A clean partition of "fitness" into three incommensurable dimensions:

growth, efficiency, and competitiveness

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Abstract

Standard population genetics models such as the Wright-Fisher model assign relative fitness values to genotypes. Normalization ensures that the absolute population mean fitness stays equal to one, keeping the population size constant. These models fail to describe extinction and evolutionary rescue; this requires a model of absolute fitness in the presence of density-dependence. Historically, the main approach to density-dependent fitness has been r- and K-selection. Canonical models of K-selection are flawed by an inappropriate choice of subscript for K, which confounds resource use efficiency with the competitive ability to win the kind of territorial contests that become most acute at high density. Here, I present a corrected version, in which fitness has three incommensurable dimensions: r gives reproductive speed at low density and has time units, K gives resource use efficiency and has units of resource and population densities, and c gives competitive high-density dominance, and is, like population genetic fitness w, always normalized and hence intrinsically unitless. Applications to experimental evolution and other data are outlined. Connections to Grime's triangle of reproductive strategies and Tilman's R* theory are described.

Introduction

The "fitness" of a genotype is its contribution to the genetic material of the next generation. It can be defined either in relative terms in proportion to the contributions of other genotypes, or in absolute terms as the expected number of surviving offspring.

Standard models of population genetics, such as the Wright-Fisher and Moran models, assign a relative fitness value w_i to each genotype i. Absolute fitnesses are calculated from the frequencies and relative fitness values of all genotypes in the population. Specifically, absolute fitness is calculated as w_i divided by the mean of the relative fitness values $\bar{w}$ in the population. This normalization ensures that the mean absolute fitness of a population is equal to 1, keeping the population size constant and equal to some assigned value N. Absolute fitness values are therefore frequency-dependent in standard population genetic models (Frank 2011; Orr 2007), rather than being an intrinsic property of a genotype in a given environment.

One obvious limitation of this standard population genetics formalism is that adaptation never leads to an improvement in the absolute flourishing of a population, nor does lack of adaptation lead to extinction. All competitive interactions are strictly relative, making population density entirely independent of the phenotypes that evolve.

Clearly, evolutionary models should also accommodate the possibility that genotypes might have a more direct effect on absolute fitness and hence population size. This is especially important when describing the limits to adaptation. Limits to adaptation can be modeled in a variety of ways, e.g. evolutionary rescue models (Bell 2013) and models of the substitutional

load (Ewens 1970; Wallace 1968; Wallace 1975). In all these models, the distinction between relative and absolute fitness effect is key. Critical limits to adaptation arise only when genotypes differ in absolute fitness.

Unfortunately for those seeking a simple model, a genotype cannot directly specify absolute fitness in the same simple way as a genotype in the Wright-Fisher model specifies relative fitness w. In all but the special case of fitness equal to one, this would lead to either exponential growth or exponential decline.

More reasonably, logistic density-dependence is assumed, where the population size N obeys $dN/dt=rN(1-N/K)$. This logistic equation led to the influential distinction between "r-selection" for rapid reproduction from a low starting point, and "K-selection" for efficient use of resources leading to a higher carrying capacity (MacArthur 1962; MacArthur and Wilson 1967). This distinction recognizes that fitness might not be a single thing that can be captured by a single number w per genotype. Where classical population genetics assumes a single dimension of fitness w, r/K-selection theory posits two dimensions. In this manuscript I focus on finding a good three-dimensional description of fitness, using the two-dimensional r/K-selection theory as my starting point. The "true" number of fitness dimensions may be much larger, but we can hope that a smaller number of simplified dimensions are enough to capture the majority of relevant phenomena.

Eco-evo synthesis

Evolutionary and ecological processes occur on similarly rapid timescales, and their synthesis is long overdue (Kokko and López-Sepulcre 2007; Pelletier et al. 2009; Reznick and Ghalambor 2001; Schoener 2011; Thompson 1998). One barrier to this synthesis is a lack of a consistently applicable and density-dependent concept of "fitness". Here I propose a revised treatment of r- and K-selection, in the process fixing known serious issues with K-selection, introducing a third dimension of c-selection, and mapping the relationship of the three-dimensional scheme with the one-dimensional population genetics w.

r- and K-selection have been more influential in the ecological literature than in the evolutionary literature. This manuscript instead takes a primarily evolutionary, population genetics approach to the subject, describing fitness and adaptation in a single population. While its immediate scope is in the realm of evolutionary studies, its foundations are however more compatible with ecological treatments than are existing evolutionary models, and amenable to eventual synthesis.

MacArthur's r- and K-selection

Concepts of r- and K-selection have a troubled history, with many definitions (Boyce 1984; Parry 1981). Some definitions focus on "fast" and "slow" life-history; the relevant concepts have since been incorporated into more sophisticated life history models of age-dependent mortality and reproduction (Reznick et al. 2002), and will not be discussed here. The use of the terms r and K in this manuscript is instead based strictly on their behavior as parameters in the density-dependence equation $\mathrm{d}N/\mathrm{d}t=rN(1-N/K)$. I make no auxiliary assumptions *a priori* about which phenotypic traits affect these parameters nor about the nature of tradeoffs between them.

