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Interim Report **IR-06-061**

Fitness

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Contents

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Abstract

The fitness concept of evolutionary ecology differs from that of population genetics. The former is geared towards dealing with long term evolution through the repeated invasion of mutants for potentially complicated ecological scenarios, the latter with short term changes in relative frequencies of types for heavily simplified ecological scenarios.

After a discussion of the conditions allowing for the definition of a general invasion fitness concept, among which that reproduction should be clonal, a framework is built within which the definition can be formalized. Recipes are given for calculating (proxies for) fitness in a large variety of instances.

The main use of invasion fitness is in ESS calculations. Only under ecologically very special conditions ESSes can be calculated from optimization principles. These conditions are detailed, as well as the, even more special, conditions under which evolution maximizes r or R_0.

The invasion fitness concept extends to any aggregates treatable as meta-individuals. Individual- and meta-individual-level invasion fitness coincide when the latter is larger than per capita within aggregate growth. Calculating invasion fitness through a meta-individual route often works beyond calculations based on inclusive fitness arguments, but provides less insight.

Mendelian diploids are aggregates of clonally reproducing genes. Conditions are given for when predictions for virtual cloning diploids coincide with those from gene-based calculations.

History and context

Darwin

Although fitness is generally perceived as the central concept of Darwinism, Darwin used the word only once in the first to the fifth, and twice in the sixth edition of the Origin of Species, and then only in the meaning of adaptedness. In the fifth edition, he, on the recommendation of Wallace, added the phrase "survival of the fittest„ due to Herbert Spencer, as synonym for natural selection. However, Darwin's reasoning was throughout qualitative and he nowhere considered quantitative measures that might determine the speed of evolutionary change.

The founders of the modern synthesis

What may be the first use of the term fitness in its modern meaning, as a quantitative measure of the contribution of a particular type to future generations, occurs in 1922 in a paper by Fisher. However, mostly the three founders of theoretical evolutionary biology, Fisher, Haldane, and Wright, were unexpectedly reticent in their use of the term. When it comes to quantitative considerations, they use words like selective value, adaptive value, or selective advantage. One gets the impression that they avoided using the term fitness in specific contexts in order not to tie it to too specific a meaning: their verbal deliberations point at a strong awareness of the complications present in real life (such as overlapping generations, spatial differentiation of populations, fluctuating environments, frequency dependence caused by competitive interactions, and complicated genetic architectures) which are only very partially represented in specific models. Although Haldane's book "The causes of Evolution„ contains a special chapter on fitness, the discussion there is wholly qualitative, stressing the dependence on the environment.

In their later work, Fisher and Wright do use the term fitness, but only when referring to populations, as in Fisher's statement of his fundamental theorem "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time„ which in modern translation reads: The rate of increase of mean fitness of any closed population at any time is equal to the additive genetic variance in fitness present at that time.

In the context of this entry it is relevant to note that Fisher was well aware of the incompatibility of a continuing increase of mean fitness (i.e., the instantaneous per capita growth rate of all different types together) with the ultimate boundedness of any population, and that he pointed to the dynamics of the community as a whole as the source of environmental deterioration compensating for such an increase. However, his attempt at a phenomenological formalization failed to capture that the feedback loop between population and environment necessarily on a community dynamical time scale brings the time averaged mean fitness of the population back to exactly zero. Precisely this consequence will be basic to the arguments below.

Although the founding fathers were well aware of the complicated life histories occurring in the real world, Wright and Haldane to a large extent restricted their calculations to genetically ever more complicated variants of viability selection in populations with non-overlapping generations (below called simple viability selection) in order to get more quickly at useful conclusions. For population dynamically more elaborate models, they compared the outcomes with those of simple viability selection models, but they made no attempts at arriving at more encompassing ecological perspectives, presumably since the genetics itself already proved sufficiently challenging.

Fisher almost from the start attempted to incorporate age structure. However, he did this on the basis of the mistaken conviction that for general age structured populations it is possible by weighing individuals with their so-called reproductive values to arrive at the differential expressions that are nowadays standard used for uncovering the consequences of weak simple viability selection (with the Malthusian parameter substituted for the logarithm of the viabilities). Malthusian parameters and reproductive values are tied to clonal reproduction, and the properties that in the clonal case justify the derivation of the differential expressions unfortunately do not extend to the Mendelian case.

Population genetics

Population genetics textbooks, for obvious didactical reasons, also tend to concentrate on scenarios akin to simple viability selection, with the relative viabilities independent of the population density and genetic constitution. In contrast with the early tradition, the textbooks refer to the viabilities as fitnesses, thus making in the minds of new generations of population geneticists fitness effectively synonymous with viability. The advantage of the so restricted universe of discourse is that one can consider fitnesses on an instantaneous and local basis. One may thus consider models in which fitnesses vary in time, over space, or with the local gene frequencies or population densities. The other advantage of the restriction to simplified life histories is that it allows population geneticist to concentrate on cataloguing the dynamic consequences of the variety of genotype to fitness maps, as well as mating and transmission rules.

Evolutionary ecology

The more recent research program of evolutionary ecology focuses on the evolution of behavioral and demographic parameters in ecologically less simplified situations. Yet, in textbooks on the subject, simple viability selection models figure heavily in any chapters devoted to genetics, although on a verbal level fitness tends to be identified unrestrictedly with expected lifetime offspring production (= average number of offspring contributed to the next generation). In addition, the Malthusian parameter, also called intrinsic rate of (natural) increase, is introduced as an appropriate measure of fitness. Usually it is left somewhat open when, and more importantly why, one or the other measure is relevant, although one finds statements to the effect that for arriving at evolutionary predictions one should maximize lifetime offspring production in the case of stable environments, and the intrinsic rate of increase in environments that are constant except for occasional decimating catastrophes. Although steps in the right direction, neither statement fully captures the intricacies of the issue.

Below it will be argued that for a fair collection of ecological scenarios and given certain minimal requirements, there exists a unique fitness concept, to be referred to as invasion fitness, that may serve as universal reference. This invasion fitness is in the first place a theoretical entity that earns its keep as tool in powerful deductive arguments and from being calculable from models fed with more concrete data. Measuring it directly is very difficult, except in the simplest possible ecologies. To make things worse, single measurements are of little use, as the interest of invasion fitness derives from what its values are for potential mutants and how these values change with changes in the environment. For general eco-evolutionary models, it is only possible to calculate invasion fitnesses by numerical means. Only under special circumstances and for purposes that are more restricted, invasion fitness can be expressed in a simple manner or replaced by simple proxies like lifetime offspring number. In a still smaller subset of cases it may even be possible to directly measure some component of fitness (say, survival probability or offspring number) that by invoking a ceteris paribus assumption can be argued to be monotone related to fitness. This proxy then may be used to rank types in order of increasing fitness. The section on uses discusses the theoretical restrictions on the application of such simplified procedures.

Setting the stage

Individuals and types

Epistemologically, fitness is not a property of individuals, but of types. Individuals do not have a probability to die before maturity; they just die or survive. Moreover, the phrase that fitness is a property of types only makes sense under an implicit ceteris paribus condition, as the fitness of a type necessarily depends on the environment in which it lives. Hence, except in very restricted cases, fitness should be treated not as a single number, but as a function of two variables, type and environment.

What objects should be considered individuals, as well as the attribution of types, depends on the evolutionary question. About the only restriction is that adaptive evolution crucially depends on the almost faithfulness of reproduction, i.e., offspring should nearly always have the same type as their parents or at least a very very similar type. If this were not the case, the smearing out over type space would overwhelm any evolutionary dynamics due to selection. This also means that the appropriate reference frame for any definition of fitness is clonal reproduction. The connection with the Mendelian world is made by observing that alleles reproduce clonally.

