantifies the ability to survive and reproduce, but is operationalized in many different ways. Generally, short-term fitness (e.g., expected number of surviving offspring) is *assigned* to genotypes or phenotypes, and used to non-trivially *derive* longer-term operationalizations of fitness (e.g. fixation probability or sojourn time), providing insight as to which organismal strategies tend to evolve due to natural selection. Assigned fitness operationalizations vary, but all summarize currently expected organismal vital rates (i.e. births, deaths, organismal growth). Derived operationalizations depend also on assumptions regarding demographic stochasticity, environmental stochasticity, feedbacks whereby births, deaths, and organismal growth cause environmental change, and the impact of migration and niche construction on which environment is experienced. After reviewing existing derived fitness operationalizations, we propose a new one tailored to balancing selection. Population genetic models generally sidestep ultra-high-dimensional phenotype space and genotype spaces by instead deriving the long-term evolutionary fate of a lower-dimensional set of genetically encoded "strategies". Strategies (e.g. costly developmental commitment to producing armaments) are causally upstream from realized phenotypes (e.g. armament size). While selection is best understood in terms of differences in *organismal* vital rates, its derived outcomes are most easily understood as properties of *genetic lineages*.

Keywords:
Invasion fitness, Malthusian parameter, theoretical population genetics, bet-hedging, life history strategy, density-dependent selection

"Fitness: Something everyone understands but that no one can define precisely" (Stearns 1976)

Introduction

Darwin’s theory of evolution by natural selection did not launch a professional discipline of evolutionary biology until the Modern Synthesis of the early twentieth century, in which the role of mathematical population genetics was key (Provine 1978). Central to this mathematization was “fitness,” which turned intuitions about “the ability to survive and reproduce” or "what tends to be favored in the struggle for existence" into more formal quantitative operationalizations. Resulting models are used to derive non-obvious insights (Servedio et al. 2014). One important historical role for fitness models was to deduce that the timescale of evolution by natural selection is fast enough to make selection a predominant factor in evolution, even with reasonably small selection coefficients (Provine 1978; Charlesworth 2020). Models of fitness can also be fit to sequence data, e.g. to detect loci under recent selection (Enard 2021); this falls outside the scope of the current manuscript.

From the outset of its mathematization, fitness has been operationalized in different ways (Ariew & Lewontin 2004; Orr 2009). Haldane (1927) used the expected *absolute* number of surviving offspring, while the influential Wright-Fisher model used the expected *relative* contribution to the gene pool in the next generation (Fisher 1930; Wright 1931). Theoretical population genetic models *assign* some version of expected short-term fitness to genotype-environment combinations, from which they mathematically *derive* longer-term outcomes. For example, Haldane (1927) assigned births per generation to a mutant genotype, and then derived its probability of fixation. Each such model thus involves at least two operationalizations of fitness: the assigned short-term fitness, and the derived long-term outcome or probability distribution of outcomes.

We review a variety of models and corresponding fitness operationalizations, their motivation, and simplifying assumptions, using annual plants and the Hawk-Dove game (Maynard Smith & Price 1973) as illustrative examples. We first focus on operationalizations that are at least sometimes assigned, then on operationalizations in which fitness is always derived. We then propose a conceptual scheme describing how models give insights into the fate, under natural selection, of the organismal strategies of interest to biologists. We argue that short-term fitness is best operationalized via *organismal* vital rates (births, deaths, organismal growth) plus organismal effects on the experienced environment through migration and/or niche construction, while long-term fitness is best operationalized for *genetic lineages*.

Assigned Fitness

Absolute fitness

Absolute fitness W describes the expected number of surviving offspring that a (hermaphroditic or asexual) individual produces after reaching reproductive maturity. Equivalently, it describes a juvenile's expected number of offspring (reversing the order of survival and reproduction). Either way, it is the expectation over one complete life cycle or 'generation' of both survival and reproduction.

The seminal use of assigned absolute, per-generation fitness was to derive the fixation probability of a new beneficial mutation. Haldane (1927) considered a resident (R) population of constant size, such that $W_R = 1$. He then considered the fate of a new lineage produced by a beneficial mutation. Individuals carrying the mutation have $W_I = 1 + s$, where the selective advantage $s > 0$. With some simplifying assumptions, including a Poisson distribution of offspring and $s \ll 1/2$, Haldane (1927) derived the probability that the beneficial mutation escapes extinction to "invade" as $2s$ (Fig. 1). Beyond the Poisson distribution, invasion probability is $2s/\sigma^2$ where σ^2 is the variance in offspring number (Barton et al. 2007, p. 25).

This example illustrates how the long-term fate of a mutant (probability of extinction) is derived from the short-term probability distribution of offspring number. Evolutionary success under natural selection cannot be reduced, even in a very simple model, to a single number such as W (Krimbas 2004). Larger variance in reproduction σ^2 increases the extinction probability, which can loosely be understood in terms of a lower signal (s) to noise (σ^2) ratio.

Haldane's assignation of absolute fitness W to genotypes is rarely used outside of this example of a rare beneficial mutant. All biological populations are density regulated, meaning that high W causes an increase in population density, which in turn reduces W (Haldane 1956; Nicholson 1957). For assigned constant W, the invading mutant lineage instead experiences unbounded exponential growth.

Relative fitness

Assigning *relative fitness* instead of *absolute fitness* sidesteps the issue of unbounded exponential growth. Relative fitness models treat the proportions of variants, rather than their absolute abundances. To motivate this, Crow and Kimura (1970, pp. 25-26) derived relative fitnesses w_k from assignations of absolute fitnesses W_k in the context of exponential population growth or decline. On this basis, they argued for simplified models in which w_k values are directly assigned, sidestepping assignations of W_k. Measurement theory has also been invoked as supporting the use of relative fitness over alternatives (Wagner 2010).