I propose a formalism in which *r*-selection acts on the speed of population expansion at low density, which is a form of absolute fitness. This is consistent with previous versions of *r*-selection. The more controversial part of *r-K* theory is *K*-selection (Mallet 2012), which I will redefine in this manuscript. My aim is a formalism in which a *K*-adapted genotype can be interpreted as a parsimonious user of resources, permitting a higher population density. Two genotypes that differ only in *K* should differ in resource use efficiency alone, and not in low-density growth rate *r*, in resource partitioning, or in interference or other forms of competitive ability.

Canonical models of *r*- and *K*-selection (MacArthur 1962; Roughgarden 1971) assume that the dynamics of genotype *i* are best described as

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{1}{K_i} \sum_j N_j \right). \tag{1}$$

I believe this treatment of *r*-selection is fine, but Eq. 1 is not compatible with the interpretation of a high-*K* genotype as a parsimonious user of resources. Troublingly, Eq. 1 would imply that all benefits from this parsimony are directed exclusively to individuals of identical genotype. However, in the absence of spatial structure, resources left unused are normally equally available to all genotypes rather than preferentially enjoyed by the high-*K* genotype (Chao and Levin 1981).

To see this clearly, consider a new mutation with $K_2 > K_1$ entering a population previously fixed for genotype 1, so that N_2 is small and N_1 is near K_1. If *K* represents resource use efficiency, a small amount of resources should now be freed, giving a minute benefit to individuals of both

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genotypes. But in Eq. 1, genotype 1 gets no benefit, while genotype 2 gets a benefit whose size is greatest when genotype 2 is rare and increased K_2 has not yet led to an increase in the total population size N.

K in Eq. 1 might instead be interpreted as competitive ability to dominate at high density, making the immediate, low-frequency benefit no longer a puzzle. However it is now unclear why a new, hawkish competitor genotype 2 should have a higher carrying capacity than the dove genotype 1 it displaces. As we will see later in this manuscript, the standard Eq. 1 formulation of K assumes a tightly coupling between resource use efficiency and competitive ability; I will propose a new formulation that disentangles these two traits.

The best interpretation of classical K-selection in Eq. 1 is that this new high-K mutant exploits a previously neglected resource (Levin 1971, p.261). Innovation in resource partitioning might or might not be common in ecological speciation. However, it is rare in adaptation. Its appearance in Lenski's experiments (Blount et al. 2008), involving the ability to exploit citrate as a result of gene duplication and associated promoter capture leading to altered regulation of the new ortholog (Blount et al. 2012), was a spectacular and newsworthy occurrence, rather than a "garden-variety" adaptation. This is despite the fact that the experimental setup, with a single species exploiting only one of two available resources, and requiring only change in the regulation of the expression of an existing gene to exploit the second, was in retrospect almost designed to make such an occurrence easy. The best interpretation of MacArthur's Eq. 1 K-selection describes an event that is extraordinarily rare in evolution.

Alternative version of *K*-selection

I propose that a more reasonable equation for selection on carrying capacity via resource use efficiency, while holding constant other factors such as competitive abilities and resource partitioning, is described by the parameter K in

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \sum_j \frac{N_j}{K_j}\right)$$

(2)

Note the change in the subscript of K. In Eq. 2, $1/K_j$ is interpreted not only as the amount of resources needed to support one individual of genotype j, but also the amount of resources consumed in the process of this support, and hence unavailable to individuals of any genotype. This issue with the interpretation of K has occasionally been pointed out (Joshi et al. 2001 p.66) but somehow does not seem to have been pursued.

Note that K-selection favoring efficiency in resource use, in my Eq. 2 formulation, requires group selection (MacLean 2008). This is because forgone resources are equally available to all members of the population, just as in a classic tragedy of the commons. In the absence of group selection in favor of higher yield, and in the absence of a pleiotropic tradeoff or genetic correlation of K with r, two lineages with different values of K in Eq. 2 have neutral evolutionary dynamics. Unlike the classic formulation of the tragedy of the commons, individual selection for greedy, less efficient resource use is not intrinsic, but must be added as an auxiliary assumption of a tradeoff between K and r, or between K and some other yet to be determined dimension of fitness.

Adding a density independent term

The logistic equation is subject to certain known pathologies. In particular, if r is negative, then when $N > K$, the population grows instead of shrinking. Even if $N < K$, when r is negative then population decline is counterintuitively slowest near K. The logistic equation is more compatible with intuitively interpretable versions of r-selection if r can be constrained to be strictly positive.

One approach to minimize this pathology is to consider both density-dependent and density-independent influences on population dynamics, via the equation

$$\frac{dN_i}{dt} = b_i N_i \left(1 - \sum_j \frac{N_j}{K'_j} \right) - \mu_i N_i \tag{3}$$

A simplistic interpretation of Eq. 3 is that birth is subject only to density-independent selection while death is subject only to density-independent selection. This simplistic interpretation ensures that the birth rate b will never be negative. Partitioning births and deaths in this way is partly justified by the observation that many density-independent selective pressures, such as surviving a transient temperature extreme, affect death rates, while many density-dependent effects, such as territorial acquisition of nesting sites, have strong effects on birth rates.