Environments

When considering environments, a strict individual centered perspective is called for. Only individuals reproduce. Hence, the description of the environment should contain all information relevant for predicting that reproduction, including any direct influences exerted by conspecifics. A second restriction is that the environment should have some stability. It should not keep changing directionally over time, nor should one consider more environmental regimes occurring with nonzero probabilities that once realized exclude each other for all time. More technically expressed: environments should be ergodic. Ergodic environments comprise point equilibria, limit cycles, and most relevant chaotic and stochastic environmental regimes.

Another point is that to cover the ubiquity of short-term environmental fluctuations, evolutionary environments should be considered as extended in time. To separate the evolutionary concept of environment from the instantaneous perspective common in ecological models, it is useful to refer to the instantaneous values taken by the evolutionary environment as environmental conditions. General evolutionary environments can then be characterized as 'ergodic stochastic processes with as realizations functions of time to the environmental conditions'.

A final restriction is that it makes only sense to look at environments that can occur in (some appropriate abstraction of) the real world, be it observed time series or the output of a community dynamical model. As this entry concentrates on the long-term view, this means that the only relevant environments are ones that can be realized as (outputs from) community dynamical attractors, including stochastic ones, either in ecological reality or in the world of ecological models.

Population structure

Usually individuals of the same type and exposed to the same environment are still not demographically equal; some are small, others large, some may be young, others old, with all these differences feeding through to their population dynamical behavior. Such diversity can be dealt with by introducing the idea of population structure. Here structure means that individuals are distinguished by their h(eterogeneity)-state. This h-state may be composed of a location in space and a physiological state. To classify as a state, (i) all population dynamical behavior of individuals at a particular point in time, be it dieing, giving birth, or impinging on the environment, should be fully determined by the current state and environmental condition, (ii) an individual's future states should be fully determined by its present state and the intervening environmental conditions. Fully determined should be interpreted here in a stochastic sense, i.e., given the indicated information, the behavior or future states are independent of any further adducible information. Conditions (i) and (ii) form a restriction on the combined choices for describing h-states and environments. Arriving at good h-state and environment descriptions is an essential step in the craft of translating from the real to the model world.

Populations in turn should be defined by the requirement that all individuals share the same environment. Populations living under spatially heterogeneous conditions may be accommodated by making spatial position a component of an individual's h-state and letting the environmental condition be a function of spatial locations to local environmental conditions, with individuals only being affected by a local environmental condition singled out according to their h-state.

The definitions of population, h-state and environment have as consequence that given the course of the environment individuals proceed through their lives independently. This conditional independence property forms the basis of all further deliberations.

Infinite dilution

The previous deliberations dealt with concept engineering. To arrive at a general fitness definition also an assumption is needed: any influences of the focal population on the environment can be neglected. This will be referred to as the infinite dilution assumption. It is needed to justify speaking of the environment as a second independent variable coordinate with the traits.

Although infinite dilution of population effects is sufficient for delimiting a framework within which to define invasion fitness, to make the resulting concept into a useful tool a more refined variant is needed: The influence single individuals exert on the environment is negligible, although for large populations the effect of the added individual contributions may be substantial. This individual-centered concept of infinite dilution has the advantage that it encompasses both large resident and small invader populations. Under the assumption that individual effects are infinitely diluted, the effect of any small focal (sub)population, be it a mutant population or any other subpopulation having our attention, will also be infinitely diluted. The individual-centered infinite dilution assumption will be operative throughout the next three sections, to be replaced by slightly extended version thereafter.

Of course, a growing focal population will not forever stay infinitely diluted. Yet, for populations starting from only a few founders, as is i.a. the case for mutants, the infinite dilution approximation often is sufficiently good for a sufficiently long time that many biological conclusions can be based on it. The fact that in most modeling contexts small invader populations as well as populations on the brink of extinction are close to infinitely diluted, allows bringing many fluctuating physiologically and spatially structured population models almost fully in line with simple viability selection counterparts.

Invasion fitness, fundamentals

Underlying mathematical structure

For expository purposes, assume for the time being that the number of h-states is finite. In that case, the expected numbers of individuals in different h-states at time t for a given realized environment **E** can be written as a column vector $\mathbf{N}(t)$. If it is moreover assumed that time runs in steps, the definitions of state and environment introduced above make it possible to write

$$\mathbf{N}(t+1) = \mathbf{A}\big(\mathbf{E}(t)\big)\mathbf{N}(t), \tag{1}$$

while for continuous time

$$\frac{\mathrm{d}}{\mathrm{d}t}\mathbf{N}(t) = \mathbf{B}\big(\mathbf{E}(t)\big)\mathbf{N}(t). \tag{2}$$

The i,j-th component of the matrix **A** equals the probability of a transition from h-state j to h-state i, multiplied with the corresponding survival probability, plus the average number of offspring with h-state i produced by an individual in h-state j. The matrix **B** is built up from per capita rates. The off-diagonal components equal the transition rates between the corresponding h-states plus the h-state dependent average rates of offspring production differentiated according to their birth h-state. The diagonal components equal minus the overall rates of state transitions from the h-states, minus the h-state dependent death rates, plus the average rates of giving birth to offspring with the parental h-state.

Equations (1) and (2) apply to populations of all sizes, large as well as small, but with different interpretations. Small populations do not influence the environment, but are subject to demographic chance fluctuations. Hence **N** in Equations (1) and (2) refers only to the expected and not to the realized population state. For large populations, the components of **N** may be interpreted as realized population densities in a large spatial area or volume. The step from expected numbers to realized densities is based on law-of-large-number considerations. Moreover, for large populations the assumption that **E** is given independent of **N** takes on the status of a thought experiment and not that of an idealized representation of reality. In reality the feedback loop is closed, that is, **E** is determined at least in part by **N**. (As example let $\mathbf{E}(t)=\mathbf{F}(\mathbf{O}(t))$ with the population output **O** given by $\mathbf{O}(t)=\mathbf{HN}(t)$, with **H** a matrix consisting of weight factors telling the extent to which individuals in different h-states impinge on various aspects of the environment and **F** determined by a fast dynamics of the environmental state plus the map from environmental states to the environmental conditions experienced by the focal individuals.)

The situation for infinitely many h-states is not different in principle, except that to deal with it more powerful abstract machinery has to be invoked. This is still an active research area. In the general case, even the appropriate law-of-large-number theorems have not been proven. However, all evidence indicates that under biologically reasonable restrictions the picture will be similar to that for finitely many h-states. Below, little distinction will be made between finite and infinite h-state spaces. However, the reader should bear in mind that the most general statements have in the strict mathematical sense only the status of conjectures.

Notational conventions

The need to keep track of many different mathematical objects could lead to a notational explosion. Adherence to strict mathematical consistency throughout the entry would have necessitated writing equation (1) as e.g.

$$\mathbf{N}\big(\mathbf{X}_\mathrm{m} \mid \mathbf{E}_\mathrm{attr}(\mathbf{X}_\mathrm{r})\big)(t+1)=\mathbf{A}\big(\mathbf{X}_\mathrm{m} \mid \mathbf{E}_\mathrm{attr}(\mathbf{X}_\mathrm{r})(t)\big)\mathbf{N}\big(\mathbf{X}_\mathrm{m} \mid \mathbf{E}_\mathrm{attr}(\mathbf{X}_\mathrm{r})\big)(t),$$

with '|' to be read as 'for the given', $\mathbf{X}_\mathrm{m}$ and $\mathbf{X}_\mathrm{r}$ the mutant respectively resident trait vectors, $\mathbf{E}_\mathrm{attr}(\mathbf{X}_\mathrm{r})$ the environment produced by $\mathbf{X}_\mathrm{r}$, and $\mathbf{E}_\mathrm{attr}(\mathbf{X}_\mathrm{r})(t)$ the corresponding environmental condition at *t*. This notational explosion is prevented by only displaying the symbols figuring in the specific argument at hand. For example, $\mathbf{A}\big(\mathbf{X}_\mathrm{m} \mid \mathbf{E}_\mathrm{attr}(\mathbf{X}_\mathrm{r})(t)\big)$ is written as just $\mathbf{A}(t)$ when the argument is only about temporal fluctuations.

