

Fitness “kinematics”: biological function, altruism, and organism–environment development

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Abstract It’s recently been argued that biological fitness can’t change over the course of an organism’s life as a result of organisms’ behaviors. However, some characterizations of biological function and biological altruism tacitly or explicitly assume that an effect of a trait can change an organism’s fitness. In the first part of the paper, I explain that the core idea of changing fitness can be understood in terms of conditional probabilities defined over sequences of events in an organism’s life. The result is a notion of “conditional fitness” which is static but which captures intuitions about apparent behavioral effects on fitness. The second part of the paper investigates the possibility of providing a systematic foundation for conditional fitness in terms of spaces of sequences of states of an organism and its environment. I argue that the resulting “organism–environment history conception” helps unify diverse biological perspectives, and may provide part of a metaphysics of natural selection.

Keywords Altruism · Development systems theory · Fitness · Function · Life history theory · Probability

Introduction

It’s often taken for granted that events occurring during the life of an organism can change its fitness. Finding a mate, food, or shelter might increase fitness, for example. Encountering a predator might decrease it. The assumption seems to be at the core of some accounts of biological function and biological altruism, but it has recently been challenged (Ramsey 2006).

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The idea that a biological function is an effect of a trait (or behavior) which increases the organism's fitness or probability of reproductive success in certain contexts has a long history. It's explicit in some accounts of function (e.g., Wimsatt 1972, 2002; Abrams 2005) and plausibly implicit in many others. For example, the idea of raising fitness provides a reasonable way of making precise the notion of "contributing" to fitness in Neander (1991, p. 174)¹:

It is the/a proper function of an item (*X*) of an organism (*O*) to do that which items of *X*'s type did to contribute to the inclusive fitness of *O*'s ancestors, and which caused the genotype, of which *X* is the phenotypic expression, to be selected by natural selection.

Other authors have adopted Neander's formulation as a starting point for further discussion (e.g., Godfrey-Smith 1994; Schwartz 2002).

Some kinds of biological altruism seem to require that behaviors change fitness as well. For example, Sober and Wilson say that "A behavior is altruistic when it increases the fitness of others and decreases the fitness of the actor" (Sober and Wilson 1998, p. 17). Thus when an animal warns others of an approaching predator, it might sometimes decrease its fitness by drawing attention to itself while at the same time increasing others' fitness by making their escape more likely. Though both functions and altruism plausibly involve changes in fitness, I'll focus mainly on the simpler context of functions.

Ramsey (2006) argues—correctly, I believe—that we can't make sense of the role that fitness plays in natural selection unless fitness remains the same over the course of an organism's life (except perhaps due to significant environmental changes); fitness must be what Ramsey calls "block fitness", or what I'll call "static fitness" here. This conclusion seems to undermine our understanding of biological function and biological altruism. I'll argue, however, that we can make sense of intuitions about fitness changes within a lifetime by understanding the "contribution" that an effect makes to fitness in terms of unchanging conditional probabilities of reproductive success—viz. probabilities conditional on that effect.

After presenting and refining Ramsey's arguments that fitness is static ("Why fitness is static") and his use of possible lives of an organism to define fitness ("Possible lives and probabilities"), I'll explain how we can make sense of intuitions about fitness's kinematics in terms of a conditional notion of biological fitness ("Conditional fitness"). Since there is not widespread agreement about how to define fitness—and some authors don't think that a single way of defining fitness is possible—I'll sketch some prominent proposals in order to argue that the idea of conditional fitness plausibly applies to a large class of views about fitness. In most of the rest of the paper ("Organism-environment history spaces") I describe a general framework for thinking about natural selection and development which helps to make sense of conditional fitness, and I'll discuss possible interpretations and implications of the resulting "organism-environment history" conception.

¹ It appears that contributing to fitness can't be understood in terms of counterfactuals in any simple way; see Wimsatt (1972, pp. 55ff) and Millikan (2002).

Static conditional fitness

Why fitness is static

Ramsey (2006) gave two arguments that fitness’s role in natural selection requires an organism’s fitness to remain the same over the course of its life.

First, an organism’s fitness should in general help to predict the reproductive success of similar organisms. However, if fitness fluctuates—perhaps severely, as when a predator notices prey—fitness at a given moment in an organism’s life need not predict the reproductive success of other, similar organisms.

Second, if fitness can change in response to events in an organism’s life, fitness could be altered by “random” occurrences, allowing even identical organisms in the same environment to have different fitnesses. In Scriven’s (1959) widely cited example, one twin reproduces but the other is killed by lightning before reproducing, apparently coming to have zero fitness—though there’s no heritable, evolutionarily relevant difference between the twins. More commonplace examples are easy to generate. A shift of the wind could affect which of two similar organisms is detected and caught by a predator, irrespective of their heritable similarities and differences. Allowing events to change fitness thus seems to allow fitness differences to be disconnected from biological properties on which natural selection acts.