A serious problem with this interpretation is that when $N > K'$, a negative number of births occur, clearly a physical impossibility. Fortunately, Eq. 3 is also compatible with a less restrictive interpretation, in which the partitioning of birth and death between density-dependent and density-independent factors is not absolute, but where the correlation between birth (death) and density-(in)dependence is nevertheless strong enough to ensure that $b > 0$. In this less restrictive interpretation, b represents all density-dependent factors rather than only those

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affecting births, and μ represents density-independent effects on both births and deaths. In particular, when $N > K'$, density-dependent death is the driver of negative population growth. In other words, $b < 0$ is not permitted, while $N > K'$ is, allowing for a single negative but not a double negative, and avoiding the pathology.

Note that Eq. 3 can be made equivalent to Eq. 2 by setting $r=b-\mu$ and $K= K'(b-\mu)/b$. K is the maximum sustainably achievable population size, while K' describes a more abstract theoretical resource limit of what the carrying capacity or equilibrium population size would hypothetically be, in the presence of density-dependence but in the absence of the constraints posed by the density-independent term (Berryman 1992). More simply, when the density-independent term can be interpreted as random mortality μ, e.g. being diluted out in a chemostat, K' rather than K is the best choice to be interpreted as the efficiency of resource use, e.g. yield. K-selection should therefore be interpreted in terms of Eq. 3 K' rather than Eq. 2 K.

Now consider a non-random component of density-independent birth and death, so that there is selection on genotypes that specify different values of μ. In terms of the logistic Eq. 2, we have $r_i=b-\mu_i$ and $K= K'(b-\mu_i)/b$. In other words, selection on the density-independent term μ affects both r and K by an equal factor (Andrewartha and Birch 1954 p.347-396; Ginzburg 1992; Mallet 2012). We will return to this important observation again below.

Competitive ability

Standard population genetic w-selection, as formalized in deterministic replicator equations and in the stochastic Wright-Fisher and Moran models, occurs at high density with population

size N constant and hence presumably equal to the carrying capacity K. w-selection can be thought of as a form of competitive ability to dominate at high density. r-selection on the "Malthusian parameter" is defined with respect to low density phenomena, and for this reason should not be equated with w-selection. Differential K' in my redefined system corresponds only to a form of group selection, and not to either r-selection or w-selection, both of which apply at the individual level. In yet another important difference, w-selection, unlike either r or K', is normalized relative to other values of w in the population. The competitive ability studied by population genetics corresponds neither to r-selection nor to K'-selection (Clarke 1973). Note, however, that both K' and w describe effects that are most important at high population density.

One of the best examples of a strictly relative competition, well-described by population genetics w, is sexual selection. Individuals choose the best mate may they can find, not the best mate on any absolute scale. Interestingly, this kind of competition is often ignored by ecologists. For example, a much-quoted definition of competition by Grime (1977, p.1170) is "the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space", a definition that clearly excludes mate choice (although, when appropriately extended to applicable organisms, it may include other forms of social selection (Lyon and Montgomerie 2012)). Sexual selection highlights the importance of describing relative competitions in any evolutionary model.

In an attempt to capture w-selection, I therefore introduce a third fitness parameter into the logistic equation, which I call c-selection. Like w, c is normalized to the mean value of c in the

population. In order to create a clean partition between r, c, and K', I propose a new formalism below which holds the values of r and K' constant across genotypes that vary only in competitive ability c.

To describe c-selection mathematically, note that the importance of relative vs. absolute competitions should vary with density. For example, at low density, organisms may "settle" for whatever rare mating opportunity comes their way, leading to weak relative competitions simultaneously with strong absolute ones. In contrast, at high density, intraspecies competitive violence and/or winner-take-all mate choice dynamics can accentuate relative competitions at the expense of absolute ones.

Let c_i be the competitive ability of genotype i to access resources under higher-density conditions, for example by winning a contest with a conspecific. (In contrast, r or b can be seen as speedy use of resources (Olson 1992), and $1/K'$ as the total absolute resource usage needed to maintain one individual.) I propose

$$\frac{dN_i}{dt} = b_i N_i \left(1 - D + \frac{c}{\bar{c}}D\right)(1-D) - \mu_i N_i \tag{4}$$

where $\bar{c}$ is population mean c, and $D = \sum_j N_j / K_j'$ is a population-averaged measure of density that can be interpreted as 1 – the amount of free resources. Eq. 4 captures a linear transition from r-dominated dynamics at low density to more c-influenced dynamics at high density. In the special case of a single c-type, we recover Eq. 3 from Eq. 4.

Note that the contrast between competitive ability c and population growth speed r can be seen as partially overlapping with the distinction between "contest" (c) and "scramble" (r) competitions (Nicholson 1954). Contest, like c is usually a relative competition, while scramble, like r, is an absolute competition. However, scramble describes competitions in which resource acquisition is potentially below-threshold, whereas contest describes competitions in which the winner is guaranteed above-threshold resources. The latter distinction is not present in my continuous-time growth model.

Relationship of *r* and *c* to population genetics *w*

In most population genetic models, death rates are constant across genotypes, while birth rates are proportional to relative fitness. In the Wright-Fisher model, all individuals die each generation and are replaced according to their relative fitness. In the Moran model, one individual at a time is chosen with uniform probability to die, and is immediately replaced via the reproduction of another (or the same) individual chosen with probability proportional to relative fitness.

By taking the limiting case of small μ in Eq. 4, we recover a scenario similar to the continuous time Moran model. As μ approaches 0, density D approaches 1 and the rates of birth and death approach zero.