Vectors are assumed to be written as columns, with the transposition operator $^\mathrm{T}$ transforming columns into rows. Differentiating a scalar for a column produces a row. In products, row vectors will be treated on equal footing with matrices. $\mathbf{1}^\mathrm{T}$ denotes $(1,\cdots,1)$ and $n=\mathbf{1}^\mathrm{T}\mathbf{N}$ total population size or density. Angular brackets, $\langle\ \rangle$, denote averaging.

Definition

Thanks to the preceding conceptual dissection of population dynamical processes it is now possible to arrive at a general fitness definition by falling back on a mathematical result that is easy to state but very difficult to prove. Luckily, a suite of mathematicians has done the latter already and the result is known as the multiplicative ergodic theorem. This theorem deals with general ergodic sequences of matrices. The matrices in (1) are restricted to having nonnegative components, and a similar result applies to the solutions of (2). From this combination the following fact emerges: Under some technical conditions

> in ergodic environments
>
> $$\lim_{t\to\infty}\frac{1}{t}\ln\big(n(t)\big)=\rho \qquad (3)$$
>
> with ρ a unique real number, which mathematicians call the dominant Lyapunov exponent and that here will be called invasion fitness (on the presupposition that **E** is generated as the output of some community dynamics).

The technical conditions are somewhat involved, but are generally fulfilled in biological applications. For example, it suffices that all the components of the matrices **A** are smaller than some uniform upper bound, and that for any initial condition after sufficient time all components of **N** are bound to be positive.

Phases of the invasion process

Invasion fitness summarizes the essential features of the initial stages of any invasion process. Two possibilities have to be distinguished. The general mathematical theory of branching processes tells that the prospective invader will die out when ρ is negative or zero, and has positive establishment probability when ρ is positive. In the latter case, there will be a short initial phase during which the effects of the initial chance fluctuations on the population structure still are discernable in the form of the population trajectory. After that phase the population grows roughly exponentially with rate constant ρ, although with possibly a good amount of wobble due to the variations in $\mathbf{E}(t)$. (This clear differentiation in phases only holds good under some technical conditions, which, however, are sufficiently relaxed that from a practical point of view there is little to worry about.) The exponential phase ends only when the infinite dilution Ansatz starts to fail due to the increase of invader numbers.

Invasion fitness, general calculation procedures

Without population structure

For a start consider the case without any population structure and with time running in steps, i.e., generations do not overlap and newborns are stochastically equal (i.e., parents do not bequeath any properties other than long term heritable traits). Then

$$\rho = \left\langle r\left(\mathbf{E}(t)\right)\right\rangle_{\text{time}} \tag{4}$$

with

$$r = \ln\left(R\right) \tag{5}$$

and

$$R\left(\mathbf{E}(t)\right) = \left\langle \text{individual offspring numbers } \right\rangle_{\text{individuals}} \Big| \mathbf{E}(t)\,. \tag{6}$$

Formula (4) also applies for unstructured populations in continuous time described by

$$\frac{\mathrm{d}n}{\mathrm{d}t} = r\left(\mathbf{E}(t)\right)n\,. \tag{7}$$

(Note that here $r\left(\mathbf{E}(t)\right)$ is itself an average over the stochastic behavior of individuals, which themselves just give birth and die.)

By letting $\square\{\mathrm{d}\bar{\mathbf{E}}\}$ denote the fraction of time $\mathbf{E}(t)$ spends in a small set $\{\mathrm{d}\bar{\mathbf{E}}\}$, the time average in (4) can be re-expressed as

$$\rho = \int r\left(\bar{\mathbf{E}}\right)\square\{\mathrm{d}\bar{\mathbf{E}}\}\,. \tag{8}$$

Formula (8) is particularly useful in the context of stochastic population models where it may be relatively easy to calculate $\square$.

Non-fluctuating environments

As next simple case, consider a structured population in a constant environment. Then in discrete time

$$\rho = \ln\left(\text{dominant eigenvalue of } \mathbf{A}\right), \tag{9}$$

and in continuous time

$$\rho = \text{dominant eigenvalue of } \mathbf{B}\,. \tag{10}$$

For constant environments ρ is sometimes called Malthusian parameter, in which case it is often written as *m*, or intrinsic rate of increase, in which case it is usually written as *r*. The corresponding right eigenvector of $\mathbf{A}$, or $\mathbf{B}$, is called stationary h-state distribution, with usually some more germane expression substituted for ‘h-state’, while the components of the left eigenvector are called reproductive values.

Expressions (9) and (10) lead to useful algebraic procedures only when either the numbers of h-states is very small or when the matrices **A** or **B** have some special structure, as is for example the case when the h-state is age. Otherwise it is necessary to take recourse to numerics.

The most efficient numerical procedure for calculating the dominant eigenvalue of a large nonnegative matrix is by iteration:

- Start from some positive vector $\mathbf{M}(0)$ with $\mathbf{1}^{\mathrm{T}}\mathbf{M}(0)=1$.
- Successively calculate $\mathbf{M}(t)$ from
  $\mathbf{L}(t+1)=\mathbf{A}\mathbf{M}(t), \quad w(t)=\mathbf{1}^{\mathrm{T}}\mathbf{L}(t+1), \quad \mathbf{M}(t+1)=\frac{1}{w(t)}\mathbf{L}(t+1)$.
- $w(t)$ then converges to the dominant eigenvalue of **A**: $\rho=\ln\left(\lim_{t\to\infty}w(t)\right)$.

Since for a population state **N**, $\mathbf{1}^{\mathrm{T}}\mathbf{N}$ corresponds to the total population size, $w(t)$ can be interpreted as a per capita increase in population size. Therefore, this iterative procedure is equivalent to estimating an asymptotic population growth rate from a deterministic simulation.

The continuous time case can be dealt with numerically by first calculating the dominant eigenvalue of the nonnegative matrix $\mathbf{B}+\beta\mathbf{I}$, with β minus the most negative diagonal component of $\mathbf{B}$, and subtracting β from the result.

Periodic environments

The previous formulas extend to *T*-periodic environments by the following ploy:

- For discrete time, define $\mathbf{C}(T)=\mathbf{A}(T-1)\cdots\mathbf{A}(0)$.
- For continuous time, calculate $\mathbf{C}(T)$ by numerically solving
  $$\frac{\mathrm{d}\mathbf{C}}{\mathrm{d}t}=\mathbf{B}(t)\mathbf{C}, \quad \mathbf{C}(0)=\mathbf{I}.$$
- Calculate $\rho=\frac{1}{T}\ln\left(\text{dominant eigenvalue of }\mathbf{C}(T)\right)$.

