



The Complex Nexus of Evolutionary Fitness

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Abstract

The propensity nature of evolutionary fitness has long been appreciated and is nowadays amply discussed (Abrams, 2009, 2012; Ariew & Ernst, 2009; Ariew & Lewontin, 2004; Beatty & Finsen, 1989; Brandon, 1978; Drouet & Merlin, 2015; Mills & Beatty, 1979; Millstein, 2003, 2016; Pence & Ramsey, 2013; Sober, 1984, 2001, 2013, 2019; Walsh, 2010; Walsh et al., 2016; etc). The discussion has, however, on occasion followed long standing conflation in the philosophy of probability literature between propensities, probabilities, and frequencies. In this paper, I apply a more recent conception of propensities in modelling practice (the ‘complex nexus of chance’, CNC) to some of the key issues, regarding the mathematical representation of fitness and how it may be regarded as explanatory. The ensuing complex nexus of fitness (CNF) emphasises the distinction between biological propensities and the probability distributions over offspring numbers that they give rise to; and how critical it is to distinguish the possession conditions of the underlying dispositional (physical and biological) properties from those of their probabilistic manifestations.

Keywords Philosophy of Biology · Philosophy of Probability · Chance · Fitness

1 Introducing the Complex Nexus of Fitness

In evolutionary biology, *fitness* has long been appreciated by many to be a probabilistic disposition, or propensity, to reproduce successfully (Popper, 1983, pp. 358ff.; but see particularly Brandon, 1978; and Mills & Beatty, 1979). This propensity interpretation of fitness (PIF) is part of a larger tradition in evolutionary thinking that takes fitness or adaptiveness to be a causally explanatory concept (Sober, 1984, 2011) – and one moreover that can be proudly traced back to the pioneering introduction of the concept of probabilistic or indeterministic causation more generally (Fisher, 1934). Yet, there has been little consensus as to the specific kind of

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propensity fitness is. On the contrary, there is much disagreement in the field as to how to formally represent fitness, how exactly it is an explanatory concept, and what exactly it explains. Critics have been quick to latch onto such disagreements to argue that fitness is not causally explanatory after all (Walsh et al., 2016), that it does not reflect causal relations (Walsh, 2010), and that there are no propensities underlying adaptation phenomena in evolutionary biology (Ariew & Ernst, 2009).

The current impasse suggests that there are some fundamental issues at stake regarding the nature of propensity and its explanatory power that stand yet to be clarified. In a recent state of the art paper, Millstein (2016) argues that there is conceptual work to do; and that debates in the philosophy of probability may feed profitably into the discussion of the nature of fitness. This paper takes up Millstein's suggestion and offers a more complex and nuanced framework than is typically assumed for modelling chancy phenomena in general, the 'complex nexus of chance' (CNC).¹ Contrary to what has been conventional in the philosophy of probability, this approach clearly distinguishes propensities from both probabilities and the finite frequency data that are used to test them. The distinction allows us to cast significant issues that are already discussed in the field in a fresh light – such as the debate about whether fitness is long-term or short-term, and the question regarding what the appropriate mathematical representation of propensities is. My claim is not that applying CNC to fitness solves all outstanding problems in the field, but the more modest claim that it bears significantly on a few important problems currently discussed in relation with the propensity interpretation of fitness (PIF). I argue merely that CNC casts both extant problems and avowed solutions within a different and hopefully more promising framework.

I shall focus upon the propensity *interpretation* of fitness; the name itself follows the standard convention in the philosophy of probability, in line with Popper's (1959) renowned propensity *interpretation* of probability. Here the word "interpretation" is to be taken seriously – propensities are meant to provide the 'semantics' for (objective) probabilities; in other words, they are meant to provide a model for what sort of entities probabilities are – one that moreover makes probability statements true. In other words, this *identity thesis* supposes that propensities provide the truth makers for probability statements. It is, however, riddled with difficulties, as is by now well known (Eagle, 2004; Humphreys, 1985; Suárez, 2013). More specifically, the reduction of probability to propensity that it involves can be proven to generate several paradoxes and contradictions, most prominently what is known as Humphrey's paradox (Humphreys, 1985). This explains why Popper's original version of the propensity interpretation has few champions in the philosophy of probability nowadays – even amongst those few of us who continue to defend a role for propensities in science generally.