In the simplified models that have become standard within population genetics, relative fitness is defined as proportional to the expected fraction of the next generation that is descended from the focal genotype or individual. In the simple case of asexual reproduction, if $p_i(t)$ is the proportion of the population with genotype i at time t, and w_i is the relative fitness of type i, then its expected proportion in the next generation is

$$p_i(t+1) = p_i(t)\frac{w_i}{\overline{w}}.$$

Normalization by the population mean of relative fitness $\bar{w} = \sum_{\text{all k}} p_k(t) w_k$ can be used either to keep the population size constant, or to impose a different demographic model such as exponential growth. Importantly, this normalization derives absolute fitness W in a frequency-dependent way from relative fitness w - the opposite direction of Crow and Kimura's justification for the assignation of relative fitness.

A classic use of relative fitness assignations is in Wright-Fisher models that select among parent genotypes to produce expected fecundity $w_i/\bar{w}$. All adults then die - a potentially appropriate model for an annual plant. The finite size N of Wright-Fisher populations enables the derivation of fixation probabilities also for deleterious mutations, which never avoid extinction under the branching process treatment of Haldane (1927). Finite population size also enables derivation of the expected "sojourn" time prior to extinction or fixation (Charlesworth 2020). Conditional on fixation, $\bar{\tau} \sim 2\,(\ln(sN) + \gamma)/s$ generations in a haploid Wright-Fisher model (Fig. 1) where $\gamma = 0.5772$ is Euler's constant (Hermisson & Pennings 2005). Sojourn times were historically key to proving that natural selection works sufficiently rapidly to be a major cause of evolution (Provine 1978). In the modern era, sojourn times (or, if backward time is considered, coalescence times) are used when inferring a population's history of selection and demography from sequence data (Gutenkunst et al. 2009; Keightley & Halligan 2011; Ronen et al. 2013; Charlesworth 2020; Liu & Fu 2020; Excoffier et al. 2021).

A key limitation of models in which relative fitness is assigned to genotypes is that they do not allow the consequences of selection to feed back onto population density. In other words, the population size N is externally set, independently of mean population fitness. Problematically, no matter how low population fitness w drops, the externally set population size N will not decline, contradicting the desired behavior that low fitness should indicate an increased tendency to go extinct. A second, related limitation is that relative fitness cannot be compared across populations.

Vital rates are the “ultimate” assigned values

Vital rates describe rates of organismal growth, deaths, and reproduction. To complete a generation, seeds must germinate and survive to become seedlings, then survive from seedlings until they reach reproductive maturity, and then produce and disperse seeds. This description of three “fitness components” encompasses three vital rates for three life history transitions: the first two include both survival and growth, while the third includes only reproduction. Per-generation absolute fitness is the product of fitness components, each describing survival and/or reproduction during a different life history transition, within a fixed sequence. However, when the sequence varies, different values of fitness components are derived from the same vital rates, e.g. for a seed that survives within a seed bank for a variable number of years, each time without growth.

Like Metcalf (2007), Doebeli (2017), and Matheson (2023), we propose making survival and reproduction core to our scheme, and assigning corresponding values of death rate d and birth rate b, rather than of “fitness”, to phenotypes in an environment. On the surface, many models assign relative or absolute fitness values. In fact, a classic model such as Wright-Fisher is better seen as assigning a variable birth rate combined with a constant adult death rate, from which per-generation fitness is implicitly and trivially derived. In more complex models, e.g. of populations perturbed away from demographic equilibrium, selection on fecundity/juveniles does not produce the same allele frequency trajectory as selection on adult death rates (Benton & Grant 2000; Bertram & Masel 2019).

Derived fitness operationalizations

The fitness operationalizations presented so far are sometimes assigned to genotypes (as a function of their current environment). Next, we consider properties that are rarely if ever assigned to genotypes, but derived from assigned fitness operationalizations. To illustrate them, we add a seed bank to our annual plant example.

The Malthusian parameter

The Malthusian parameter (Malthus 1798; Fisher 1930) or intrinsic growth rate r (Lotka 1907) quantifies how quickly a genetic lineage tends to grow or shrink, in absolute time units (e.g. days), rather than in the per-generation time units of the relative and absolute fitness operationalizations above. While usually specified as a form of absolute fitness, a relative fitness version can be obtained as $r_i' = r_i - \bar{r}$ where r is the mean Malthusian parameter, with r_i' analogous to $w_i/\bar{w}$ discussed above. Occasionally, r is an assigned parameter as a technical matter to allow the use of differential equations (Desai & Fisher 2007). In most studies, however, r is a derived fitness operationalization. Doebeli et al. (2017) argue that r should always be derived rather than assigned.

For the non-overlapping generations treated by the Wright-Fisher model, r and W contain the same information, albeit in different units. However, consider a simple scenario of overlapping generations, where individuals produce offspring at rate b and die at rate d. The Malthusian parameter is $r = b - d$ with time units, whereas per-generation absolute fitness is $W = b/d$ (births occurring during expected lifespan $1/d$). For example, when $b = 0.2$ and $d = 0.1$, then $W = b/d = 2$ (average of 2 offspring per generation), while $r = b - d = 0.1$ (lineage is growing with exponential growth rate 0.1 per external time unit such that $y(t) = y(0)e^{rt}$).When generations overlap, neither W nor r can be derived given information only about the other, and they provide information about different things (De Jong 1994). The Malthusian parameter tells us what allele frequencies to expect at a specified time in the future (r is a *rate*). For example, sojourn time (Fig. 1, $\bar{\tau}$ in mutation 4) depends on differences in r, whereas differences in W, combined with σ^2, tell us the *probability* that a rare beneficial mutation will escape extinction (Fig. 1, mutations 1-4).

Selection can act on differences in one quantity (r or W) even given equality for the other. For example, consider a trade-off between b and d such that $W = b - d$ remains constant. Importantly, r need not be constant under this constraint. In the wake of a disturbance that kills many individuals from a population previously at equilibrium, selection will favor larger b and d, because this increases $r = b - d$, enabling the type with the faster life history strategy to more quickly rise back up to carrying capacity (Stearns 1992).