General fluctuating environments

For general fluctuating environments ρ can be calculated through the following scheme:

- Start from some positive vector $\mathbf{M}(0)$, with $\mathbf{1}^{\mathrm{T}}\mathbf{M}(0)=1$
- Successively calculate vectors $\mathbf{M}(t)$ and numbers $w(t)$, $t=1,2,\cdots$, from:
  - As an intermediate step, first calculate a vector $\mathbf{L}(t+1)$ from
    for discrete time,
    $$\mathbf{L}(t+1)=\mathbf{A}(t)\mathbf{M}(t),$$
    for continuous time,
    $$\frac{\mathrm{d}\mathbf{L}}{\mathrm{d}\tau}=\mathbf{B}(\tau)\mathbf{L} \text{ with } \tau \text{ running from } t \text{ to } t+1 \text{ and } \mathbf{L}(t)=\mathbf{M}(t).$$
  - From $\mathbf{L}(t+1)$ calculate the average per capita population growth $w(t)$ over that step
    $$w(t)=\mathbf{1}^{\mathrm{T}}\mathbf{L}(t+1).$$
  - Normalize to
    $$\mathbf{M}(t+1)=\frac{1}{w(t)}\mathbf{L}(t+1).$$
- Calculate fitness as
  $$\rho=\lim_{T\to\infty}\frac{1}{T}\sum_{t=0}^{T-1}\ln\left(w(t)\right).$$

Beyond matrix models

For general structured population models a procedure similar to the last described one may be used, with $\mathbf{M}(0)$ any normalized h-state distribution, from which then the h-state distribution

$\mathbf{L}(t+1)$ and the total population growth over one time step, $w(t)$, are calculated by some numerical technique appropriate for that model. For constant environments the last step can be simplified to $\rho = \ln\left(\lim_{t\to\infty} w(t)\right)$.

The section on constant environments treats a number of halfway analytical procedures pertaining to restricted model classes.

A fitness perspective on the resident environment

Residents have fitness zero

For any long existing community, at the **E** generated by that community the invasion fitnesses of all composing types equal zero. This is because any type that has invasion fitness different from zero either explodes or dies out, and therefore cannot be a permanent member of the community. For community models having equilibria corresponding to non-fluctuating environments, setting the invasion fitnesses of all types equal to zero produces as many equations for **E** as there are types. These can be combined with the equilibrium equations derived from the mechanisms that produce the environmental condition from the population outputs to the environment. The latter output can be calculated from the population sizes times the corresponding normalized stationary h-state distributions. The resulting set of equations precisely matches the set of unknowns, so that it is possible in principle through this route to determine the environments that can be generated by the community.

Generalized Lotka-Volterra communities

Generalized Lotka-Volterra communities are toy models for which it is very easy to calculate the invasion fitness for new potential community members. Although these models are biologically rather unrealistic, their easy accessibility makes them ideally suited for the initial exploration of ideas, and the construction of examples or counterexamples. In continuous time, for $i = 1,\cdots,k$,

$$\frac{\mathrm{d}n(\mathbf{X}_i)}{\mathrm{d}t}(t) = \left[b(\mathbf{X}_i) - \sum_{j=1}^{k} c(\mathbf{X}_i,\mathbf{X}_j) e(\mathbf{X}_j, n(\mathbf{X}_j), \mathbf{E}_1)(t) \right] n(\mathbf{X}_i)(t),$$

with $\mathbf{E}_1$ consisting of some additional environmental variables, like the weather, various weighted sums of the $n(\mathbf{X}_i)$, etc., and e some recipe that when fed with a trait vector $\mathbf{X}$ and scalar and vectorial time functions n and $\mathbf{E}_1$ produces a scalar time function $e(\mathbf{X}, n, \mathbf{E}_1)$. Similarly in discrete time

$$n(\mathbf{X}_i)(t+1) = \mathrm{e}^{\left[b(X_i) - \sum_{j=1}^{k} c(\mathbf{X}_i,\mathbf{X}_j) e(\mathbf{X}_j, n(\mathbf{X}_j), \mathbf{E}_1)(t) \right]} n(\mathbf{X}_i)(t).$$

For these models the invasion fitness for a new type $\mathbf{X}_{k+1} = \mathbf{Y}$ equals

$$\rho(\mathbf{Y}) = b(\mathbf{Y}) - \sum_{j=1}^{k} c(\mathbf{X}_i,\mathbf{X}_j) \bar{e}_j,$$

with the $\bar{e}_j = \left\langle e(\mathbf{X}_j, n_j, \mathbf{E}_1)(t) \right\rangle_{\text{time}}$ determined from the *k* linear equations in *k* unknowns resulting from setting $\rho(\mathbf{X}_i) = 0$ for $i = 1,\cdots,k$.

Uses

Predicting individual characteristics

The reason to spend effort on arriving at a proper fitness definition is primarily pragmatical. Prediction of evolutionary outcomes by maximizing fitness is a huge industry. Literally interpreted, a fair part of the older evolutionary ecology literature makes no sense as it (a) recommends maximizing the Malthusian parameter without ever mentioning environments and (b) invokes Fisher's fundamental theorem as justification. Yet, in practice it did a good job. The reason is that at evolutionary stops, invasion fitness cannot be but maximal for the environment generated by the corresponding population dynamics, for if it were not, there would be many possible mutants that by invading could set evolution moving again (an idea first put forward by Hamilton, and made popular through the efforts of Maynard Smith). Hence, if one does not account for the dynamics of the environment but just measures it, it is possible to predict the properties of organisms through fitness maximization. Such predictions can work when environments stay unperturbed, but not if one wants to predict the consequences of e.g. climate change, as then any evolutionary change necessarily carries population dynamically generated environmental change in its wake.

The above characterization of evolutionary stops is usually referred to as the ESS criterion. ESS is an abbreviation of “Evolutionarily Stable Strategy„ which, however, is a misnomer as the so defined strategies need not be evolutionarily stable in the standard meaning of the word stable. The latter requires that the ESS through the continued substitution of mutations be approached from nearby strategies. Evolutionary attractiveness can only be judged by seeing how the fitness landscape changes with a change in the resident strategy. Hence, the abbreviation will here be supposed to read Evolutionarily Steady Strategy. For evolutionary predictions only attracting ESSes, often called CSSes, matter.

When will long-term evolution maximize some fitness-related measure?

Given the stress on fitness maximization in the literature, it is relevant to know when there do exist properties of types that are maximized at CSSes. This is the case if and only if ‘the trait values affect fitness effectively in a one-dimensional monotone manner’. The term ‘effectively’ here means that the specified properties only need to pertain to the range of fitness values closely surrounding the change from negative to positive. More precisely, if $\boldsymbol{X}$ denotes the potential trait vectors, $\boldsymbol{E}$ the realizable environments and $\mathbb{R}$ the real numbers:

An eco-evolutionary model is governed by an optimization principle if and only if

(A) there exists a function ψ : $\boldsymbol{X} \rightarrow \mathbb{R}$ and a function g : $\mathbb{R} \times \boldsymbol{E} \rightarrow \mathbb{R}$, increasing in its first argument, such that

$$\operatorname{sign} \rho(\mathbf{X} \mid \mathbf{E}) = \operatorname{sign} g\big(\psi(\mathbf{X}), \mathbf{E}\big). \tag{11}$$

Condition (A) can be proved equivalent to

(B) there exists a function ϕ : $\boldsymbol{E} \rightarrow \mathbb{R}$ and a function h : $\boldsymbol{X} \times \mathbb{R} \rightarrow \mathbb{R}$, decreasing in its second argument, such that

$$\operatorname{sign} \rho(\mathbf{X} \mid \mathbf{E}) = \operatorname{sign} h\big(\mathbf{X}, \phi(\mathbf{E})\big) \ , \tag{12}$$

which can be paraphrased as ‘the environment acts effectively in a one-dimensional monotone manner’.

Relations (11) and (12) can be related to each other by the observation that,

if an optimization principle exists,

(C) it is possible to choose the functions ϕ and ψ such that

$$\operatorname{sign} \rho(\mathbf{X} \mid \mathbf{E}) = \operatorname{sign}\big(\psi(\mathbf{X}) - \phi(\mathbf{E})\big) \ , \tag{13}$$

where ϕ and ψ are connected through the relation

$$\psi(x) = \phi\big(\mathbf{E}_{\text{attr}}(\mathbf{X})\big) \ . \tag{14}$$

Of course, results (A) to (C) hinge on the interpretation of the term ‘optimization principle’. The latter should be interpreted as a function from trait values to real numbers such that for any possible constraint on the traits the ESS(es) can be calculated by maximizing this function. The proviso in the previous sentence mirrors the usual practice of combining an optimization principle, derived from the population dynamics, with a discussion of the dependence of the evolutionary outcome on the possible constraints. What matters here is that, while condition (A) is close to trivial, the equivalent condition (B) and relation (14) provide a useful tool for either deriving optimization principles or proving the non-existence of such principles for large families of eco-evolutionary models.