In the discrete equivalent to the continuous Eq. 4, then following each rare death at rate μ, individuals compete to replace the missing individual, with probability of success proportional to bc. In other words, relative fitness w at high density $D \rightarrow 1$ is equal to the product of two

fitness components, reproductive speed b and reproductive competitiveness c. At low density D → 0, the relative fitness of genotype i is b_i. Intermediate densities represent a linear transition between these two extreme cases.

In the Moran model, death and replacement are discrete processes involving single individuals, whereas in Eq. 4 they are continuous, with fractional numbers of births and deaths. A continuous model is chosen because it avoids unstable dynamics and the pathologies associated with $N > K'$. When μ is larger, this distinction between discrete and continuous interpretations becomes unimportant.

Note that given a continuous model, the population size N in Eq. 4 is arguably best interpreted as biomass rather than as number of individuals, and is therefore agnostic with respect to body size considerations.

Relationship to resource competition and other ecological models

The speed of resource use is the critical factor underlying Tilman's (1980) resource ratio or R* theory. Tilman's theory explicitly assumes the absence of direct interactions between types, i.e. the absence of differences in c, such that the only form of species interaction is to quickly deplete a resource and make it unavailable for others. Under this assumption, all selection in a well-mixed population is best interpreted as r-selection in Eq. 4. Resource abundance in Eq. 4 is assumed to equilibrate rapidly enough to be at quasi-equilibrium, and so is implicit within the population density term of the Lotka-Volterra dynamics, rather than being explicitly modeled as in Tilman's theory. By adding explicit resource density back into a scheme based on Eq. 4, my

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scheme and Tilman's could be made compatible, while relaxing Tilman's exclusion of direct interaction effects. The explicit tracking of resource density also defines the difference between the logistic equation approach to microbial growth, and that based on Michaelis-Menten kinetics (Clarke 1973; Dean 1988; Monod 1950). The extension of Eq. 4 to include at least one explicit resource, while clearly important, is nevertheless beyond the scope of the current manuscript, and is left for future work. Here it must suffice to observe that this reconciliation is possible.

Grime's (1977) universal adaptive strategy theory, with a triangle of competitive, stress-tolerant, and colonizing traits, is often contrasted with Tilman's (e.g. (Grace 1991)). In Eq. 4, high density selection on the product of b and c acts on Grime's competitive traits, while pure r-selection acts on Grime's colonization ability. Grime's stress-tolerance traits are arguably best related to density-independent μ-selection (acting proportionately on both r and K). Eq. 4 can therefore also be viewed as a population genetic formulation of Grime's theory (Figure 1).
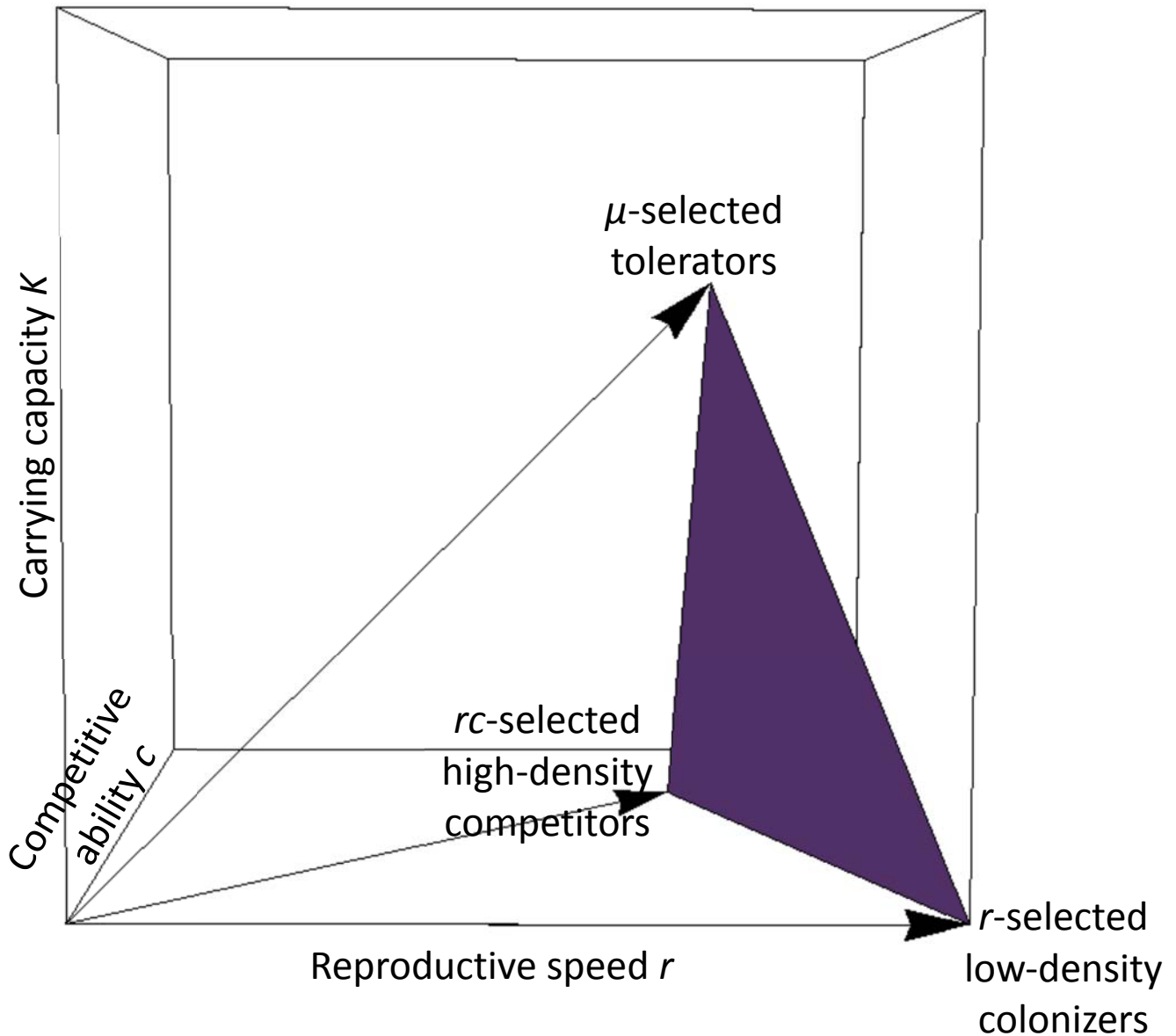
Figure 1: Grime's triangle of three extreme reproductive strategies arises within the three-dimensional