The Malthusian parameter generally depends on all three kinds of vital rate: deaths, births, and growth. For example, consider adult plants (A) that die at rate d and give birth at rate b to seeds (S) that grow into reproductively mature adults at rate g. For simplicity, we neglect seed death. This yields the following differential equations:

$$\begin{matrix} dS(t)/dt \\ dA(t)/dt \end{matrix} = \begin{pmatrix} -g & b \\ g & -m \end{pmatrix} \begin{pmatrix} S(t) \\ A(t) \end{pmatrix}$$

The Malthusian parameter is the dominant eigenvalue of the 2×2 matrix above: $r = \frac{1}{2}\left(\sqrt{4bg + d^2 + g^2 - 2dg} - d - g\right)$. This summary of the short-term fitness consequences of vital rates illustrates the need to include g; note that $r \to b - d$ as $g \to \infty$. In contrast, $W = b/d$, with no dependence on g.

A common use of the Malthusian parameter is to describe “invasion fitness”, meaning whether and at what speed a new mutant genotype I deterministically invades a population of “resident” genotype R at equilibrium abundance $\widehat{N_R}(t+1) = \widehat{N_R}(t)$ (Metz et al. 1992). To illustrate this, consider an annual plant population in which a seed germinates with probability g per year to produce an expected f seeds, or else survives with probability $1/d$ in the seed bank. Now our vital rates are f, g, and d. We capture the dependence of fecundity on seedling density using parameter α. In external timesteps $t = 1$ (rather than per-generation terms), types $k = R, I$ (resident and invader) obey:

$$E[N_k(t+1)] = \underbrace{(1/d)(1 - g_k)N_k(t)}_{\substack{\text{Number of non-germinating} \\ \text{seeds that survive}}} \quad + \quad \underbrace{N_k\, f\, g_k \frac{1}{1 + \alpha \sum_{\text{all } j} g_j N_j(t)}}_{\substack{\text{New seeds produced by germinating} \\ \text{individuals that survive density effects}}} \qquad (1)$$

For a rare invader ($N_I(0) \ll \widehat{N_R}(t)$), invasion fitness is equal to the absolute Malthusian parameter:

$$r_I = E\left(\ln\frac{N_I(1)}{N_I(0)}\right) \qquad (2)$$

which depends on resident density $\widehat{N_R}$ via the denominator in the rightmost term of Equation 1. Invader I tends to invade if and only if $r_I > 0$.

So far, the optimal strategy is always to germinate, i.e. $r_I > 0$ if and only if $g_I > g_R$. This is because there is so far no advantage to being dormant, to offset the risk of dying while in the seed bank. This changes when we consider fluctuating environments below, in which germination is sometimes futile.

Fitness across a variable environment

Most organisms experience environmental heterogeneity that affects their vital rates. E.g., plant seed production f depends on abiotic (e.g. rainfall), and biotic density-dependent (MacArthur 1962; Tilman 1982; Travis et al. 2023) and frequency-dependent (Tilman et al. 2020) environmental factors. The social environment (e.g. pollinators and/or interference competition) is included within the biotic density-dependent and frequency-dependent factors. Environmental variation can be spatial and/or temporal.

Given spatial environmental variation, migration enables organisms to affect which environment(s) they encounter. Some forms of migration, e.g. seed dispersal, are closely coupled to a life history transition, but can be conceptually separated into a migration phenotype in the old location, followed by vital rates of birth, death, and growth in the new location. Similarly, organisms can indirectly modify their vital rates via phenotypes that physically alter their local environment (niche construction; Odling-Smee et al. 1996). Selection on migration and niche construction phenotypes is included within the Malthusian parameter calculated across spatial environmental variation. I.e., the Malthusian parameter is derived not just from assigned vital rates, but also from assigned migration and niche construction rates.

We consider temporal variation in the environment $e(t)$ via an extension of Equation (1) in which germinating seeds produce zero offspring during drought years, such that fecundity

$$f(e(t)) = \begin{cases} f \text{ in good years with probability } p \\ 0 \text{ in bad years with probability } 1-p \end{cases}.$$

Instead of the instantaneous Malthusian parameter in a single environment, we take, as invasion fitness, its expected value across the distribution of environments $e(t)$:

$$r_I = E_{e(t)}\left(\ln \frac{N_I(t+1)}{N_I(t)}\right). \tag{3}$$

This is known as the *geometric mean fitness* because it corresponds to the geometric mean of absolute per-generation or per-time-step W. It is equivalent to the arithmetic mean of the Malthusian parameter over environments (Takacs & Bourrat 2022, 2024). In more complex scenarios when multiple life stages are affected by the environment, a generalization of the Malthusian parameter known as the Lyapunov exponent can be used (Cohen 1979; Metz et al. 1992; Kussell & Leibler 2005).

While germination probability $g = 1$ maximizes r_I in a constant environment, it results in complete extinction in a bad year, and so a more conservative $g_I < 1$ maximizes r_I in a temporally varying environment. This is an example of evolutionary *bet hedging* (Cohen 1966; Seger & Brockmann 1987; Frank 2011a).

In adaptive dynamics (Metz et al. 1995), the standard practice is to assume that evolution moves in the direction that maximizes invasion fitness, given infinitesimal perturbations to parameters controlling strategies (e.g., g_I infinitesimally differs from g_R). In the seed bank model, evolved g_R then achieves $r_I < 0$ for all $g_I \neq g_R$ (an “evolutionary stable strategy"; Geritz et al. 1998).

Fixation Probability Ratio

Derived fitness operationalizations attempt to capture which strategies will become prevalent, if present, under evolution by natural selection. Although individuals die within a short timescale, they embody a strategy/type (e.g., germination probability) that lasts over a longer timescale, due to being genetically encoded.

Consider a genetic lineage (Akçay & Van Cleve 2016; Graves & Weinreich 2017) consisting of all gene copies descended from a new mutation encoding a change in germination probability. Independent mutations creating the same allele found separate lineages. A subsequent mutation to the derived allele creates a sublineage that is still part of the original lineage. Due to recombination, different genetic lineages at different loci are nested within a common organismal genealogy (Kelleher et al. 2018). In the long term, each lineage either fails (goes extinct), or succeeds (fixes in the population). The probabilities of lineage fate can be used to construct a derived operationalization of fitness.

By equating $r_I > 0$ with success, invasion fitness (equations 2-3) neglects chance extinction. Recalling that the probability of invasion $2s/\sigma^2$, invasion fitness does nothing to capture genetic variation affecting demographic stochasticity σ^2. Stochasticity in the series of environments also contributes to extinction (King & Masel 2007).