What do optimization principles tell?

If an optimization principle ψ exists, each successful mutant increases $\psi(\mathbf{X})$, and hence any ESS attracts. Moreover, $\phi\left(\mathbf{E}_{\text{attr}}(\mathbf{X})\right)$ increases with each increase in $\psi(\mathbf{X})$. Since fitness decreases with ϕ where it counts, i.e., around zero, ϕ may be dubbed pessimization principle. When a pessimization principle exists, in the end the worst attainable world remains, together with the type(s) that can just cope with it.

The following example may give a more concrete feel for the issue. Consider a structured population in continuous time regulated through an additional h-state independent death rate d_{E} and with all other demographic parameters independent of **E**. Then the mean death rate $\left\langle d_{\text{E}}\left(\mathbf{E}(t)\right)\right\rangle_{\text{time}}$ associated with an environment provides a pessimization, and the asymptotic relative growth rate ρ_0 calculated on the assumption that $d_{\text{E}}=0$ an optimization principle. A special case is where the environment is constant except for occasional decimating catastrophes, provided the latter kill totally indiscriminately (so that ρ_0 may be identified with *r* for that constant environment). But for the (essential, but generally unmentioned) indiscriminateness, this is the condition touted in the textbooks as supporting *r*-maximization.

Optimization principles come closest to the textbook intuition for the meaning of fitness, which generally fails to account for the fact that the fitnesses of all possible types are bound to change with any change in the character of the residents. The results above show that optimization principles, although frequently encountered in the literature, are exceptions rather than the rule.

When will evolution just maximize the Malthusian parameter, average offspring number?

The results from the previous subsection can be used to characterize the ecological scenarios for which evolution will just maximize the Malthusian parameter or lifetime offspring number. Here 'just maximizing a function of **X** and **E**' should be interpreted as maximizing that function by varying **X** for an unspecified choice of **E** (the latter as reflection of the absence of any mention of **E** in the usual statements in the non-epidemiological literature). Under the presupposition that the community dynamics engenders constant environments so that the Malthusian parameter *r* and the lifetime offspring number R_0 are well defined, it can be proved that

evolution just maximizes *r* if and only if

(D) the combination of life histories and ecological embedding is such that *r* can be written as $r(\mathbf{X}\,|\,\mathbf{E})=g\left(r(\mathbf{X}\,|\,\mathbf{E}_0),\mathbf{E}\right)$ for some function g that increases in its first argument, and $\mathbf{E}_0$ some fixed, but otherwise arbitrary, environment,

and

evolution just maximizes R_0 if and only if

(E) the combination of life histories and ecological embedding is such that $\ln(R_0)$ can be written as $\ln\left(R_0(\mathbf{X}\,|\,\mathbf{E})\right)=g\left(\ln\left(R_0(\mathbf{X}\,|\,\mathbf{E}_0)\right),\mathbf{E}\right)$ for some function g that increases in its first argument, and $\mathbf{E}_0$ some fixed, but otherwise arbitrary, environment.

In contrast to the criterion for the existence of an optimization principle, the present criterion is relatively easy to check in specific situations.

Individual level conditions

A fair fraction of textbook statements, if taken literally, applies only when condition (D) or (E) is fulfilled. Condition (D) is fulfilled on the rare occasions that the only influence of the environment is through an h-state- and type-independent death probability, or rate, on top of any h-state- or type-dependent ones. Condition (E) is fulfilled in the rather more common cases that the life history can be decomposed into a number of subsequent stages that connect only through single h-states (so that no information about the past is carried over between stages) and no stage is influenced by both **X** and **E** together.

Non-fluctuating environments: proxies and approximations

From lifetime offspring number to intrinsic rate of increase and invasion probability

Most ESS calculations consider situations where the environment can be assumed constant over community dynamical time, as these are about the only cases where analytical results can be obtained. For the remainder of this section the same assumption will be operative.

In non-fluctuating environments, life histories with everybody born equal always allow an age representation, characterized by an average age-dependent effective birth rate (or ratio) $\lambda(a)$ (often seen decomposed into an age-dependent survival $l(a)$ and conditional fecundity $b(a)$ as $\lambda(a)=l(a)b(a)$), from which the intrinsic rate of increase r can be calculated by solving

$$1=\int_0^\infty \mathrm{e}^{-ra}\,\lambda(a)\mathrm{d}a \qquad \text{(respectively} \qquad 1=\sum_{a=1}^{\infty}\mathrm{e}^{-ra}\,\lambda(a)\ . \tag{15}$$

From here on only the continuous time formulas will be displayed.) Lifetime offspring production equals

$$R_0=\int_0^\infty \lambda(a)\mathrm{d}a\,. \tag{16}$$

The two quantities are related through

$$R_0 \gtrless 1 \;\Leftrightarrow\; \ln(R_0)\gtrless 0 \;\Leftrightarrow\; r\gtrless 0. \tag{17}$$

For not too large R_0, or when births concentrate around a single parental age,

$$r\approx \ln\left(R_0\right)/T_b\,, \tag{18a}$$

with T_b the average age at giving birth,

$$T_b=\int_0^\infty a\lambda(a)\mathrm{d}a\Big/\int_0^\infty \lambda(a)\mathrm{d}a\,, \tag{18b}$$

For small positive $\ln(R_0)$ the establishment probability, p, can be approximated, under some mild conditions on the offspring number distribution, as

$$p\approx 2\ln\left(R_0\right)/\sigma^2\,, \tag{19a}$$

with σ^2 the variance of the lifetime offspring numbers. For mutations with small effect the more easily determined resident values can be substituted for T_b and σ^2, without affecting the order of the approximation.

More than one birth state

When individuals can be born in different birth states (think e.g. of different patches), the previous results generalize with little change. Let $\lambda_{ij}(a)$ be the average rate (or ratio) at which an individual born in state j gives birth to offspring in state i, and $\mathbf{\Lambda}(a)=\left(\lambda_{ij}(a)\right)$. Then r has to be determined from

$$\left[\text{dominant eigenvalue of } \tilde{\Lambda}(r)\right]=1, \tag{20a'}$$

or as the rightmost solution of

$$\text{determinant}\left(\mathbf{I}-\tilde{\mathbf{\Lambda}}(r)\right)=0 \tag{20a''}$$

with

$$\tilde{\lambda}_{ij}(r) = \int_0^\infty \mathrm{e}^{-ra}\, \lambda_{ij}(a)\mathrm{d}a\,. \tag{20b}$$

For ease of reference, denote $\tilde{\mathbf{\Lambda}}(0)$ as $\mathbf{A}$, and denote the dominant right eigenvector of $\mathbf{A}$ as $\mathbf{U}$ and the dominant left eigenvector as $\mathbf{V}^{\mathrm{T}}$. Both eigenvectors are supposed to be normalized such that $\mathbf{1}^{\mathrm{T}}\mathbf{U} = 1$ and $\mathbf{V}^{\mathrm{T}}\mathbf{U} = 1$. $\mathbf{U}$ can then be interpreted as a generationwise stable birth state distribution, and the components of $\mathbf{V}$ as generationwise reproductive values.