We can refine Ramsey’s points by noting that the sort of fitness relevant to natural selection must attach to alternative types present in a population (genes, phenotypes, etc.), since it’s types, not tokens, which can be inherited. It’s hard to see, though, how behaviors which may or may not occur during different organisms’ lives could suddenly change the fitness of the type they share.²

Possible lives and probabilities

Ramsey (2006) ultimately characterized static fitness as a function of probabilities over numbers of offspring (pp. 487f), where the relevant probabilities are to derive from “the number of successful reproductive events in the sum of [an organism’s] possible lives...” (p. 492).³ I think this is on the right track, but it is at best unclear about a crucial point: The number of possible lives of any organism will usually be infinite since, among other things, location varies continuously (cf. Lewis 1973, p. 20). Thus the number of reproductive events in all of the possible lives of any organism would usually be infinite. I see no way to define probabilities of numbers of offspring *directly* in terms of such numbers. Rather, a definition of fitness must assume a probability distribution over sets of possible lives; this will allow finite

² Some models (e.g., Ewens 2004) and general accounts of fitness (e.g., Mills and Beatty 1979; Sober 1984) define type fitness as an average of token fitnesses. If this were correct in general, arbitrary fluctuations in token fitnesses should sometimes accumulate and force type fitnesses to diverge from what’s biologically appropriate (Abrams 2007).

³ Ramsey also described two notions of fitness, ratchet fitness and flux fitness, which do allow fitness changes, but argued that neither is relevant to natural selection. Ramsey didn’t describe relationships between these notions. As I mention below (footnote 8), my approach allows the possibility of seeing static fitness as deriving from flux fitness along with other information.

fitness values to be derived from infinite numbers of possible lives.⁴ I'll eventually argue that the relevant probabilities are over "organism–environment histories": sequences of states of an organism and its environment. My approach explicitly concerns organism types rather than tokens, however, and allows the possibility of clarifying the appropriate notion of possibility.

Conditional fitness

I'll argue that any member of a broad class of plausible accounts of static fitness will allow us to define a notion of static *conditional* fitness. Such conditional fitnesses will include fitnesses conditional on the occurrence of an event of a particular type. Though these fitnesses do not change during an organism's life, they reflect the effects of possible events on organisms' reproductive success, and I'll argue that static conditional fitnesses suffice to capture the intuitions behind the assumption that fitness can change during an organism's life. I won't attempt to deal here with all controversies concerning fitness, however.

Let's begin with the simplest case, conditional viability. Consider an animal which uses carotenoids to improve disease resistance, e.g., the jungle fowl (Zuk et al. 1990). Carotenoids usually must be acquired from foods, but carotenoid-rich foods are rare in some environments (Olson and Owens 1998). It's natural to think that when a young jungle fowl experiencing a carotenoid shortage encounters a ready source of these substances, the animal's viability could thereby increase. Though, as we've seen, this kind of fitness can't really play a role in natural selection, there's nevertheless a difference in what I'll call "conditional viability"—a difference between viability conditional on being a young carotenoid-depleted jungle fowl which finds a source of carotenoids and being one which finds no such source.

We can illustrate the idea most simply by supposing that all jungle fowl of a particular (geno- or pheno-) type go through a period of carotenoid depletion while immature, and that this contributes to some of them succumbing to disease before reaching maturity. Then the conditional probability of survival to adulthood—the *conditional viability*—given finding a carotenoid source is plausibly greater than the corresponding conditional probability of survival given not finding a carotenoid source. Allowing "S" to represent the condition of surviving to adulthood, "C" the condition of finding a good source of carotenoids, and representing negation (complementation) by an upper bar,

$$P(S|C) > P(S|\bar{C})$$

⁴ Ramsey (2006, pp. 492f) does acknowledge that the number of possible lives could be infinite, but only in order to argue that this doesn't present an epistemological problem for his account of fitness. My point here is that Ramsey's characterization of what fitness *is* leaves out an important aspect: the probability distribution over possible lives. Note that this probability distribution may be over an uncountably infinite number of element—lives—but this is mathematically unproblematic; in such cases probabilities are defined by integrals over a probability density function rather than by sums of finite or countably infinite probabilities.

is the relation between these conditional viabilities. We might then use this idea as part of a characterization of biological function, requiring, say, that:

A kind of effect C of a behavior or trait is C 's function if and only if viability conditional on C exceeds that conditional on not- C in certain restricted conditions....

This formulation would obviously need to be revised in line with one or another existing account of functions.

Importantly, claims about viabilities conditional on behaviors don't require that probabilities change over time. They require only a probability distribution over possible lives for an organism *type* in an environment, where probabilities are assigned to sets of lives classified by circumstances such as finding a carotenoid source. Representing conjunction (intersection) by concatenation, the conditional probability $P(S|C)$ is by definition equal to $P(CS)/P(C)$. Thus $P(S|C)$ is the probability (for a given organism type) of the set of those possible lives in which carotenoids are found early and there is survival to maturity, divided by the probability of the set of possible lives in which carotenoids are found early.