Consider an extension of the annual plant example in which genotype abundance is a discrete random variable, X

$$N_k(t+1) = X(\mu, \sigma^2). \tag{4}$$

Equation 1 is the special case with $\sigma^2 = 0$. As in Haldane (1927), $N_k(t+1)$ can be 0 even if $\mu > N_k(t)$. The maximal probability that an invader lineage fixes requires at a lower value of g_I than the maximal geometric mean growth rate (Fig. 2). Larger g causes greater fluctuations in N – the strategy with largest r therefore increases extinction risk (Adler & Drake 2008; Constable et al. 2016; Pande et al. 2020; Pande et al. 2022). Invasion fitness r thus does not fully capture the long-term fates of lineages.

To capture demographic stochasticity, we can compare fixation probabilities to those of neutral alleles (Nowak et al. 2004). To also capture environmental stochasticity, we can use the ratio of the probability with which allele 1 invades a population in which allele 2 is resident : the probability with which allele 2 invades a population in which allele 1 is resident (Masel 2005). When mutation between the two alleles is symmetric and rare, the fixation : counterfixation ratio describes the odds with which a population will be found fixed for allele 1 vs. allele 2. This makes it directly applicable to empirical situations such as quantifying preferences among codons (Bulmer 1991), in which there is sufficient data across an ensemble of comparable instances.

Note that when mutation is not symmetric, the direction and degree of mutational asymmetry also affect the odds with which a population will be found fixed for allele 1 vs. allele 2, which are given by $\mu_{j\to i}p_{\mathrm{fix}}(j \to i) : \mu_{i\to j}p_{\mathrm{fix}}(i \to j)$. This ratio includes both our fitness operationalization $p_{\mathrm{fix}}(j \to i) : p_{\mathrm{fix}}(i \to j)$, and mutation bias $\mu_{j\to i} : \mu_{i\to j}$. The relative mutation rates matter because a variant must first appear in the population before it can be subject to natural selection. Fitness cannot be equated with quantifying “what evolution makes prevalent”, because natural selection is not the only cause of evolution (Stoltzfus & Yampolsky 2009).

The evolved mutation rate is a good example of an outcome determined in part by mutation bias. There are more mutations that increase the mutation rate (mutators) than decrease it (antimutators). However, indirect selection against deleterious mutation load favors a lower mutation rate (Johnson 1999a, b). This results in a mutation-selection-drift balance at some fairly low mutation rate (Lynch 2008). Operationalizing fitness as the ratio of fixation : counterfixation probabilities readily handles the complexities of indirect selection that arise during the evolution of mutation rate.

How do we operationalize fitness under balancing selection?

Balancing selection is a challenge to all three derived operationalizations presented above. Sometimes two alleles can each invade an equilibrium population of the other, such that both variants are maintained by balancing selection (Fig. 3A). Characterizing cases of *mutual invasibility* is common in evolutionary game theory (Maynard Smith & Price 1973), adaptive dynamics (Metz et al. 1995), and theoretical community ecology (Turelli 1978; Chesson 2000). While coexisting at equilibrium, both types have a geometric mean fitness of 1. Both fixation probabilities are much lower than the neutral $1/N$ or $1/2N$, and taking the ratio of fixation probabilities contains little information about the outcomes natural selection tends to produce.

The qualitative intuition that “both types are fit” can be operationalized in stochastic terms by noting that both types invade with a high probability of “establishment” (rather than fixation) when rare. Establishment means reaching high enough abundance such that deterministic dynamics dominate, with subsequent stochastic extinction being rare (Desai & Fisher 2007). A “high” establishment probability can be operationalized by comparing an invader’s probability of reaching a given frequency to that of a neutral reference invader (i.e. one indistinguishable from the resident).

To quantitatively operationalize fitness under balancing selection, we propose taking the time-integral of mutant lineage abundance from introduction into a resident population of the other type, until stochastic extinction. We then take the ratio of these integrals, switching which is the resident and which is the invader. This is illustrated in Fig. 3 for the Hawk-Dove game. The time-integral is slightly larger than the product of three informative components: establishment probability, sojourn time from introduction until extinction conditional on establishment, and mean abundance during its sojourn (Fig. 3B-G). Minor deviation of overall fitness from the product of these three components comes from neglecting abundance conditional on non-establishment. As a technical matter to prevent the sojourn time from being inflated by fixation events, a model should disallow transitions to the absorbing boundary of invader fixation. Our metric captures the potential vulnerability of an abundant type to extinction e.g. from disturbance (Tilman et al. 1994), which would be missed if we used abundance or biomass (Van Valen 1975) from the corresponding mean field model.

The role of fitness within evolution by natural selection

Fig. 4 illustrates how models describe causality during evolution by natural selection. We distinguish between three aspects of the environment. The *selective environment* interacts with phenotypes to give rise to a particular organism's vital rates. (Note that our use of "selective environment" better corresponds to the "ecological environment" of Brandon (1990).) Here, we restrict the term *phenotype* to realized organismal properties (e.g., body size) or behaviors (e.g., migration, aggression). Extended phenotypes (Dawkins 1982) are captured by feedback from phenotype to the environment (Fig. 4). We refer to aspects of the environment that directly change phenotypes as the *developmental environment*. Organismal *strategies* describe allocation of scarce resources in pursuit of phenotypes. Strategies are shaped by genotype and/or by a plastic response to the *informational environment* – the cues that organisms respond to, prior to the direct effects of the environment on development. Responses to the informational environment (e.g., using locally low resource levels as a cue to migrate), if any, reflect the history of adaptation. In contrast, we consider intrinsic effects of the environment on phenotypes (e.g., reactions proceed faster at higher temperatures; Brown et al. 2004) to be part of the developmental environment. Note that the same environmental factor (e.g., temperature) can be part of all three aspects of the environment, by giving information, altering development, and imposing selection.