The average lifetime offspring number can be found by averaging the total number of offspring begotten by individuals born in the various birth states:

$$R_0 = \mathbf{1}^{\mathrm{T}}\mathbf{A}\mathbf{U} \quad = \quad \text{dominant eigenvalue of } \mathbf{A}\,. \tag{21}$$

Relation (17) applies without change, while (18b) and σ^2 in (19a) have to be modified. In the case of mutants that are not too different from the resident:

$$T_b = \int_0^\infty a\mathbf{V}_{\mathrm{r}}^{\mathrm{T}}\mathbf{\Lambda}_{\mathrm{r}}(a)\mathbf{U}_{\mathrm{r}}\mathrm{d}a \Big/ \int_0^\infty \mathbf{V}_{\mathrm{r}}^{\mathrm{T}}\mathbf{\Lambda}_{\mathrm{r}}(a)\mathbf{U}_{\mathrm{r}}\mathrm{d}a\,, \tag{18b′}$$

with the index r indicating the resident values, and

$$\sigma^2 = \sum_h u_h \operatorname{Var}\left(\sum_i v_i \xi_{ih}\right), \tag{19b}$$

where ξ_{ih}, v_i and u_h denote the stochastic number of offspring in state *i* produced by a resident individual that itself was born in state *h*, respectively the corresponding components of $\mathbf{V}_{\mathrm{r}}$ and $\mathbf{U}_{\mathrm{r}}$.

Cyclic environments can be treated like constant ones through the ploy of making the phase of the cycle a component of the birth state.

Applications

In ESS calculations, including the calculation of population dynamical equilibria, any function of **X** and **E** that has the same sign as invasion fitness may be substituted for it without affecting the answer. Hence,

> for the calculation of evolutionary outcomes $\ln(R_0)$ does as good a job as invasion fitness.

More quantitative precision is needed for dealing with evolutionary transients. The time needed for a gene substitution is largely determined by the initial fitness of the mutant allele and the final fitness of the allele it replaces, with the two fitnesses determined by the heterozygote's demographic behavior in the resident environments set by the two homozygotes. For mutants that are sufficiently similar to the resident, both quantities can be determined by means of (18). The speed of long-term evolution is largely determined by the establishment probabilities of favorable mutants. For mutants with small effect these probabilities can be determined from (19).

A still simpler proxy

Multiple birth states still necessitate the calculation of an eigenvalue. Luckily, for a number of calculations it is possible to use as fitness proxy the explicitly calculable quantity

$$q(\mathbf{X}_{\mathrm{m}} \mid \mathbf{X}_{\mathrm{r}}) = P(\mathbf{X}_{\mathrm{m}} \mid \mathbf{X}_{\mathrm{r}})(1) \tag{22}$$

with

$$P(\mathbf{X}_{\mathrm{m}} \mid \mathbf{X}_{\mathrm{r}})(z) = -\text{determinant}\big(z\mathbf{I} - \mathbf{A}(\mathbf{X}_{\mathrm{m}} \mid \mathbf{X}_{\mathrm{r}})\big) \tag{23}$$

In particular,

> provided the set $\boldsymbol{\mathcal{X}}$ of potential trait vectors is connected,
> $\mathbf{X}^*$ is a global ESS if $q(\mathbf{X} \mid \mathbf{X}^*) < 0$ for all $\mathbf{X} \neq \mathbf{X}^*$, and only if $q(\mathbf{X} \mid \mathbf{X}^*) \leq 0$ for all **X**.

(A strategy is called a local ESS when it cannot be invaded by nearby mutants and a global ESS when it cannot be invaded by any mutant.) Moreover,

> any local ESSes can be calculated and their attractiveness determined by substituting q for invasion fitness.

Only when it comes to the calculation of evolutionary transients there is a difference. For small mutational steps

$$r(\mathbf{X}_\mathrm{m} \mid \mathbf{X}_\mathrm{r}) \approx \frac{\partial r}{\partial \mathbf{X}_\mathrm{m}}(\mathbf{X}_\mathrm{r} \mid \mathbf{X}_\mathrm{r})(\mathbf{X}_\mathrm{m} - \mathbf{X}_\mathrm{r}) \approx \kappa \frac{\partial q}{\partial \mathbf{X}_\mathrm{m}}(\mathbf{X}_\mathrm{r} \mid \mathbf{X}_\mathrm{r})(\mathbf{X}_\mathrm{m} - \mathbf{X}_\mathrm{r}) \text{ with } \kappa = \frac{1}{T_b(\mathbf{X}_\mathrm{r})} \frac{1}{\frac{\mathrm{d}P(\mathbf{X}_\mathrm{r} \mid \mathbf{X}_\mathrm{r})}{\mathrm{d}z}(1)} > 0 \tag{24}$$

with progressively more complicated corrections appearing in the higher order terms.

Similar results hold good for models described in terms of (1) or (2), with $T_b = 1$ and in the case of (2):

$$q(\mathbf{X}_\mathrm{m} \mid \mathbf{X}_\mathrm{r}) = P(\mathbf{X}_\mathrm{m} \mid \mathbf{X}_\mathrm{r})(0) \text{ and } P(\mathbf{X}_\mathrm{m}, \mathbf{X}_\mathrm{r})(z) = -\operatorname{determinant}\big(z\mathbf{I} - \mathbf{B}(\mathbf{X}_\mathrm{m} \mid \mathbf{X}_\mathrm{r})\big).$$

Matrix models with *T*-Periodic environments can be brought into the fold by in (23) replacing $\mathbf{A}$ with $\mathbf{C}(T)$, as defined in the subsection on calculation procedures, and in (24) replacing T_b with T.

Aggregates

Meta-individuals

The infinite dilution assumption allows proving the asymptotic exponential growth of the focal population. The definition of invasion fitness only requires this growth pattern. Such a pattern also occurs when individuals aggregate, with individuals in an aggregate interacting with each other for extended periods of time, provided the aggregates are infinitely diluted (so that, although the individuals appreciably influence their immediate environments, they only infinitesimally influence the environment outside the aggregate). Some examples of aggregates are (i) diploid individuals, or more generally genets, (ii) family groups (with singles treated as families of size one), (iii) patches in a structured meta-population, and (iv) pairs in so-called pair approximation calculations for a population supposedly living on the nodes of a graph. For the invasion problem only aggregates with at least one individual of the focal type count. Such aggregates will be referred to here as meta-individuals.

It is always possible to define an h-state of a meta-individual in the form of a list of the types and h-states of all individuals in it, plus a scheme of their possibilities for interaction. In the case of a mutant, one other type of individuals are the residents, but in (i) they may in addition be alleles on additional polymorphic loci, and in (iii) and (iv) any other species in the meta-community. The existence of at least one h-state representation, however impractical, allows invoking the multiplicative ergodic theorem. In special models more practical simplified representations may be possible. For instance, when the individuals in (iii) are all the same but for a distinction between mutants and residents, a patch can be characterized with just the mutant and resident numbers, and when moreover the total number of individuals in a patch is constant, only the number of mutants is needed.

The disappearance of all focal types from an aggregate can be interpreted as a meta-death, the new appearance of aggregates with at least one individual of the focal type as meta-births. In (i) meta-births correspond to fertilizations, in (ii) to the splitting of families, in (iii) to the immigration of an individual of the focal type into a patch not yet containing such individuals (the infinite dilution assumption guarantees that a meta-individual once born does not experience further immigrations of the focal type), and in (iv) to having a pair of adjacent nodes on the graph filled with non-focal type individuals replaced by a pair with at least one focal type.

Since meta-individuals reproduce clonally and are infinitely diluted,

> all recipes for the calculation of invasion fitness and of proxies thereof equally apply to meta-individuals.

In addition,

> if the asymptotic per capita growth of the expected number of focal individuals in meta-individuals is less than the invasion fitness of the latter, the asymptotic per capita rate of initial increase of a type equals the invasion fitness of meta-individuals for that type, and hence can rightfully be called the invasion fitness of the type.