The CNC is one amongst other recent developments in the philosophy of probability that rejects Popper's reduction of probability to propensity. But, unlike other rejections of Popper's views, the CNC does not reject the concept of propensity

¹ The CNC is developed fully in Suárez (2020), although the 'tripartite conception' of objective probability that lies at its core goes back to Suárez (2011, 2013, 2017).

altogether: It does not throw the baby out with the bathwater. Instead, CNC embraces a plural metaphysics, where propensities exist independently and give rise in appropriate environments to single case chances or objective probabilities. It is these single case chances – represented as probability distributions within statistical models – which in turn account for frequencies in the data. This ‘tripartite distinction’ between propensities, probabilities and frequencies is unusual in the philosophy of probability literature, since it explicitly abandons the *propensity identity* at the heart of Popper’s view. It favours a distinct and more substantial role for propensities to play in the explanation (rather than merely the interpretation) of probabilities. While most defenders of propensities believe them to explain observed frequencies, the claim that they also explain single case chances is much rarer in the philosophy of probability literature – and has to my knowledge never been applied to evolutionary fitness.

In this paper, I argue that the application of this framework to evolutionary biology yields what may be called the complex nexus of fitness (CNF), which by necessity starts from the assumption that ‘fitness’ is an ambiguous term referring to i) statistical data regarding organisms’ actual offspring numbers and their frequencies; ii) probability distributions within population models representing expected or hypothetical reproductive successes; and iii) the physical and biological supervenience bases of such model-based probabilities, which are taken to include the dispositional properties of the relevant organisms. It is critical that CNF does not collapse ii) into iii) as does Popper’s identity thesis, and as is often assumed for propensity probabilities (Suárez, 2017, 2018). The claim at the heart of the CNF is thus that, in considering evolutionary fitness, we must at all points keep neatly distinct the propensities from the single case chances that they give rise to, and then both in turn from the frequencies that may be observed. I then argue that the careful application of this ‘tripartite conception’ allows CNF to overcome some of the objections raised against the PIF, by making it explicit that propensities cannot be merely in the business of interpreting probabilities, as suggested by the *identity thesis*, but that they must be invoked as separate explanatory entities with respect to single-case chances.

2 Fitness as a Propensity to Adapt: The Issues

My aim is thus to inject some conceptual clarity into the discussion, by offering new light on some of the extant answers to the outstanding objections to PIF. The first objection I shall focus on concerns the exact formal or mathematical representation of fitness as propensity. The relevant discussion here broaches two technical aspects of statistical modelling, informing what are sometimes known as the *moments problem* and the *delayed selection problem* (Beatty & Finsen, 1989; Pence & Ramsey, 2013; Sober, 1984). On the one hand there is the demonstrable empirical fact that fitness is often sensitive to higher moments of the statistical distribution for reproductive success. Hence identifying fitness with just the statistical mean average (the *expected value*, or *expectation*) of a probability distribution will often miss out critical differences down the lineage. The differences can be so critical as to entirely reverse judgements of relative fitness between individual organisms (or traits, or

genes – more about this later). But the idea that fitness, understood as a propensity, must necessarily be identified with some or other moment of a probability distribution presupposes that all propensities are statistical functions, or formal moments of these distributions. This would be in accordance with the conventional wisdom deriving from Popper, but it is nowadays questionable in the philosophy of probability, and it is indeed rejected by the CNC. In section four of the paper, I consequently suggest that CNF accounts for the statistical modelling of fitness without such assumptions, and thus delivers us from the problem of moments.²

The second narrow technical issue concerns whether fitness is short or long term, i.e., whether it involves reproductive success in the most proximate generations, or perhaps even just the next generation; or whether, by contrast, fitness refers meaningfully only to reproductive success down the generations – or perhaps even hypothetical success in some infinite reproductive limit. On a propensity interpretation, the issue may at first sight seem merely a version of the debate regarding ‘single case’ versus ‘long run’ propensity interpretations of probability (Gillies, 2000). If so, the *delayed selection problem* would boil down merely to a difference regarding the appropriate type of propensity involved, where those advocating long term fitness would be implicitly if not explicitly adopting a ‘long run’ propensity account. However, I argue in section five of this paper that these distinctions are in fact tangential. Long term fitnesses are perfectly compatible with ‘single case’ propensities, as advocated by the CNC. This has consequences for the precise mathematical definitions that are appropriate when modelling fitness in different contexts, and whether they issue in contradictions.

Then there is the second and more general issue, namely the explanatory role of fitness. Advocates of the PIF typically defend the view that fitness is a causally explanatory property of biological entities – and for this reason they are sometimes known as ‘causalists’ (Abrams, 2012). Critics of the PIF by contrast, tend to view fitness as not particularly an explanatory concept – certainly not a causally explanatory one –, but rather a descriptive or generalising concept.³ In the last substantial

² As a referee points out, Sober (2001, 2011) already addresses the problem and provides a similar solution for it; and there are similar views voiced in Beatty and Finsen (1989), Brandon (1990) and Millstein (2003, 2016). However, the complex nexus of chance (CNC) allows us to systematize the solution properly within a general philosophical account of probability.