Different models simplify the Fig. 4 scheme in different ways. Commonly assigned fitness operationalizations, e.g. per-generation absolute fitness $W = b/d$, summarize the differential *vital rates* that embody natural selection in the short-term (Fig. 4, small shadow). In the Wright-Fisher model, genotypes vary in b, whereas in Haldane's model and the Moran model (Moran 1958), they could also vary in d. Haldane holds the environment constant, whereas the Wright-Fisher model lets the selective environment (represented by allele frequencies) affect the absolute vital rate b produced by a given genotype.

Derived fitness operationalizations are more complex summaries of the longer-term fate of genetic lineages, including the influences of demographic stochasticity, migration, niche construction, and spatial and temporal environmental variation (Fig. 4, large shadow). Natural selection produces differential vital rates, while the long-term outcomes of natural selection are embodied in long-term lineage fate. Simple population genetic models provide insights into the efficacy and timescale over which natural selection may operate (e.g., invasion probability $\sim 2s/\sigma^2$, and sojourn time $\sim 2\,(\ln(sN) + \gamma)/s$. However, phenotype-agnostic assigned fitness operationalizations do not provide insights into the underlying biological mechanisms through which natural selection favors particular traits.

Directly assigning vital rates enables us to ask, for example, how natural selection acts during the evolution of dormancy, operationalized as a genetically encoded 1-locus strategy to germinate with probability g per year. More sophisticated strategies might involve active sensing to exploit the informational environment (Kussell & Leibler 2005). For example, selection might favor a reaction norm of higher g given higher soil moisture. A sufficiently reliable environmental cue begets a shift from bet hedging to plasticity (Botero et al. 2015). Selection acts on phenotypes (germinating vs. not) as a function of both biotic environment (population density) and abiotic environment (drought vs. non-drought year), to produce vital rates whose impact on genetic lineages, over time, can be summarized by derived fitness operationalizations. This type of model provides insights into the biological mechanism through which a lineage with a mutation (g_I) "wins".

Fromhage (2024) categorize five properties that have motivated fitness operationalizations: predictors of short-term (A) phenotypic change and (B) gene-frequency change, (C) "improvement" criteria, and performance measures of (D) phenotypic strategies and (E) individual organisms. We emphasize assigning vital rates (E), then deriving lineage properties (D). B is fulfilled by relative Malthusian fitness, a derived short-term fitness operationalization, while its interpretation as invasion fitness is a short-term approximation of D. Fromhage (2024) argue for the “folk definition of inclusive fitness” to address (C-E) as a “design principle”. Strategies instead play the role of design principle(s) within our scheme.

Social interactions are often treated as *the* key complication for defining fitness; Fromhage’s (2024) scheme is correspondingly focused on debates about the role of inclusive fitness, neglecting e.g. complications from non-overlapping generations. Inclusive fitness is a derived fitness operationalization, traditionally viewed as a short-term organismal property. However, the same inclusive fitness operationalization can be viewed as a lineage property, namely the mean reproductive success of individuals across the probability distribution of lineage fates (Akçay & Van Cleve 2016). In our view, social interactions are simply one form of the density- and frequency-dependence of the biotic environment, and our same scheme of deriving lineage properties from organismal vital rates applies.

Strategies

Strategies are intermediate between genotype and phenotype. In a broader sense, strategies are a form of phenotype, describing what an organism prioritizes given constraints, often entailing commitment to developmental pathways and/or behaviors. Strategies can be seen as setting organismal goals (at least in organisms capable of cognition). The decision to commit is informed by genotype and by the informational environment, with its success in achieving the anticipated phenotype affected by the developmental environment.

As a simple example, consider a “Hawk” strategy from the Hawk-Dove game in evolutionary game theory (Maynard Smith & Price 1973). Briefly, Hawks fight for resources while Doves avoid conflict. In classic models, the developmental environment is neglected, and having a Hawk strategy fully specifies behavioral phenotypes. One’s opponent (Hawk or Dove) constitutes one’s selective environment, and knowledge of their past behavior (if included in the model variant) constitutes the informational environment. In contrast, we conceptualize a Hawk *strategy* not just as behaviors within the narrow confines of game theory, but as a developmental commitment toward *developing a set of phenotypes* (both armaments and behaviors) that are relevant for implementing aggression. This allows for the possibility that developmental conditions (e.g., insufficient resources) may prevent a Hawk from e.g., achieving large enough body size or armaments to be successful. The individual may then switch strategies, treating developmental inputs as part of the informational environment.

Applying our distinction between strategy and phenotype to the seed bank model (equation 1) is more subtle. A seed's realized phenotype is defined by germination (or lack thereof) while its strategy is embodied in the stochastic gene circuitry that is an adaptation for achieving a probability of germination g within the historical range of environments. An organism’s realized phenotype arises from the latter via a noise within the developmental environment (Frank 2011b). An unanticipated developmental environment (e.g. a prolonged hard freeze) could cause the outcome (germinating with probability g) to deviate from the strategy.

Strategies include investing in rapid growth given low population density, or in competitiveness or persistence given high population density (Grime 1988; Bertram & Masel 2019). This was originally formalized as r- vs. K-selected “strategies” (MacArthur 1962; Roughgarden 1971), where r is the Malthusian parameter at low density (and a prefactor of it also at higher densities), and K describes susceptibility to density-dependence (similar to $1/\alpha$ in equation (1)). A trade-off between investment in r vs. K was assumed, with the resulting “strategy” reflecting an organism’s position along that trade-off. However, r and K are often positively correlated with slope near 1 in empirical studies (Luckinbill 1978, 1979; Valle et al. 1989; Kuno 1991; Hendriks et al. 2005; Fitzsimmons et al. 2010), in agreement with some process-based theoretical models (Travis et al. 2023). While there does seem to be a fast-slow continuum, contemporary life history theory categorizes strategies in other ways (Salguero-Gómez et al. 2016; Healy et al. 2019; Malik et al. 2020; Bruggeman et al. 2023).

Organisms are capable of an extraordinary variety of phenotypes. The “functional trait” literature in community ecology attempts to reduce this dimensionality, by focusing on phenotypes (e.g., wood density, seed size, metabolic rate) that are most closely tied to strategies and vital rates (McGill et al. 2006; Yang et al. 2018). In contrast, vital rates come in only three key varieties, applied to different life history stages. Organismal strategies might have far lower dimensionality than downstream functional traits or other organismal phenotypes, in a manner that helps provide generalizable insights. Strategy space might be both small enough and concrete enough to give coherence to the organism’s developmental commitments, as well as to scientists studying them. Assigned and derived fitness operationalizations are key components of the models that serve to clarify how natural selection acts on strategies.