More general compounds

For non-fluctuating environments, births were given a special role in the bookkeeping. This focus allowed a considerable simplification of the calculations thanks to the fact that at birth individuals usually pass through a subset of states that is much smaller than the h-state space as a whole. Birth thus provides a bottleneck for the passing on of information from previous stages through the life cycle. Such bottlenecks may sometimes also occur elsewhere. For example, when in (ii) families may split only when above a certain size, the most parsimonious calculations result from treating the reaching of the size threshold as if this were the birth-events. There often is considerable freedom in the compounds that can be chosen for the role of meta-individual. In making such choices, it pays to build in the severest possible bottlenecks.

In meta-populations consisting of clonally reproducing individuals, the calculations are simplest for meta-lifecycles going from new disperser to local colonies founded by dispersers to the dispersers produced by such colonies. This leads to taking as fitness proxy for constant environments (of the meta-individuals) the probability of surviving dispersal times the average number of dispersers produced over the lifetime of an invader colony. For diploid meta-populations with small local population sizes the new dispersers are no longer equal but should be distinguished according to their birth state: heterozygote or homozygote.

Inclusive fitness

Although the concept of meta-individual is mathematically elegant, arguments expressed in more conventional biological terminology are usually more cogent. The concept of inclusive fitness is based on a decomposition of the (exponential of) invasion fitness into an individual component and a component that derives from the change in the reproductive output of other individuals of the same type caused by interactions with the focal individual. At the invasion stage, infinite dilution guarantees that other individuals in a meta-individual only have the focal type when those individuals are related by descent. The idea then is that the change in reproductive output of non-focal individuals is weighed with the probability that these individuals are identical by descent to the focal one.

For simple ecological scenarios, with e.g. non-overlapping generations, fixed size aggregates and mutants that closely resemble the residents, it is possible to separately calculate the various contributions before combining them. (The close resemblance is needed to guarantee that selection does not affect the probabilities of identity by descent and that fitness effects are approximately additive.)

When possible, calculations through the inclusive fitness route are preferable, as the resulting decomposition helps in interpreting trait evolution. When higher cognitive abilities do not come into play, meta-individual-based techniques usually have a larger reach than inclusive-fitness-based ones. When meta-individual-based techniques work, it is possible in principle to reconstruct the ingredients occurring in an inclusive fitness calculation, at least numerically. However, doing so often is far more complicated than directly calculating invasion fitness, and hence may contribute less insight than one has come to expect from the simple cases.

Mendelian diploids

Setting the stage

Many biologists' prime concern are traits characterizing the sort of individuals they can hold in their hand instead of traits of underlying clonally reproducing genes, of which the visible bearers are but uneasy coalitions. This section considers how the invasion fitness of genes relates to the traits of their carriers. Part of that story is contained in the developmental map from genotypes to traits and in the ecological processes translating traits into demographic parameters. Here, it is only considered how transmission genetics and demography conspire in determining invasion fitness. And that only for a few ecological scenarios akin to those usually considered in population genetics: unstructured populations in discrete time or structured ones with a single birth state and non-fluctuating environmental attractors, all with randomly uniting gametes.

A second aim of this section is exemplifying the calculation of invasion fitness when there is more than one birth state.

The arguments will be couched in the well-honed formalism of population genetics, as this is far more efficient than working in terms of the population dynamics of alleles. (The reason for the earlier stress on the population dynamical viewpoint is that the latter is conceptually more encompassing.) The initial growth ratio of a population of mutant alleles is independent of whether this ratio is calculated from the approximate dynamics of low allele frequencies or from the dynamics of expected population sizes.

The trait vector produced by a genotype *G* will be denoted as $\mathbf{X}_G$, with $f(\mathbf{X}_G \mid \mathbf{E})$, also abbreviated as f_G, the corresponding average per capita lifetime macrogametic output, and $m(\mathbf{X}_G \mid \mathbf{E})$, abbreviated as m_G, the average per capita lifetime output of microgametes times their fertilisation propensity. Thus, f_G equals the average number of kids mothered by a randomly chosen *G*-individual and m_G is proportional to the average number of kids fathered.

Monomorphic residents

Let the mutant allele be denoted as *A*, the resident allele as *a*, and their frequencies in the micro- and macrogametes as p_A, p_a respectively q_A, q_a. The recurrences for the unstructured case are, with the next generation indicated by a prime,

$$n' = \bar{f}\, n\,,$$

$$\bar{m} p'_A = m_{AA} p_A q_A + \tfrac{1}{2} m_{aA} (p_A q_a + p_a q_A)\,,$$

$$\bar{f} q'_A = f_{AA} q_A p_A + \tfrac{1}{2} f_{aA} (q_A p_a + q_a p_A)\,,$$

with (25)

$$\bar{m} = p_A q_A m_{AA} + (p_A q_a + p_a q_A) m_{aA} + p_a q_a m_{aa}\,,$$

$$\bar{f} = q_A p_A f_{AA} + (q_A p_a + q_a p_A) f_{aA} + q_a p_a f_{aa}\,.$$

Substituting $p_a = 1 - p_A$ and $q_a = 1 - q_A$ and dropping quadratic terms gives for the frequencies of the two states in which allelic meta-individuals can be born

$$p'_A \approx \frac{1}{2}\frac{m_{aA}}{m_{aa}}\left(p_A + q_A\right), \qquad q'_A \approx \frac{1}{2}\frac{f_{aA}}{f_{aa}}\left(p_A + q_A\right), \tag{26}$$

which on adding give

$$\left(p_A + q_A\right)' \approx \frac{1}{2}\left(\frac{m_{aA}}{m_{aa}} + \frac{f_{aA}}{f_{aa}}\right)\left(p_A + q_A\right). \tag{27}$$

Hence, in unstructured populations

$$\rho\left(\mathbf{X}_{aA} \mid \mathbf{X}_{aa}\right) = \left\langle \ln\left(\frac{1}{2}\left(\frac{m(\mathbf{X}_{aA} \mid \mathbf{X}_{aa})}{m(\mathbf{X}_{aa} \mid \mathbf{X}_{aa})} + \frac{f(\mathbf{X}_{aA} \mid \mathbf{X}_{aa})}{f(\mathbf{X}_{aa} \mid \mathbf{X}_{aa})}\right)\right)\right\rangle_{\text{time}}, \tag{28}$$

and in non-fluctuating environments

$$R_0\left(\mathbf{X}_{aA} \mid \mathbf{X}_{aa}\right) = \tfrac{1}{2}\left(\frac{m(\mathbf{X}_{aA} \mid \mathbf{X}_{aa})}{m(\mathbf{X}_{aa} \mid \mathbf{X}_{aa})} + \frac{f(\mathbf{X}_{aA} \mid \mathbf{X}_{aa})}{f(\mathbf{X}_{aa} \mid \mathbf{X}_{aa})}\right), \tag{29}$$

a result known as the Shaw-Mohler formula. Formulas (28) and (29) lie at the hart of the calculation of phenotypic ESSes and evolutionary trajectories (on the suppositions that the former are effectively genetically homozygous, respectively of effective mutation limitation).

Polymorphic residents, allelic evolution

Now assume that the resident population is dimorphic on the A-locus, and that the traits of the three corresponding genotypes are subject to modification either by the invasion of other alleles or by new alleles on other, previously monomorphic, loci, generically called B. To keep the formulas simple, the standard textbook assumption is made that m and f are proportional for all values of their arguments. Moreover, it will be assumed that the resident environment does not fluctuate. In that case, if $\overline{m}_{\mathrm{r}}$ and $\overline{f}_{\mathrm{r}}$ denotes the values of $\overline{m}$ and $\overline{f}$ at the resident equilibrium, $m/\overline{m}_{\mathrm{r}} = f/\overline{f}_{\mathrm{r}} = f$ (since at equilibrium $\overline{f}_{\mathrm{r}} = 1$). Their common value is indicated as w in accordance with population genetical tradition.