³ See Matthen and Ariew (2009), and Walsh, Ariew and Matthen (2016), but also Sober (1984, Ch. 3) which arguably anticipates the statisticalist view in his critique of the causal role of fitness. In more recent work Sober (2011) develops his view and argues that some of the causal explanations provided by evolutionary fitness are a priori. Sober appeals to precisely the sort of powers that I invoke as part of propensity explanations of single case chances, i.e. dispositional properties (akin to Molière’s ‘dormitive virtue’). However, as Sober points out, these dispositions are probabilistic: Given the appropriate testing circumstances these powers give rise not to particular events (as in Molière style deterministic dispositions), but to the *probabilities* of particular events (Mellor, 2005; Suárez, 2014). Sober’s further distinction between *sources* and *consequences* of fitness differences is also grist to my mill: On a CNC account, ‘fitness differences’ amount to differences in single case chances for survival and for reproductive success. The sources of such differences are propensities, which – as in Sober’s view –, may be said to ground and causally explain such chances a priori; while the consequences of fitness differences are the observed or predicted differences in traits -- which are of course the ultimate empirical facts, and explananda, in evolutionary biology. Thus Sober (1984, 2011) anticipates the tripartite conception, and the CNF may be understood to be systematizing and providing precision for some of his distinctions.

section six of the paper, I argue that CNF shows both ‘causalists’ and ‘statisticalists’ to be in part right.⁴ Propensities are indeed explanatory entities but, in accordance with CNC they explain not only the frequencies in data: They also explain the single case chances that they give rise to within given chance set-ups. However, these explanations are of a very different type: While propensities may be said to *causally explain* frequencies, they cannot, on pain of contradiction (Humphreys, 1985; Suárez, 2013), be said to *cause* single case chances.⁵ Instead, propensities may be said to *ground* such chances (Suárez, 2018). Thus ‘fitness’ is indeed often a name for explanatory propensities, but these are typically a set of properties that are explanatory in diverse ways. In addition, ‘fitness’ is also a name used for the formal probability distributions within statistical models that are adequate for the purpose of representing the single case chances manifested by those propensities. Here statisticalists are surely right: Such formal probabilities are bereft of any causal powers. Finally, ‘fitness’ is also sometimes somewhat confusingly used by practicing biologists to refer to the finite frequencies in the data for reproductive success that propensities aim to explain. Thus, the disambiguation of these three distinct but mutually related uses of fitness is essential for a better understanding of its explanatory power.

My proposal of a complex nexus of fitness is a straightforward application of a particular approach to objective chance within the philosophy of probability, the complex nexus of chance (CNC). Therefore, it helps to first provide some background and motivation on the CNC, as it emerges in discussions over the last decade within the philosophy of probability and statistical modelling. The next section introduces some of the relevant considerations in the foundations of probability that motivate CNC in the first place. It turns out that many of the objections to the propensity account of evolutionary fitness are similar to those raised against the propensity and frequency interpretations of probability over the decades. These objections have led many to abandoning both propensity and frequency *interpretations* of probability (for a compendium of the reasons, see Hájek, 1997, 2009; Eagle, 2004; and many of the essays contained in Hájek & Hitchcock, 2016).

CNC answers the objections by following original leads from Paul Humphreys himself (1985): It abandons the interpretation of objective Kolmogorov probabilities as propensities (thus rejecting the flawed *identity* thesis); yet it refuses to discard the notion of propensity altogether. Instead, CNC recommends using propensities differently, as the explanatory grounds for objective single case chances, and this retort gets around the objections to propensities in general (Suárez, 2013, 2017, 2018, 2020). It is thus unsurprising that the same retort also serves to respond to some of

⁴ This follows Millstein’s (2006) strategy to combine some claims from each of the ‘causalist’ and ‘statisticalist’ camps, although the CNF combines them differently – not at the level of the natural selection of populations versus the level of individual organisms, but by insisting that propensities at either level non-causally ground single case chances.

⁵ Contrary to what e.g., Brandon and Beatty (1984) are led to assert in their response to Rosenberg (1982). More generally, any monistic account that follows Popper’s identity thesis will inevitably be led to assert that propensities explain causally whatever frequencies they explain; and there is nothing over and above for them to explain in any other way.

the objections to earlier propensity interpretations of fitness. Indeed, my purpose in this essay is to construct an alternative CNF view of fitness that not only dispenses with the objections to the propensity interpretation (PIF), but systematically rationalises the responses that have been offered to such objections, by showing them to be proper application of a more nuanced and complex framework for understanding objective probability in science in general.