We find the 3-dimensional scheme of Grime to be a promising starting point for characterizing strategies. Grime (1977, 1988, 2001) hypothesized that trade-offs shape species into three types of specialization – “ruderals” tolerate harsh abiotic environments, “competitors” excel at high population density, and “colonizers” rapidly disperse to ephemeral resources. Each strategy is closely tied to vital rates. High-dimensional phenotype space among e.g., coral species can be simplified via a space of just these three strategies (Darling et al. 2012). Our simple example of a seed bank illustrates how organismal strategies can be described with reference to vital rates (and potentially also migration and niche construction phenotypes) in order to gain insight into how populations evolve within strategy space.

Conclusion

Both genotype space and phenotype space are huge and must be simplified to produce generalizable biological insight. Organismal “strategies”, intermediate between genotypes and phenotypes, capture biological questions of interest, and give rise to vital rates, migration rates, and niche construction phenotypes, which influence the quantifiable fate of genetic lineages. Traditional relative fitness and absolute fitness implicitly assign vital rates to organisms. From assigned vital rates, other fitness operationalizations (i.e. ways of quantifying what natural selection favors) are derived to describe evolutionary outcomes. Variations on the Malthusian parameter capture adaptation speed, while the probability of invasion is captured by the fixation : counterfixation probability ratio. We build on the latter to propose a new, lineage-based fitness operationalization suitable for describing fitness under balancing selection.

Figures

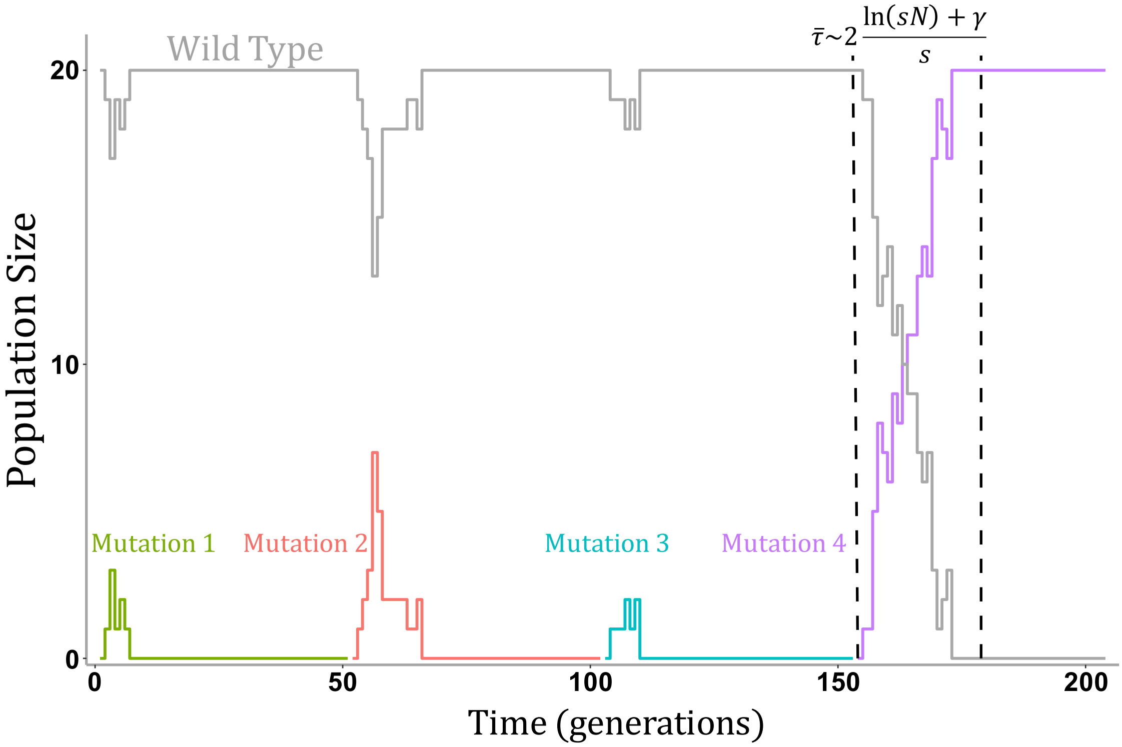

Fig 1: Fixation probability and sojourn time capture different long-term consequences of natural selection. Representative Wright-Fisher simulation of a population of size $N = 20$ in which an allele with selection coefficient $s = 0.125$ appears repeatedly by mutation. The mutant fixes with probability $\approx 2s/\sigma^2 = 0.25$. The sojourn time τ describes the number of generations before a mutation fixes (given it does not go extinct) with mean $\bar{\tau} = 2\,(\ln(sN) + \gamma)/s$. Each color indicates a different mutation. The interval between the dashed lines depicts $\bar{\tau}$; slightly shorter than the realized value of τ in this simulation.