rcK model even in the absence of tradeoffs. Selection in three environments favoring the three most

extreme strategies is shown as three vectors of equal length in directions *r*, *r+K*, and *r+c* within a cube

whose axes are defined by Equation 4. All three forms of selection lead to increases in *r*, but because the

vectors are of equal length, the increase in *r* is greatest in the pure-*r*-selecting low-density environments

encountered by colonizers.

Adding more dimensions

This manuscript begins with a model with n r-parameters and n K-parameters (Eq. 2), then adds

a third vector of n c-parameters (Eq. 4) that describe relative fitness competitive ability, where

n is the number of genotypes. In an alternative approach to describing competitive ability,

MacArthur's $2n$-parameter Eq. 1 is sometimes expanded by introducing an additional n^2 α-

parameter values (Gill 1974; Matsuda and Abrams 1994; Osmond and de Mazancourt 2013) to

obtain

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{1}{K_i} \sum_j \alpha_{ij} N_j \right) \tag{5}$$

My Eq. 2 can be seen as a special case of Eq. 5 that is obtained by setting $\alpha_{ij}=K_i/K_j$, in the process

removing n^2 parameters to collapse the system back to $2n$ parameters, albeit a differently

defined $2n$ parameters than in MacArthur's original scheme.

Given the implicit redundancy of K and α in Eq. 5, it is more transparent to abandon K

altogether, and use the equivalent formulation, with $n+n^2$ rather than $2n+n^2$ parameters, of

(Kuno 1991; Mallet 2012)

$$\frac{dN_i}{dt} = N_i \left(r_i - \sum_j \alpha_{ij} N_j \right) \tag{6}$$

Eq. 6 is a very general description of genotype (or species) interactions. Unfortunately, $n + n^2$ is

a large number of parameters, making Eq. 6 difficult to use in full generality. Most models

implicitly or explicitly simplify the structure of the α-matrix in order to focus on phenomena of

interest. My argument here is that if resource use efficiency is acknowledged to be a phenomenon of interest, then Eq. 2, rather than Eq. 1, is a better way to simplify Eq. 6 in order to isolate this effect.

In Eq. 4, I propose the use of a model with $3n$ parameters, in order to capture resource use efficiency, maximum reproductive speed, and competitive ability. Eq. 4, unlike Eq. 6, is not a competitive Lotka-Volterra equation: its density-dependence is quadratic rather than linear. But because competitive Lotka-Volterra equations of the Eq. 6 form are so common in the theoretical ecology literature, I next attempt to obtain a $3n$-dimensional special case of Eq. 6 whose parameters can also be interpreted as low-density reproductive speed r, resource use efficiency K', and some version of high-density competitive ability c'. In particular, I seek a special case of the Eq. 6 α-matrix using only $3n$ parameters instead of $n+n^2$. The most reasonable option I could come up with is

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{1}{c_i'} \sum_j \frac{c_j' N_j}{K_j} \right)$$
(7)

Here, N_j/K_j represents the demand on resources coming from all individuals with genotype j. Multiplying this by c_j takes into account genotype j's ability to obtain those resources. Dividing by c_i puts genotype j's competitive ability into a context that is relative to the focal genotype i, representing the extent to which a genotype's own competitive abilities protect it from the attempts of others to take those resources. The term inside the parentheses describes the extent to which genotype i's growth is inhibited as a consequence of resource demands made by other members of the population, across all genotypes.

Eq. 7 has problems, and I consider it inferior to Eq. 4 for the purposes of describing three intuitive axes of selection, namely speed, efficiency, and competitiveness. In particular, the total quantity of resources used in Eq. 7 is a function of genotype frequencies even in the absence of genotypic differences in K. Nevertheless, the vector c' in Eq. 7 captures something with the flavor of competitive ability. Eq. 4 lacks this flaw, but is not a special case of the α-matrix; values of α are density-dependent rather than constant.