Suppose though that fitness is not mere viability, but expected of number of offspring, as in the original propensity interpretation of fitness (Brandon 1978; Mills and Beatty 1979). Letting “ $O_A = i$ ” refer to the condition that an organism of type A has i offspring, the fitness of a type A would be:

$$\begin{aligned} \text{Fitness of } A &= \\ E O_A &= \sum_{i=0}^{\infty} i P(O_A = i) \\ &= 0 \times P(O_A = 0) + 1 \times P(O_A = 1) + 2 \times P(O_A = 2) + \dots \end{aligned}$$

This makes fitness a mathematical expectation or arithmetic mean, a particular mathematical function E of a set of probabilities of a random variable O_A taking on various values.

There will then be analogous differences between expected numbers of offspring conditional on locating a source of carotenoids and conditional on failing to do so. These are just conditional expectations, which are routine in probability theory; they can be understood as expectations using conditional probabilities instead of simple probabilities. The expected number offspring of a type A conditional on finding carotenoids (C) would be

$$E(O_A|C) = \sum_{i=0}^{\infty} i P(O_A = i|C).$$

Fitness conditional on finding carotenoids would then be greater than that conditional on failing to do so when

$$E(O_A|C) > E(O_A|\bar{C}).$$

This captures the idea that although not all jungle fowl which find carotenoids have many offspring and not all of those which fail to do so have few offspring, the average number of offspring among possible lives which include finding of carotenoids is greater than the average for lives which don't.

Several authors have argued that fitness is not always expected number of offspring and that it may be some more complex mathematical function of probabilities and numbers of offspring (Beatty and Finsen 1989; Brandon 1990; Sober 2001; Rosenberg and Bouchard 2008),⁵ or a function of probabilities of numbers of later descendants (Cooper 1984; Beatty and Finsen 1989), or of probabilities of numbers of offspring along with other factors (Sober 2001; Krimbas 2004; Ariew and Lewontin 2004).⁶

For example, Brandon (1990) argued that fitness is some mathematical function of the expectation of number of offspring and the variance of number of offspring, though the appropriate way of combining expectation and variance won't be the same in all evolutionary contexts. Variance, though, is defined in terms of expectation,

$$\text{Var } O_A = \text{E}(O_A - \text{E}O_A)^2 = \sum_{i=0}^{\infty} (i - \text{E}O_A)^2 \text{P}(O_A = i),$$

and conditional variance can easily be defined in terms of conditional expectation by substituting conditional probabilities for simple probabilities:

$$\text{Var}(O_A|C) = \text{E}([O_A - \text{E}(O_A|C)]^2|C) = \sum_{i=0}^{\infty} (i - \text{E}(O_A|C))^2 \text{P}(O_A = i|C).$$

Thus if variance of number of offspring is relevant to fitness, variance conditional on locating (or not locating) carotenoids plausibly is, too.

More generally, it seems reasonable to think that if fitness can be defined in terms of some mathematical function $\text{F}O_A$ of probabilities of numbers of offspring for a given type A , then the effect on fitness of events of some particular kind in organisms' lives should be definable in terms of corresponding conditional probabilities:

$$\begin{aligned} \text{Fitness of } A \text{ given the occurrence of } C &= \text{F}(O_A|C) \\ &= \text{F}O_A \text{ calculated using } \text{P}(\cdot|C) \text{ rather than } \text{P}(\cdot). \end{aligned}$$

⁵ Much of this discussion was inspired by Gillespie (1977), summarizing other work by Gillespie.

⁶ It may be that different definitions of fitness are needed in different contexts (Stearns 1989; Brandon 1990; Krimbas 2004; Ariew and Lewontin 2004; Rosenberg and Bouchard 2008); see Abrams (2009a) for a contrary view. Note that biologists often define fitness as a "deterministic" scalar which doesn't depend on probabilities; this usually seems to be a simplification for modeling convenience. I don't deal here with arguments that fitness only summarizes actual reproductive success (e.g., Walsh 2007); see Rosenberg and Bouchard (2008) for further references and critiques.

Where fitness must be defined partly in terms of numbers of later descendants of a current organism, the relevant probabilities would still be conditional on a kind of event in the current organism’s life.⁷

As with conditional viabilities, the relevant probabilities—conditional and unconditional—are for a given organism type in a given environment, and these probabilities don’t change within organisms’ lives, since they already take into account everything that can happen in a life, i.e., in various possible lives. Thus the fact that conditional fitness is defined in terms of such probabilities means that conditional fitness is static as well. Rather than an organism’s fitness literally changing when an effect C occurs, there is instead a relationship between conditional probabilities: a type’s fitness conditional on the occurrence of C is different from its fitness conditional on C ’s non-occurrence.

Thus a notion of biological function of a heritable (perhaps behavioral) trait might be defined in part by requiring that a trait A have an effect C in many possible lives, such that in certain restricted circumstances the (static) fitness of A conditional on C is greater than on not- C :

$$F(O_A|C) > F(O_A|\bar{C})$$

Similarly, we can understand the negative effect of an altruistic behavior B on actors of type A in terms of the difference between A ’s fitness conditional on performance of the behavior and its fitness conditional on lack of performance:

$$F(O_A|D) < F(O_A|\bar{D}).$$

(I’ll discuss the positive effect of an altruistic behavior on others’ fitness at the end of Section “Core ideas.”)