3 The Complex Nexus of Chance in the Philosophy of Probability

It is nowadays widely accepted⁶ that probability is formally defined through the four classical Kolmogorov axioms, which can be non-technically summarised (in the discrete and finite case) as follows:

Axiom 1: Probability is a mathematical function or mapping from the domain of a logically closed set of propositions $\{A\}$ onto the range of the unit interval of the real numbers: $f : \{A\} \rightarrow [0, 1] \subseteq \mathfrak{R}$.

Axiom 2: The probability of a tautology (a logical truth) is always 1: $P(Taut) = 1$

Axiom 3: The probability of a logical disjunction of mutually exclusive elements (say a and b , where each one rules the other out) is the sum of the probability of each disjunct: $P(a \vee b) = P(a) + P(b)$. (This axiom has a notorious generalisation to the infinite or infinitesimal case, in the so called *axiom of countable additivity*).

Axiom 4: The conditional probability of some proposition A given another proposition B is given by Bayes' theorem:

$$P(A|B) = \frac{P(A \wedge B)}{P(B)} = \frac{P(B|A)P(A)}{P(B)}$$

The philosophical debates have traditionally concerned the *interpretation* of this probability function. According to one school, all probability is subjective degree of belief, hence a measure of agents' ignorance regarding events (or the initial conditions that would give rise to such events in a deterministic or Laplacean universe). We shall instead assume here that probability at least partly – at least in some domains –, refers to the objective chances of events, which they possess independently of any agents' knowledge of them. (The assumption that there are such chances is innocuous for our purposes, since routine in most natural sciences, including evolutionary biology). But what is objective chance, and how can it be an *interpretation* of probability?

The two main philosophical approaches are the frequency and the propensity interpretations. Both have played some role in debates regarding the nature of evolutionary fitness. On a frequency interpretation, probability is identified with a ratio of

⁶ Widely but not universally accepted, as is made clear by the raging debates regarding probabilities based upon fuzzy, quantum, and intuitionist logic. There is also considerable debate regarding the fourth axiom for conditional probability which is ill-defined when the conditioned upon proposition has zero probability (i.e. when $P(B)=0$) – see Hájek (2003) for discussion.

outcomes of a type within the full sequence of all outcomes. We may refer to this as the *frequency identity* of probability (Reichenbach, 1934/1949). Thus, the probability that a coin may land heads, on this interpretation, is simply the ratio or frequency of head outcomes in the full set of (either heads or tails) outcomes. If the coin is fair, then that ratio is just $\frac{1}{2}$. However, there are some very serious problems with this attempt to interpret probability, which are by now well known to philosophers, and which many of us think make any frequency interpretation untenable.⁷

One problem that I like to emphasise (Suárez, 2020, pp. 36–49) is the *explanatory circularity* problem: frequencies cannot explain other frequencies, so the frequency identity renders probabilities explanatorily ineffective vis a vis frequency data. This seems contrary to the statistical modelling practice to invoke probabilities precisely to explain frequencies in the data. The problem is, as we shall see, acute for the kinds of probabilities involved in evolutionary fitness. Another classic objection is the *reference class* problem: the fact that the relevant class of outcome events within which one should seek a ratio or frequency of the salient type is always underdetermined. Consider the coin toss example again: Is the outcome space the set of all outcomes of all tosses of all coins, of just some subset of coins, of just the one coin? Should we include the outcomes where the coin bounces off, or rebounds, or falls on the edge, or is simply not tossed? Should we include all possible outcomes of a similar kind, since any set of actual outcomes is finite and may always diverge from the underlying probability (a phenomenon known as *frequency tolerance*)?

An alternative that gets around such problems is the propensity *interpretation* of probability, advocated by philosophers such as Karl Popper (1959). On this view, probability is not to be identified with any frequency but with the underlying propensities or dispositional properties (what we have called above the *propensity identity*). In the case of a coin toss, this identifies the chances with either the full set of physical properties of the coin, or the toss, or some subset of both. It is often claimed that the propensity interpretation is explanatory in a way that the frequency interpretation cannot be since it is firmly linked to the conditions or underlying properties that give rise to the frequencies in the first place. Change the conditions, or the properties of the coin (or the coin toss, or its setup), and you will also change the frequencies. Yet, whilst the propensity identity overcomes some of the objections to the frequency identity, it has problems of its own too, related to what is known in the literature as Humphreys' paradox.