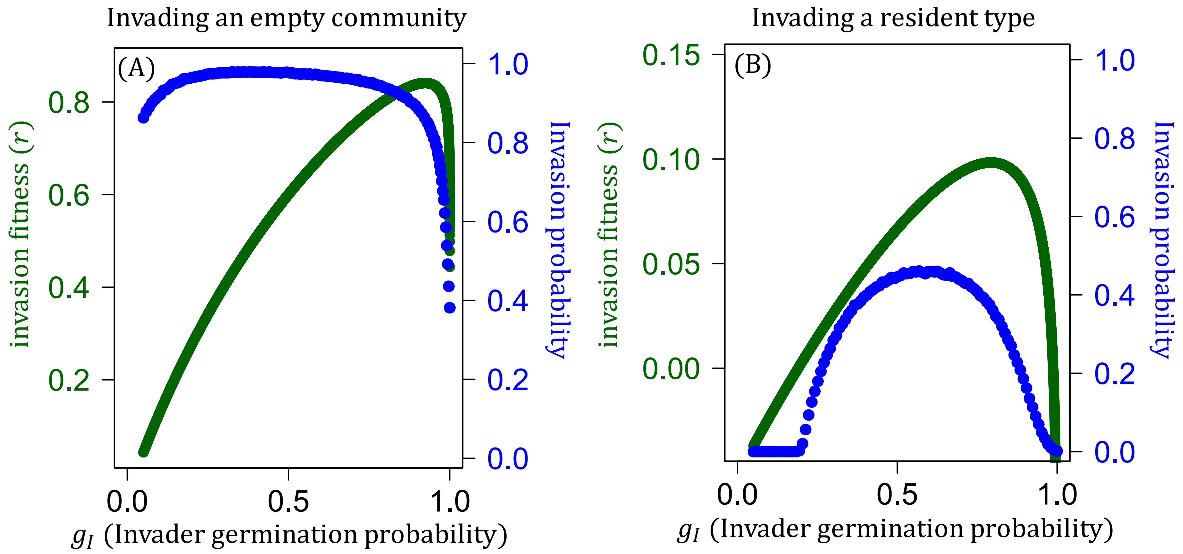

Fig 2: The invader's initial geometric mean growth rate is maximal for a higher germination probability than that which maximizes invasion probability. Seed banks are simulated given demographic stochasticity, and probability $p = 0.95$ that a given year allows reproductive success. An invader with germination probability g_I is introduced into an empty community (A) or a resident population of $g_R = 0.2$ (B); note the different y-axis scales for r in green. Invasion probability (blue) is defined in A as the probability that invader persists for at least 20 generations, and in B as the resident going extinct before the invader does. Invasion fitness (green) peaks at $g \sim 0.8$, but invasion probability (blue) is highest for moderately low values of g_I. Invasion fitness relative to a resident (B) is only positive for $g_I > g_R$. Invasion probability peaks at an intermediate value for which $g_I > g_R$ and is ≈ 0 when $g_I < g_R$. Adaptive dynamics models consider only infinitesimal changes in g_I relative to g_R, and only consider the invasion fitness. Parameters: $d = 1.053, f = 3, \alpha = 0.025$.