Organism–environment history spaces

Initial motivation

We’ve seen how to make sense of “changes” of fitness in terms of static conditional fitnesses for simple cases. However, the conditional fitnesses relevant to biological functions and altruistic behaviors rarely depend only on whether a simple property is instantiated in the organism’s life. Effects on fitness are enormously varied, depending on a wide variety of subtle interactions between different environmental,

⁷ Abrams (2009a) argues that probabilities of numbers of later descendants can be replaced by probabilities of occurrences in a current organism’s life. Ramsey, Neander, and others use inclusive fitness (Hamilton 1964), which incorporates reproductive probabilities for kin; my view is that effects of kin on reproductive probabilities are special cases of more general contextual effects: group selection, frequency- or density-dependent selection, etc. (Michod 1982; Sterelny 1996; Sober and Wilson 1998). Rosenberg and Bouchard’s arguments that fitness might be defined by a token organism “solving the design problems set by [an environment] more fully” than another organism (Rosenberg and Bouchard 2008, and references given there) is not intended to apply to types, but I suspect that an analogous notion of fitness for types would ultimately have to be cashed out in terms of probabilities of reproductive events or other events in possible lives.

physiological, and behavioral factors; effects which “increase” fitness in one circumstance needn’t do so in another.

The literature on costs and benefits of carotenoid use provides numerous illustrations; it’s likely that several of the functions of carotenoids and conditions affecting their functionality apply to any given carotenoid-using species. Olson and Owens (1998) list nineteen known physiological functions of carotenoids, along with the substances’ use to produce various pigments in feathers and scales. Such pigments can have a variety of communicative functions including species recognition, sexual display, conflict resolution, etc. Carotenoid functions can vary at different stages of an organism’s life (Olson and Owens 1998); for example, male American goldfinches have bright yellow carotenoid-based pigmentation only as adults during summer months (Hill and McGraw 2004; Cornell Lab of Ornithology 2003), and female blue-footed boobies use carotenoids for egg production (Morales et al. 2009). Carotenoid use incurs costs, including time, energy, and risks involved in locating carotenoid-rich foods, energetic costs of processing, and possible toxicity (Olson and Owens 1998). Use of carotenoids involves other physiological resources, illustrated by the fact that poor nutrition can interfere with their processing (Navara and Hill 2003). Moreover, different carotenoid substances may have different costs even when used for the same function (Hill and McGraw 2004). Finding a new source of carotenoids in a carotenoid-rich environment might provide no additional benefit, but an organism whose condition limits carotenoid processing might receive no benefit from a new source anyway.

Thus fitnesses relevant to biological functions will often be conditioned on complex, subtle properties of an organism’s life and its environment over extended periods of time. Altruism is no different—for example, an altruist’s fitness conditional on giving an alarm call might depend on subtle conditions such as the location of a predator in relation to conspecifics which have had specific kinds of past interactions with the caller, in a terrain with a particular structure. Our understanding of facts like these would be helped by a systematic conception of the structure of relevant sets of “possible lives”, or more properly, of possible sequences of states of an organism and its environment. I’ll sketch such a conception next, first presenting its main ideas (“Core ideas”). I then discuss various theoretical roles the resulting conception can play (“Theoretical roles”), including ways that it can play a role in unifying diverse ideas in biology and philosophy of biology (“Instrumental meta-model”), and including the possibility of using the conception as part of a metaphysics of evolutionary processes (“Realist metaphysics”). The more precise characterization of organism–environment histories in the latter section will suggest what counts as a possible life of an organism.

Core ideas

To a first approximation, an *organism–environment history* is a sequence of states of a possible organism and its environment which are consistent with a given type of organism and environment. The set of all organism–environment histories for a specified environment and biological (geno-, pheno-, etc.)type form an *organism–environment history space*, or simply a *history space*. I’ll provide informal details of

this conception next, and a more precise account—including a discussion of what determines the relevant environment—in Section “Realist metaphysics.”

An organism–environment history should often be considered to begin at conception and end at the time of death, but histories may have to last longer when fitness is defined in terms of numbers of near-generation descendants. What sorts of variations in states are included in organism–environment histories? If we were trying to study an actual population in an actual environment, we’d focus on some small set of properties of the organisms and of their environment, represented by a small set of variables. A stripped-down version of this idea comes from life history theory (Stearns 1989), which models differences between organism types along dimensions of organism size, time of reproduction, clutch size, offspring size, etc. Cooper (2001) extends the life history idea to include arbitrary properties and environmental circumstances in organisms’ lives, but still focuses on a relatively small number of properties of lives at various times—for example encountering a predator, nearby soil being hard or soft, etc. My remarks about carotenoids suggest that real-world evolution depends on interactions between diverse environmental and organismic properties. The large number of variables (or determinables) defining the dimensions of states in fully detailed histories might range across sets of positions and properties of small but relatively high-level parts of organisms—both parts of the organism in question and parts of other organisms (including conspecifics) in the environment—and over configurations of abiotic aspects of the environment. Minutiae like the rate of flow and cell positions in blood near a point in a vein of an organism might count as aspects of the organism–environment state as well. Even though in practice it’s unrealistic to try to capture all such variation in a model, I’ll argue below that such a rich conception of organism–environment histories is nevertheless useful.