First consider allelic evolution, with the mutant allele denoted as α. For small p_α

$$p'_\alpha = w_{\bullet\alpha} p_\alpha \quad \text{with} \quad w_{\bullet\alpha} = w\left(\mathbf{X}_{a\alpha} \mid \mathbf{X}_{aa}, \mathbf{X}_{aA}, \mathbf{X}_{AA}\right) p_a + w\left(\mathbf{X}_{A\alpha} \mid \mathbf{X}_{aa}, \mathbf{X}_{aA}, \mathbf{X}_{AA}\right) p_A . \tag{30}$$

Hence,

$$R_0\left(\begin{pmatrix}\mathbf{X}_{a\alpha}\\ \mathbf{X}_{A\alpha}\end{pmatrix} \middle| \begin{pmatrix}\mathbf{X}_{aa}\\ \mathbf{X}_{aA}\end{pmatrix}, \begin{pmatrix}\mathbf{X}_{Aa}\\ \mathbf{X}_{AA}\end{pmatrix}\right) = w_{\bullet\alpha}, \tag{31}$$

where the form of the formula brings out that the phenotype engendered by an allele consists of two components, expressing the dependence on the two intra-aggregate environments that it may encounter. In population genetics $w_{\bullet\alpha}$ is known as the marginal fitness of the α-allele.

Polymorphic residents, modifier driven evolution

The final example considers a mutant B on a so-called modifier locus that previously was monomorphic for b. The rule that symbols playing no role in the argument are dropped lets aa stand for $aabb$, aaB for $aabB$, etc. When B is rigidly coupled to a the pair aB behaves like a new A-allele, with invasion fitness $w_{\bullet aB}$ defined by (30) with $\alpha = aB$. A similar consideration applies to a pair AB. In general the standard rules of transmission genetics give for the gamete frequencies p_{aB} and p_{AB}

$$\begin{aligned} p'_{aB} &= w_{aaB} p_a p_{aB} + w_{aAB}(1-c) p_A p_{aB} + w_{aAB} c p_a p_{AB} \\ p'_{AB} &= w_{AAB} p_A p_{AB} + w_{aAB}(1-c) p_a p_{AB} + w_{aAB} c p_A p_{aB} \end{aligned} \tag{32}$$

with c the recombination probability and p_a and p_A calculated from the equilibrium equations corresponding to (25). In vector-matrix form:

$$\begin{pmatrix} p_{aB} \\ p_{AB} \end{pmatrix}' = \mathbf{A} \begin{pmatrix} p_{aB} \\ p_{AB} \end{pmatrix} \quad \text{with} \quad \mathbf{A} = \begin{pmatrix} w_{\bullet aB} & 0 \\ 0 & w_{\bullet AB} \end{pmatrix} + c w_{aAB} \begin{pmatrix} -1 & 1 \\ 1 & -1 \end{pmatrix}. \tag{33}$$

Hence

$$q\left(\begin{pmatrix}\mathbf{X}_{aaB}\\ \mathbf{X}_{aAB}\\ \mathbf{X}_{AAB}\end{pmatrix} \middle| \begin{pmatrix}\mathbf{X}_{aa}\\ \mathbf{X}_{aA}\\ \mathbf{X}_{AA}\end{pmatrix}\right) = -\left(w_{\bullet aB} - 1\right)\left(w_{\bullet AB} - 1\right) + c w_{aAB}\left(w_{\bullet aB} + w_{\bullet AB} - 2\right). \tag{34}$$

A polymorphism is evolutionarily steady if it is uninvadable by both alternative alleles and modifiers. The first can be judged from (31). Since q is linear in c, q is maximal for $c = 0$ or $c = \frac{1}{2}$. Therefore, it suffices to consider q for those values of c only. The case

$c = 0$ is already covered by the condition that no alternative allele is able to invade. So all that has to be done to deal with modifiers is to consider q for $c = \frac{1}{2}$.

Ideal free evolutionarily steady polymorphisms
ESS arguments may often be further simplified by the observation, due to Eshel and Feldman, that (c.f. (21))

$$R_0(B) = \mathbf{1}^{\mathrm{T}}\mathbf{AU} = u_{aB}w_{\bullet aB} + u_{AB}w_{\bullet AB} = p_a u_{aB} w_{aaB} + (p_A u_{aB} + p_a u_{AB}) w_{aAB} + p_A u_{AB} w_{AAB}. \quad (35)$$

Hence, if $w(X \mid X_{aa}, X_{aA}, X_{AA})$ is maximal and equal to 1 at $X = X_{aa}$, $X = X_{aA}$ and $X = X_{AA}$, the triple (X_{aa}, X_{aA}, X_{AA}) is evolutionarily steady. Evolutionarily steady polymorphisms that equalise the reproductive output of the morphs are called ideal free. Hence,

> ideal free evolutionarily steady genetic polymorphisms can be calculated by treating each phenotype as if it reproduces clonally, with the additional constraint that at birth the phenotypes should occur in Hardy-Weinberg proportions.

Similar statements apply to the sexually differentiated case and to polymorphisms in more than one locus.

Coda

Why initial growth rates?
One consideration behind the definition of invasion fitness is that the resulting quantities should link evolutionary features for arbitrary ecological scenarios with similar features for the classical simple viability selection model. In the latter model with viabilities $v_{AA} > v_{aA} > v_{aa}$, the time taken for a gene substitution is largely determined by the initial and final exponential phases, which have as time constants the invasion fitnesses $\ln\left(v_{aA}/v_{aa}\right) > 0$ and $\ln\left(v_{aA}/v_{AA}\right) < 0$. Gene substitutions in more general ecologies generally follow the same pattern. Similarly, two alleles will coexist if they have positive invasion fitness in the environment set by the other allele, which for simple viability selection reduces to the classical $v_{aA} > v_{aa}$ & $v_{aA} > v_{AA}$. Making the quantitative links requires (invasion) fitness to be defined as the asymptotic per capita growth rate.

For long-term evolution, invasion probabilities are the most important. However, for their full quantitative determination less accessible life history details are needed, while the essential qualitative information, as well as a good quantitative estimate for small mutational steps, can be extracted (up to a proportionality constant) from invasion fitness.

Under weak selection invasion fitness even does the full job of population genetical fitness
When the phenotypes under consideration are sufficiently similar, a case can even be made to drop the epithet 'invasion'. Under the similarity assumption, for fairly general classes of eco-genetic models the change in the genetic make-up of the population approximately follows the differential equations standard derived for simple viability selection, with log-viabilities replaced by invasion fitnesses in the environment that would be generated by a clonally reproducing population with the average phenotype. This in retrospect vindicates Fisher's use of differential expressions mentioned in the introductory section, but only under the assumption of like phenotypes, and with a reference to the environment thrown in. (Note also that under the similarity assumption alleles on the different loci and h-states are all (almost) independent, so that there is no need to consider reproductive-value-weighted allele frequencies; moreover, $\ln\left(R_0\right)/T_b$ can replace the Malthusian parameters.) Under the same assumption, although the mean fitness of the population stays (approximately) zero, this lack of change can be decomposed into two opposing terms, the first corresponding to the expression brought to the fore in Fisher's fundamental theorem, and the second equal to the average change of the phenotypic fitnesses caused by the environmental change resulting

from changes in the population composition, consonant with Fisher's verbal exegesis of his theorem.

Not the last word
Apparently, invasion fitness, as defined in this entry, does a good job. Only one assumption, infinite dilution, was needed for its definition. Perhaps the reach of the concept can be extended still a little further. However, there will certainly remain ecological scenarios where the extension fails. This does not mean that under those scenarios there never will be adaptive evolution, only that it is not possible to deduce its outcomes by means of the conceptual precision tool called invasion fitness.

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