I introduce Eq. 7 primarily in order to make clearer what is going on in MacArthur's classical Eq. 1. Specifically, by setting $c'_j = K_j$ in Eq. 7, we recover Eq. 1. In other words, MacArthur's classical formulation of "K-selection", when expressed in terms of our Eq. 7 model, is equivalent to the simultaneous presence of both c'-selection and true K_j-selection on resource use efficiency alone. Instead of a tradeoff, selection on competitive ability c' has the side effect of increasing the efficiency of resource use K (and vice versa). It is therefore not surprising that MacArthur's K-selection has been found to be extremely potent. I do not believe that MacArthur's approach to K-selection leads to a sensible separation of traits into natural categories.

The range of behaviors open to a single density-dependent population with a fixed genotype can be described using only two dimensions, r and K (or equivalently but arguably more usefully, density-independent r and density-dependent r/K (Kuno 1991; Mallet 2012)). Interactions between multiple genotypes can greatly increase the dimensionality of the system. In this work, for maximum simplicity while still meeting my goals, I introduce only a single additional dimension, bringing the total to three.

My three-dimensional Eq. 4 model can in the future be extended to use more parameters to describe more phenomena, while still remaining below the $n + n^2$ parameter ceiling given by Eq. 6. The simplifying choice of three-dimensional structure for Eqs. 4 and 7 is driven by the intent to study directional selection within a single species. More diverse forms of α are common in the ecology literature, to capture factors other than three I focus on. For ecological interactions between different species, as opposed to evolutionary interactions between different genotypes, terms can be added to describe resource partitioning, and resulting disruptive selection, speciation and coexistence. Co-evolutionary arms races between interference and resistance mechanisms can create nontransitive interactions, greatly complicating the α matrix, and demanding the explicit modeling of tradeoffs specific to the mechanism of interference that is assumed. Another possible axis of selection is that on variance in the number of offspring (Gillespie 1974; Lambert 2006; Shpak and Proulx 2007), which affects the establishment probability of a new beneficial mutation.

I do not deny the importance of any of these phenomena, although note that highly complex α matrices are more important in interspecies ecology contexts. In experimental evolution, most invading mutants either sweep to fixation or are outcompeted via clonal interference. I seek to model these simple and "typical" adaptive sweeps, where mutations are far more often simply good or bad, rather than altering the delicate balance between competing goals. Adaptive mutants leading to coexistence do occur, but are rare enough to be highly remarkable (Blount et al. 2008).

My intention is to propose a conceptual breakdown that is rich enough to be interesting on its own, and also useful as a starting point against which still more complex scenarios can be compared. I focus on the benefits of switching from one or two fitness dimensions to three, in the process unifying population genetics with a simple form of density-dependence. I hope that this work will provide a firm basis for extensions to even more dimensions.

Defining correlations and tradeoffs between *r*, *K*, and *c*

Eq. 4 attempts to make a natural partition of incommensurable dimensions of fitness. Their incommensurability can be seen via their disparate units: *r* has units of time, *K* of population density per resource, and *c* is intrinsically unitless. Evolution takes place in a high-dimensional space; I hypothesize that the first three principal components of this space can be well approximated through an appropriate rotation of these three dimensions.

This choice of *r*, *K* and *c* is designed to be conceptually clean, rather than to presuppose the nature of genetic correlations and phenotypic tradeoffs, i.e. the exact rotation of the space. In contrast, non-constancy of *r* and/or *K* is often built into models of competitive ability because phenotypic tradeoffs and costs are assumed to accompany competitive strategies (Case and Gilpin 1974). The model presented here allows tradeoffs to be added later, rather built in *a priori*.

The nature of any tradeoffs is evolutionarily important. For example, if competitive relative fitness comes with an absolute fitness cost, then "evolutionary suicide", a special case of the tragedy of the commons, can sometimes occur (Ferrière 2000; Haldane 1932; Matsuda and

Abrams 1994; Rankin and López-Sepulcre 2005). Understanding the appropriate rotation of the space by defining the principal components within a fitness space of r, K, and c (and potentially additional dimensions) will inform the nature of tradeoffs, and hence the likelihood of such scenarios.

Principal components can be defined with respect to the distribution of new mutations, with respect to the distribution of adaptive fixation events, or with respect to standing genetic variation within or between populations. The principal components may be different in different cases. In particular, mutations and adaptations are more likely to define axes of better vs. worse, albeit as shaped by genetic correlations. Variation among populations is more likely to lie along lines of almost equally fit phenotypic tradeoffs (perhaps shaped by even stronger genetic and/or environmental correlations), although the Pareto front nature of this variation may be obscured by measurement in a single environment in which some populations perform better than others.

The principal components between species may be radically different to the various kinds of within-species comparisons listed above. In ecology, unlike evolution within a species, resource partitioning is likely to be a key player. Evolution has sometimes been seen to differ from ecology primarily in its slower timescale, albeit in a view that is now much disputed (Carroll et al. 2007; Hairston et al. 2005). I propose that a more substantive difference between ecology and evolutionary processes lies in the nature of newly introduced variation. In evolution, novelty enters by mutation, whereas in ecology it generally enters by migration or, in special and rarer circumstances, sympatric speciation. I hypothesize that the first three principal

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components of evolution, but not necessarily of ecology, can be well approximated by a rotation of a space defined by only by the three dimensions *r, K*, and *c*.

Measuring correlations and tradeoffs between *r, K*, and *c*

Finding the appropriate rotation of the three-dimensional space is a solvable empirical problem. *r* can be measured by fitting a logistic growth curve, *K* by measuring equilibrium population size or biomass, and the product *rc* by the outcome of pairwise, high-density competitions.