The state of a possible organism of a given type in a given environment at a moment in time thus may be a point in a very high-dimensional space. The change in the organism–environment configuration from moment to moment is movement through this space, producing, over time, a path winding through it. Each such path is an organism–environment history, a sequence of states of an organism and its environment, where each state produces the next one (Fig. 1). The set of such sequences which are consistent with a given environment and organism type then form an even more complex space, an organism–environment history space.

Some biologists and philosophers think that biological processes are roughly deterministic (e.g., Graves et al. 1999; Abrams 2007). This implies that a state of the organism and its environment at one time determines the subsequent path through the organism–environment history space (Fig. 1a). Other writers think that at least some of the stochasticity in biological processes is due to fundamental indeterminism; advocates of the propensity interpretation of fitness sometimes take this position (e.g., Mills and Beatty 1979; Brandon and Carson 1996). On this view an initial state at conception would often determine probabilities of producing two or more subsequent states, each subsequent state in turn determining probabilities of producing further states (Fig. 1b). Either way, the present picture may require a probability distribution over initial organism–environment states at the time of conception (Abrams 2007). Such a distribution would itself defined probabilities of

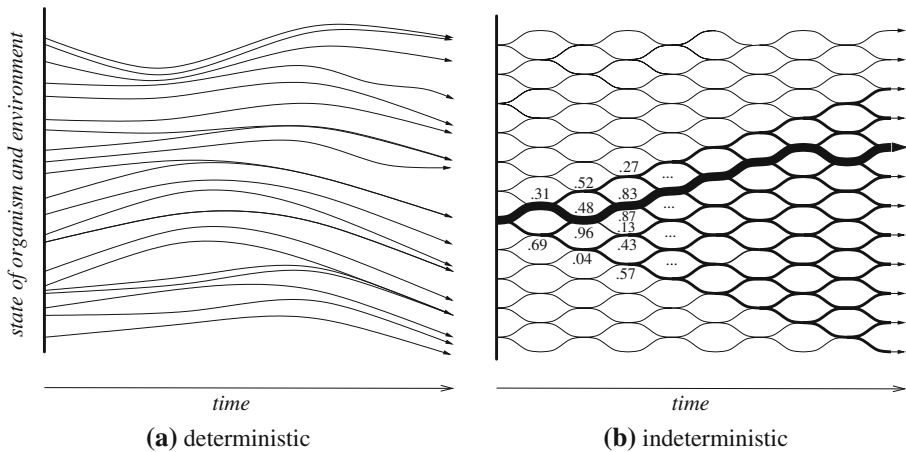


Fig. 1 Deterministic, indeterministic organism–environment history spaces: Idealized representations of organism–environment history spaces assuming that biological processes are deterministic (a) or indeterministic (b). Only one dimension of variation in states at a time is represented, and only two-way branching is represented in (b) (where histories beginning from one initial state are highlighted, one history is further emphasized, and probabilities of some branches are indicated)

sets of histories for a deterministic history space; in an indeterministic history space, the probability of a set of histories would also be determined by within-history indeterminism.⁸

If we take fitness to be a mathematical function of probabilities of numbers of offspring for alternative heritable organism types in a common environment E , we get the following picture. The environment E along with a given organism type (e.g., A) constrains and determines what histories are possible and helps to determine their probabilities. A probability of a certain number of offspring for a given biological type (A) is then a probability of a set of A -in- E histories which include production of exactly that many offspring. A 's fitness is a mathematical function FO_X of such probabilities (and perhaps other factors). If B 's fitness is different from A 's, this is because histories for the B trait wind through the possible states in a different way, with different probabilities, than do those for the A trait.

For example, suppose two competing heritable traits A and B in a population of small mammals produce different tendencies to remain still upon seeing a moderately distant predator; such “freezing” behavior may lower the probability that a predator will notice an animal of either type. The two traits A and B define two

⁸ Probabilities of branchings are probabilities conditional on the previous state, and they would satisfy a Markov condition, i.e., the probability of an event conditional on a prior event is unaffected by still earlier events. This implies that the probability of a single history would be the product of probabilities of branchings along the way. The probability of an entire set of histories beginning from particular initial conditions would be the sum, or more likely integral over probabilities of individual histories beginning from those conditions. Finally, the probability of a set of histories beginning from a variety of initial conditions would be a sum or integral of products of probabilities of initial conditions and probabilities of histories conditional on the various initial conditions (cf. Abrams 2007). This provides a way of connecting Ramsey's (2006) notion of flux fitness with his notion of block fitness, defining the latter in terms of the former along with probabilities over initial conditions.