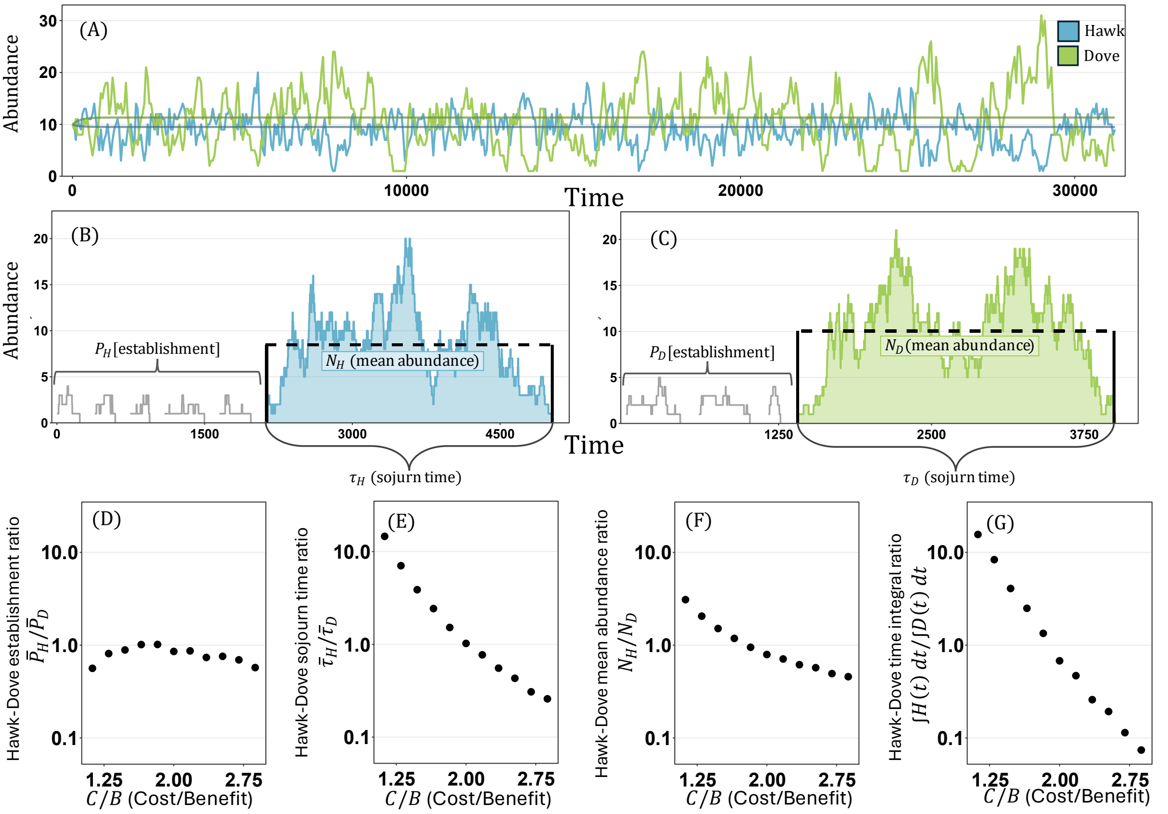

Fig 3: Our proposed operationalization of long-term fitness for a balanced polymorphism. We simulated a discrete-time stochastic Hawk-Dove game, code available on GitHub. A Hawk competing against a Dove always obtains the contested resource and receives a benefit B; a Hawk competing with a Hawk either gains the benefit B, or experiences a cost of fighting C, with equal probability; competing Doves split the benefit B evenly. Each timestep, individuals (1) die with probability d and then, if alive (2) produce offspring according to a Poisson distribution. The mean of the Poisson distribution for a type (Hawk or Dove) is determined by a baseline birth rate, payoffs that depend on the frequencies of Hawks and Doves in the population as well as B and C, and a density-dependent parameter such that births decrease with increasing density. A stable polymorphism requires $B - C < 0$. All points shown are in the parameter regime for which coexistence occurs under a mean field approximation. (A) Throughout most of the time series, Hawks and Doves coexist with abundances near the corresponding mean (horizontal lines). However, occasionally, one type falls to low abundance, and would go extinct in the absence of the reflecting boundary used in the simulation. The three components of our novel fitness operationalization are illustrated for the Hawk (B) and Dove (C). When a previously absent Hawk or Dove is introduced by mutation or migration, it must establish (increase from rarity when the other type is at equilibrium). We operationalized establishment as reaching the equilibrium frequency in the corresponding mean field model. Establishment probability (P_H and P_D) depends on various parameters of the model; gray time series data depict failures to establish. After establishment (colored blue and green time series data), the Hawks and Doves persist for a sojourn time (τ_H and τ_D) until eventual extinction. During the sojourn, the abundance of Hawks and Doves fluctuate around the mean (N_H and N_D). (D) – (E) show the ratio of the fitness components as a function of C/B. Each point shows the ratio of mean values from 7500 simulations of the Hawk invading the Dove and *vice versa*. (D) represents the establishment : counter-establishment probability ratio, which captures the relative tendencies to invade. (E) is the ratio of expected sojourn times conditional on establishment, which captures the relative tendency of each type to evade extinction over time. (F) is the ratio of average abundances throughout the sojourn. Our proposed fitness operationalization (G), the ratio of time-integrals from introduction to extinction, is negligibly different than the product of its components (D) – (E).

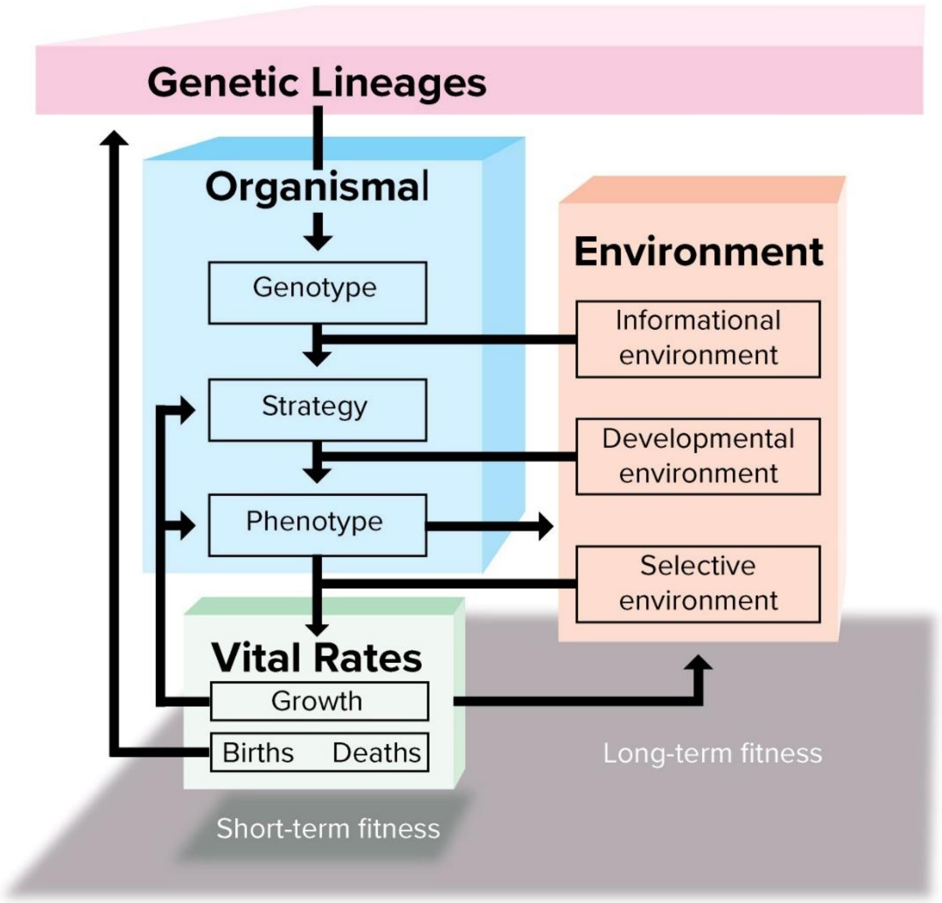

Fig. 4: Causal diagram of the key components/factors underlying operationalizations of fitness. All arrows imply causality. Evolution by natural selection involves feedback between genes, environment, organismal phenotypes, and vital rates. Short-term fitness operationalizations (e.g. traditional assigned relative or absolute fitness, or derived Malthusian parameter) are summaries of current vital rates, while long-term, derived fitness operationalizations reflect lineage fate within more complete feedback systems. Both are illustrated here as shadows, indicating projections in a mathematical sense. Short-term fitness reflects instantaneous vital rates, while long-term fitness reflects longer-term projections of the fate of genetic lineages. The environment experienced by an organism broadly includes all abiotic factors (mean physical conditions, including the effects of biotic resource depletion and ecosystem engineering) and biotic factors (direct effects of conspecific and heterospecific abundances). Births, deaths, and organismal growth all feed back to the environment, because population density and its consequences are important aspects of the environment. Note that all three vital rates feed back into all three aspects of the environment, as do phenotypes. Genotypes and the informational environment (i.e. interpretable cues that organisms plastically respond to, via phenotypic plasticity and epigenetics) give rise to the strategies used by organisms. Strategies consist of investment allocations subject to life history trade-offs such as Grime’s CSR triangle (Grime 1977), the competition-colonization trade-off (Tilman 1994), and bet-hedging. Phenotypes emerge from strategies deployed within a developmental environment. Niche construction and migration phenotypes affect the environment, or which environment is experienced, respectively. Selection on phenotypes gives rise to differences in vital rates. While the authors differ in their metaphysical interpretations of this figure (i.e., whether the objects shown in 3D are in fact appropriately depicted as “real” objects with fitness as a mere shadow (Byerly & Michod 1991; Krimbas 2004), or whether the objects shown in 3D are rather themselves shadow-like, imperfect measures of fitness as a “real” property), what the figure shows regarding various considerations for operationalizing fitness and the relationships among alternative operationalizations is compatible with either metaphysical picture (Pence & Ramsey 2013; Walsh et al. 2017).

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