Interestingly, a number of empirical studies, in direct contradiction to MacArthur's hypothesis of an *r-K* tradeoff, have found that *r* and *K* are positively correlated with a slope close to 1. This result has been found for different species and strains of Paramecium (Luckinbill 1979), during group selection for high *r* in Paramecium (Luckinbill 1979), during selection for high *K* in *E. coli* (Luckinbill 1978), for a range of bacterial species-stressor combinations (Hendriks et al. 2005), for different *Nephotettix* leafhoppers species at different temperatures (Kuno 1991; Valle et al. 1989), and among antibiotic resistant mutants of *Pseudomonas fluorescens* (Fitzsimmons et al. 2010). This points to a tight *r-K* link exists along a "better-worse" axis. A principal "better-worse" axis can explain why a mutation that improves fitness in one environment so often also improves it in others (Ostrowski et al. 2005).

This finding is not universal. In Lenski's experimental lines, *r* and *K* initially went up in tandem, but then eventually spread out across a tradeoff curve (Novak et al. 2006). *K*-selection led to a correlated decrease in *r* in *Lactococcus lactis*, corresponding in part to a switch away from

lactate production and towards acetate, formate, and ethanol metabolic end products (Bachmann et al. 2013). A tradeoff between r and K has been observed during the experimental evolution of haploid but not diploid *Saccharomyces cerevisiae* (Jasmin et al. 2012). Note that a negative r-K correlation was also found for variation among clones from the same yeast strain; this negative correlation was also found in replicate studies of the same clone, pointing to an environmental cause that could confound this and other assays of closely related genotypes (Jasmin and Zeyl 2012).

Notwithstanding the exceptions, there remains substantial evidence that a tightly coupled r-K axis is common, with a slope often near 1. Recall that changes in the density-independent death rate μ affect r and K by an equal factor. The frequently observed slope of 1 between r and K therefore suggests that the density-independent death rate μ describes a first principal component across a range of circumstances, from standing variation among strains tested in the same environment, to the variety of adaptive mutations arising in the same ancestral genotype.

Competitive ability is an obvious candidate for a second principal component. The ability to emerge victorious from a high-density competition is described by the product rc in Eq. 4. Competitive ability is negatively correlated with r among Paramecium strains and species (Luckinbill 1979). High density *Drosophila* populations evolve competitive ability that also trades off with low-density growth rate r (Mueller et al. 1991; Mueller and Ayala 1981). In some cases, e.g. high density populations of *E. coli*, the evolution of a costly inhibitory substance may

be responsible for this tradeoff (Luckinbill 1978). A principal component of *c* or *rc* is a serious contender, subject to a tradeoff with μ.

Recent advances in high-throughput robotics-based experimental evolution have the potential to go beyond these literature-inspired speculations, and define the principal components more precisely in a range of different circumstances. As well as increased rigor and precision, this can increase the subtlety of the questions asked. For example, is the *r-K* relationship following *r*-selection the same as the relationship following *K*-selection? For these purposes, we need to be able to vary both the nature of selection and the measurement of fitness.

Note that *K*-selection on microbial yield is group selection, which is absent from most experimental evolution setups. But it need not be. Microbial metapopulations can be created in an emulsion, where many small and separated droplets of growth medium are seeded with only one cell per droplet, allowing growth up to the carrying capacity of the droplet, and then remixing and diluting to seed a new generation of droplets (Bachmann et al. 2013). This protocol selects for both increased biomass (*K*) and reduced cell size.

Microfluidics also allow for more complex protocols at the level of the droplet (Agresti et al. 2010). For example, premature colony death and/or more complex droplet "colonization" protocols introduce an additional component of *r*-selection, and the resulting balance between *r*- and *K*-selection can be altered through these parameters and/or via droplet size (Frank 2010). Seeding droplets with more initial cells of potentially different genotypes introduces c-selection and increases *r*-selection (Frank 2010).

If batch culture is used, frequent transfers at fixed times yield approximately *r*-selection, while less frequent transfer (Becks and Agrawal 2013), or transfer only once a given density is reached (Yi and Dean 2013), yields a mix of *r*- and *c*-selection. Different conditions can yield qualitatively different evolutionary outcomes; for example, when both *r*-selection and *c*-selection are present, a temporally varying environment allows coexistence rather than competitive exclusion (Dean 2005; Yi and Dean 2013). But quantitative analysis is difficult in batch culture, especially when the mix of *r*- and *c*- itself evolves over the course of an experiment.

Chemostat options

A turbidostat seems ideal for the quantitative study of fitness dimensions, maintaining a microbial combination at a defined and constant density via rapid but variable dilution. At the limit of low density, we achieve something close to pure *r*-selection. As the turbidostat is adjusted to higher density, we move along a continuous scale of falling *r*-selection and rising *c*-selection, until at very low dilution rates, the product *rc* dominates.