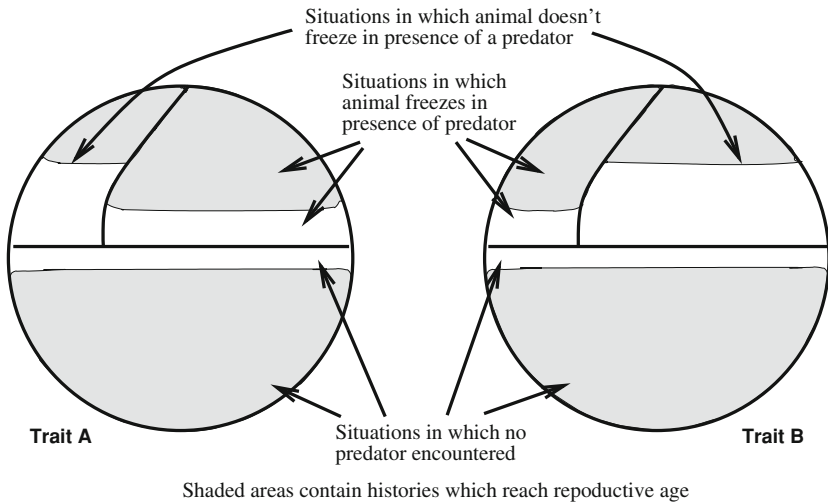


Fig. 2 Type A is fitter: A’s perform a functional behavior with greater probability. Each point represents an entire history; roughly speaking, the time axis is perpendicular to the page

different organism–environment history spaces (Fig. 2): In both, the probability of surviving conditional on freezing in the presence of a predator is greater than conditional on not freezing in the same situations. However, in the history space for A, the set of histories with a moderately distant predator includes a greater proportion (probability) of histories including subsequent freezing.

We can also characterize an altruistic behavior’s benefit to a non-actor in terms of organism–environment histories. (“Conditional fitness” only discussed the behavior’s detrimental effect on the actor.) Note that a history includes a sequence of states of (1) a “focal” organism of the type which defines the history space and (2) an environment—which may include other conspecifics, whether of the same type or not. Thus probabilities of histories can be conditioned on behaviors of conspecifics other than the focal organism, treating these behaviors like any other environmental condition. That conspecifics’ behaviors D' benefit the A type then just means that fitness conditional on the existence of such a behavior D' is greater than conditional on its absence,

$$F(O_A|D') > F(O_A|\bar{D}'),$$

i.e., that among histories which include D , fitnesses are higher on average.

Theoretical roles

We began with arguments that fitness can’t change during an organism’s life; this led to the view that what appear to be changes in fitness are really differences in static conditional fitnesses. The organism–environment history conception fills out this picture, but it raises further questions. Should we really take history spaces

seriously, given that most details of real-world history spaces would be unknowable in practice?

My view is that our thinking about approximations to reality and their relations to each other can be clearer with a systematic conception of what sort of thing it is that diverse approximations ... approximate. Such a conception, when available, can allow us to understand how seemingly incompatible models and theoretical perspectives capture aspects of the same underlying abstract structure. I'll suggest that the organism–environment conception can help unify a broad set of theoretical and philosophical perspectives concerning evolution, providing a common conceptual framework which can be specialized for various existing perspectives (“Instrumental meta-model”). I'll then refine the picture above in order to explore the possibility of a realist interpretation of history spaces (“Realist metaphysics”).

Instrumental meta-model

Organism–environment history spaces corresponding to competing biological types can plausibly play a role analogous to Hutchinson's (1957) niche concept. Hutchinson characterized a niche as a region in an abstract space of combinations of conditions which allow members of a species to persist. For example, different plant species might require concentrations of minerals in soil within different ranges. A species' niche was supposed to incorporate a great many such conditions, yet Hutchinson didn't imagine that any ecologist would be able to fully characterize the true niche of a species. Hutchinson's niche concept was nevertheless widely influential because it organized thinking about niches and provided a conceptual framework in which tractable approximations of complete niches could be developed and put in relation to each other. It gave a picture of an ideal which could be approximated to one degree or another in different ways in practical work.

Similarly, the organism–environment history conception can serve as an abstract framework to be approximated in various concrete ways for different empirical, theoretical, and philosophical purposes. My earlier remarks have already conveyed that the conception can provide a unifying framework for thinking about fitness, biological functions, altruism, mainstream life history theory, and Cooper's extended version of life history theory. I'll suggest a few other connections here.

Developmental Systems Theory (e.g., Oyama et al. 2001) advocates that we take the role of development in evolution more seriously, take the possibility of non-genetic physiological inheritance more seriously, and consider some environmental states and relations themselves to be heritable and subject to selection. DST fits easily into the organism–environment history conception, unlike accounts of selection explicitly tied to genotypes or phenotypes. Nothing in the picture that I've sketched depends on a distinction between events inside and outside the organism boundary; their roles in the overall state of organism and environment at a time are equivalent. Further, nothing in the picture I've sketched implies that heritable types must be genetically determined. Differences between competing history spaces can just as well be due to differences in inherited maternal cell structures or inherited environmental properties, e.g., due to niche construction (Laland et al. 2001).

It's worth comparing the history conception with Waddington's (1957) metaphorical conception of epigenesis as a landscape in which a canvas, its shape determined by points pulled in different ways, manages to direct a marble to various points on the surface. Waddington's metaphor can be seen as a restriction to developmental processes of ways in which a biological type biases the probabilities of organism–environment histories. Similarly, Wimsatt's concept of generative entrenchment (e.g., Wimsatt 2007) and discussions of properties of functional hierarchies (Wimsatt 1972, 2002) can be viewed as partly concerned with probabilities of various sets of possible organism–environment histories.

Finally, note that though in this paper I generally take a new history space to be tokened when a new instance of a genome occurs, the framework could just as easily be applied to heritable properties of groups of organisms or cells or non-biological entities which exhibit inheritance and biased proliferation.

To summarize: A variety of scientific and philosophical models involving biological function, altruistic behaviors, life history theory, and developmental systems can be viewed as specializing and approximating organism–environment history spaces in various respects. The history conception can easily be applied to heritable types for groups or non-biological entities as well. Viewing these diverse perspectives as involving focus on different aspects of organism–environment history spaces makes it clearer what it is they have in common and how they relate to each other. Note that this way of thinking about organism–environment history spaces doesn't require that we assume that they have any sort of reality, nor that it be possible, even in principle, to determine what factors count as possible variations in organism–environment states. Where more precision is useful, researchers can work out the details in whatever way is appropriate, negotiating cross-disciplinary differences as needed.

Realist metaphysics

While an instrumentalist stance toward the history conception makes it analogous to the Hutchinsonian niche concept, a realist stance makes it analogous to the propensity interpretation of fitness's (PIF) claim that fitness depends on propensities.⁹ This aspect of the PIF does not appear to have changed scientific practice, but its warrant never depended on practical consequences; it was proposed to resolve difficulties in evolutionary theory's conceptual foundations. Among other things, since propensities are dispositions, the PIF has the potential to explain how fitness differences could be causes. Nevertheless, propensities do not seem to be empirically distinguishable in practice from any other potential source of stochasticity in biology¹⁰; for example, quantum mechanical tests which might distinguish propensities from other sources are impractical in most biological contexts. I claim that a realist account of organism–environment history spaces can play a role similar to the PIF's propensities. A detailed organism–environment

⁹ I'm skeptical about this aspect of the PIF (Abrams 2007) despite my appreciation of its intended theoretical role.

¹⁰ Such as a deterministic mechanism which systematically generates outcomes in certain frequencies.

history space hypothesis would be testable in principle, but many simplifying assumptions would be needed for any practical tests. However, the history space conception helps to make sense of existing biological intuitions and practices.

Here I'll briefly sketch a framework that might allow organism–environment history spaces to count as real aspects of the world. This will go at least part of the way toward specifying criteria which could specify ranges of allowed variation in states of organisms and an environment—thus constraining the histories which are sequences of these states (and thereby specifying what counts as a “possible life”). The ultimate goal would be to make the organism–environment history conception precise enough that we could say what *would* be involved in determining the properties of a history space if practical limitations did not intrude.

The history spaces for two (or more) competing biological types in a population should depend on many shared environmental and organismic properties—e.g., for competing genotypes, on many genetic and physiological factors. Thus much of what determines the structure of the history spaces for the two types will be the same. On the other hand, the two history spaces will differ in structure because when instances of different types interact with identical circumstances, they produce different consequences. What makes a history space the particular space it is therefore includes both (a) those environmental and organismic conditions which are common for all organisms in the population, and (b) one of the alternative types.

More specifically, a history space for a member of a set of competing biological types in a population is constituted by three kinds of conditions: long-term, static environmental conditions; recurrent population-specific conditions; and biological type-specific conditions.

- *Static conditions*: These are aspects of the environment which remain the same, for all members of the actual population, for a long period of time. Boulders do not move very often and the gravitational constant does not change. Trees change constantly, but they do not hop around from place to place. Though weather patterns are variable, they remain within certain limits for long periods of time. In general static conditions can be fairly abstract, including limits to environmental variation and even probability distributions over variations.
- *Recurrent conditions*: These are recurrent conditions, usually common to every member of the population—often to every member of a species. DST allows environmental states which recur in each generation to play the same role as heritable properties of an organism; these could count, too.
- *Type-specific conditions*: These are heritable conditions common to every organism (developmental system, unit of selection, etc.) *with a given type* (e.g., for organisms, a genotype or a phenotype). Defining history spaces in terms of such conditions allows us to characterize fitness differences of alternative biological types.