Failing that, a chemostat, with a fixed dilution rate, is simpler and more practical. In a chemostat, the exponential growth rate adjusts until it is equal to the externally set dilution rate. Consider a chemostat with a single genotype, dilution at rate μ and negligible other cell death, such that $dN/dt = bN(1-N/K)-\mu N$. Then the population size N rapidly adjusts to an equilibrium value of $K(b-\mu)/b$. By varying μ, values of K and b can be calculated for that single type. This was done in *Saccharomyces cerevisiae* by Brauer et al. (2008), who saw very linear dilution-biomass density relationships for chemostats limited by leucine or uracil, somewhat

linear relationships for limitation by ammonia, phosphate or sulfate, and a non-monotonic

relationship for glucose limitation. For further analysis, environmental conditions showing a

linear relationship should be chosen. For example, $K \sim$ 150 Klett units for uracil limitation, with

$b \sim 1$ h^{-1}.

Now consider the introduction of a new allele. When rare, its Eq. 4 dynamics are can be

approximated by

$$\frac{dN'}{dt} = b'N'\left(1 + \frac{K(b-\mu)}{b}\left(\frac{c'}{c}-1\right)\right)\left(1 - \frac{K(b-\mu)}{b}\right) - \mu N' \tag{8}$$

This equation is quadratic in μ, allowing values of b' and c'/c to be calculated from a curve of

invasion rate as a function of μ. If the results do not fit a quadratic, this would suggest that the

quadratic density-dependence of Eq. 4 is not the best choice, and point to improved

quantitative models for competition vs. growth tradeoff as a function of density.

The experiment just described is designed to study density-dependence. Many other

experiments also study density-dependence, but unwittingly. Any time that pleiotropy is

studied by exposing the same genotypes to different environments, it is possible that

environment-specific performance is a function not of the deliberately manipulated

environmental variable, but instead of the unwittingly manipulated total population density.

This is a confounding factor any time that population density depends on the environment – in

other words, almost all of the time.

One approach to this confounding problem is to fine-tune the permissiveness of conditions and hence match density in the different environmental conditions. The alternative approach advocated here is to first focus on understanding how the fitness of alleles depends on density, and only turn to different abiotic environments once we have a baseline understanding to basic questions, e.g. whether Eq. 8 does fit a quadratic.

Understanding density-dependent fitness means assembling a panel of closely related genotypes of interest, and assaying their values of r, c and K. Assays of random mutants define the fitness axes of mutation bias. Note that different loci may consistently map to different axes (Agrawal 2010; Laffafian et al. 2010). Assays of polymorphisms within adapted populations define selective tradeoffs. Assays of adaptive substitutions define the axes of adaptation, constrained both by mutation bias and by selective tradeoffs. Substantial evolutionary insight can be obtained by comparing these different cases.

Usefulness as a conceptual framework

The model presented here can be used as a framework for detailed and quantitative studies of density dependence using rich datasets designed for the purpose, ideally combining chemostat and emulsion experiments, as described in the section above. But the model is also useful in a more basic way, as a conceptual framework to replace vestiges of the flawed r/K scheme. Here I briefly mention two examples from the literature, one microbial and one not, where this struggle with the flaws of r/K selection was evident in a published paper. I have no doubt that many more such conceptual struggles occur within research groups without making into the final published works.

First, killifish populations with genetic backgrounds adapted in the wild to low density had higher r, equal carrying capacities, and lower competitive ability than those adapted to high density (Travis et al. 2013). In my three-dimensional scheme, the finding of equal carrying capacities in populations adapted to different densities is no longer a puzzle. This is not the case in two-dimensional r/K schemes, when high-density is falsely equated with selection on carrying capacity.

Similarly in an experimental microbial system, Bull et al. (2006) noted results that could be interpreted as initial r-selection at low viral density, followed by "K-selection" later on in the experiment after density rose. However, while mentioning this r/K interpretation, the authors then explicitly distanced themselves from it, primarily because of problems regarding the interpretation of K (which in their case corresponds to my c). My model would not only provide a more suitable conceptual framework for interpreting their results, but would also suggest further experiments to measure r, K and c for isolated genotypes of interest. Metapopulation systems (Kerr et al. 2006; MacLean and Gudelj 2006) can bring true K-selection into stories such as this.

Many anomalies are the result of confounding c and K (Joshi et al. 2001), and disappear when the three dimensional scheme of Eq. 4 is adopted as a conceptual framework.

The multidimensional nature of fitness itself

A good description of evolution must take both relative and absolute competitions into account. Clearly, fitness is sometimes relative; evolution is subject to zero-sum arms races. But not all selection can be relative, or else extinction would never occur. This manuscript explores the possibility that the best description of evolution is not *in-between*, but *both* relative and absolute competition (Clarke 1973). In other words, not only phenotype, but fitness itself is a multi-dimensional construct. The incommensurability of the dimensions can be seen by their different units: time for reproductive speed r, resource and population densities for resource use efficiency K', and no units for the normalizable axis of competitive ability c. Evolution takes place in a multidimensional fitness space defined by these and perhaps other dimensions.

The literature on incommensurable fitness components has been characterized by binary comparisons, each of which is subsumed into my three-dimensional scheme. The relative fitness w of the Wright-Fisher model is in my c dimension, while absolute fitness (with units) is in r and K. MacArthur's high density K-selection is divided into c and K components as well as being contrasted with low density r-selection. Group selection is described by K'-selection, while r- and c-selection act on individuals. Sexual selection acts on c, while a very classic view of natural selection acts on μ, representing a common axis of r and K.

A basic understanding of the nature of density-dependent fitness is accessible not only conceptually, but also experimentally in the era of high-throughput experimental evolution. It is essential building block for the unification of evolutionary and ecological theories.

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