A particular history space is thus defined by a set E of static environmental conditions, a set R of recurrent, population-specific, usually organismic conditions, and a type A which usually wouldn't be universal within the population (since the point here is to understand evolutionary processes). A realization of a particular history space exists whenever all of these constituting conditions obtain in the

world. For example, if A and B are alternative alleles at a locus for haploid organisms in a population with common characteristics R in environment E , a pair of history spaces are defined by $\langle E, R, A \rangle$ and $\langle E, R, B \rangle$. An instance of the first history space is realized whenever an A organism with characteristics R is conceived under conditions E —and similarly for the second space. Note that multiple A or B history spaces can be tokened at the same time within the same environment.

Each history space allows a large range of variation in both initial conditions at conception and states later during a focal organism’s life. Among other things, in comparing genotypes produced by alternative alleles at a locus, genetic differences at other loci might count as differences in initial conditions for the history spaces. Similarly, although each actual organism in an environment experiences conditions which are similar, each also experiences different environmental circumstances, since the actual environment is always changing and no two organisms in a population are ever at exactly the same place and time.

History spaces have a particularly sharp version of what I call “the problem of the reference environment”, which can be addressed in roughly the same ways as other versions (Abrams 2009b). The actual organisms of a specified type within a population and its surroundings realize several history spaces simultaneously, all shared by the entire population: history spaces defined by minimal sets of static environmental conditions which are realized for longer periods of time, and ones defined by more complex, restrictive sets of static environmental conditions which are realized only for shorter periods of time. Fitnesses relative to these different history spaces need not be the same, however. Consider a population of desert insects with two alternative, heritable behavioral phenotypes, one better for surviving rare rainstorms (Abrams 2009b). Static conditions which exclude rain are realized for shorter periods than those allowing rain. History spaces relative to these two sets of static conditions might reverse the fitness ordering of the two competing types. Excluding or allowing histories which include rain determines whether fitness conditional on rain contributes to overall fitness. What then determines the “right” set of static conditions—the right reference environment for the whole population? A similar reference environment problem exists for nearly any account of fitness (Abrams 2009b), but the history space conception’s problem seems more acute because this conception makes the environment’s role in determining fitness relatively precise.

Applying arguments from Abrams (2009b) to the present framework, my claim is roughly that researchers in effect get to choose which static conditions are relevant to their concerns, but that history spaces are no less real because of that: Evolutionary effects over distinct time intervals count as distinct effects and distinct explananda, any of which can become the focus of investigation. Distinct effects/explananda, however, may have distinct causes/explanations—in this case involving different static environmental conditions. For example: Changes in frequencies of types in the desert insect population over a short interval (in which rain won’t occur) will be caused/explained by fitness differences relative to history spaces with rain-excluding static conditions. Changes in frequencies over a longer interval are explained by fitnesses relative to history spaces involving static conditions which allow rain. This scheme works for evolutionary effects over intervals short enough

that none of the competing types is likely to go extinct; for evolution over longer periods, I argue that relevant environmental (static) conditions are determined in a more complex way (Abrams 2009b).

Finally, in order for this picture to work, we need a probability distribution over histories. A realist construal of organism–environment history spaces, like most realist accounts of fitness, in the end needs to resolve deep problems concerning the source of biological probabilities (cf. Abrams 2006, 2007). A benefit of the organism–environment history conception, however, is that it makes it clearer exactly what work biological probabilities must do.

Conclusion

We've seen how Ramsey's arguments and the fact that fitness must attach to types mean that the kind of fitness that's directly relevant to natural selection is static—thus challenging well-known ideas about biological function and altruism. I argued, however, that since fitness is plausibly definable in terms of probabilities of numbers of descendants of an organism type, we can define a sense of conditional fitness in terms of probabilities conditional on the occurrence of events in organisms' lives. This approach captures intuitions about fitness changes in terms of static fitness, and preserves existing ideas about function and altruism with minimal modifications. The basic idea of conditional fitness is implicit in some discussions of evolution, e.g., in life history theory, and senses of conditional fitness have been defined for particular models in various contexts. However, I don't know of any previous general discussion of conditional fitness.

The organism–environment history conception, which views the fitness of a type as defined by a space of sequences of events—“histories” of an organism and its environment—provides a systematic framework for intuitions about conditional fitness which is also sensitive to the complexity of the determinants of fitness. On this view, competing types' fitness differences are the result of differences in the causal structures of their history spaces.

Full-fledged organism–environment history spaces would be too complex for practical investigation. I argued that organism–environment histories can nevertheless play an instrumental role analogous to Hutchinson's niche concept, providing unifying conceptual connections between diverse models and frameworks in evolutionary theory. In addition to supporting clearer understandings of fitness, natural selection, biological functions, and altruism, I suggested that the organism–environment history conception can help unify ideas concerning standard and extended versions of life history theory, developmental systems theory, aspects of niche construction, and other ideas about development. I also outlined a more precise account of organism–environment history spaces which could provide part of a metaphysics of natural selection. I argued that this account might help to provide conceptual foundations for evolutionary theory, playing a role analogous to part of the propensity interpretation of fitness.

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