Paul Humphreys (1985) produced an influential argument that the explanatory asymmetries that characterize propensities cannot be represented in terms of classical Kolmogorov conditional probabilities – and that this renders impossible any *propensity identity*. More generally the *propensity identity* fails both ways (Suárez, 2013, 2014), as follows. Probabilities are invertible via the fourth axiom of conditional probability: if $P(A | B)$ is well defined then so is $P(B | A)$. Yet, if the former has a propensity interpretation, whereby B describes the conditions, or dispositional properties of the chance setup, and $P(A | B)$ represents the probability that the chance setup yields outcome A, then $P(B | A)$ does not have a propensity interpretation, and in fact has no meaning at all from a propensity point of view, as the

⁷ See Hájek (2009) or Suárez (2020) for a description of this and other problems.

coin toss example illustrates: whatever properties of the coin explain its probability of heads, they are not themselves explained, or determined by, the heads outcome. On the other hand, Humphreys' ingenious thought experiment (involving subatomic particles being transmitted through a half-silver mirror) shows that some, perhaps most, propensities fail to have a coherent representation in terms of conditional probabilities. There are some responses to Humphreys' argument, but the most convincing ones (including Humphreys' own) abandon any attempt to reduce at least some of the relevant physical probabilities to propensities or vice-versa.

The complex nexus of chance (CNC) is on board with these recent rejections of the frequency and propensity *identities*. Instead of trying to reduce the notion of probability to either frequency or propensity, CNC fully embraces metaphysical pluralism regarding objective chance, accepting the need for propensities, single case chances, and frequencies (Mellor, 2005; Suárez, 2011, 2014, 2017). They are all required to make full sense of the diverse uses of chance in the practice of model building: Propensities give rise to the probability distributions in models standing for single case chances that are then empirically confirmed by the frequency data obtained in observational and experimental trials.⁸ The point of a philosophy of science in practice is not to interpret away these categories, but to understand them, and, if necessary, to suggest changes in their intricate and productive synergies within the practice of model building (Suárez, 2020). In this spirit I now turn to attempts to represent fitness probabilities as either frequencies or propensities, to some of the problems they give rise to, and to my argument that an account of fitness as a more complex nexus (CNF) involving all three of them is required.

4 Momentous Paradoxes and the Nature of Statistical Distributions

One initial difficulty in finding an appropriate mathematical representation of fitness is the inconvenient fact that there are different statistics that fitness may quite generally be identified with. The first attempts at a propensity interpretation of fitness (PIF) identified fitness with the *expected value* or *expectation* of the statistical distribution for offspring (Brandon, 1978; Mills & Beatty, 1979). Suppose the possible offspring of an organism O_1 are given by Q_i with $i=0, 1, \dots, n$. The statistical distribution over O_1 's possible offspring $\{Q_0, Q_1, \dots, Q_n\}$ in some environment E is then given by some probability function indexed to organism and environment and defined over the possible offspring numbers: $Prob_{O_1 \& E}(Q_i)$. The expected value or expectation of this probability

⁸ It is important here to understand that while frequency ratios within observed – hence finite – sequences of outcomes can provide evidence for or against propensity and single case chance ascriptions, this is not their only function. Those frequency ratios do of course objectively independently exist, and they provide factual knowledge of the phenomena regardless. In including those frequencies within the tripartite division that makes up the complex nexus of chance, I am thus not including *the means* of testing propensity ascriptions within the concept. It is true that such testing will typically involve comparison of the probability distributions that represent the theoretical single case chances with observed frequencies (also sometimes known as ‘experimental probabilities’), but the comparison is not part of the concepts involved. (This consequently has the implication that, in the CNF, ‘fitness’ does not include the means of ‘testing’ it; even if the term aptly refers also to those experimental probabilities that biologists label ‘measured’, ‘observed’ or ‘experimental’ fitness. I thank a referee for pressing me on this point).

function is its average, or population mean μ , the so-called *first central moment* of the distribution (Krzanoski, 1998, pp. 14ff.; Grimmett & Stirzaker, 1982, p. 51):

$$\mu_{O_1 \& E} = \text{Exp}_{O_1 \& E}\{Q\} = \sum_i \text{Prob}_{O_1 \& E}(Q_i) \cdot Q_i.$$

Suppose the organism O_1 in question has in the given environment either no offspring or two offspring with probability $\frac{1}{2}$ in each case. The expected value of O_1 's offspring in environment E is then exactly one since: $\sum_i \text{Prob}_{O_1 \& E}(Q_i) \cdot Q_i = \frac{1}{2} \cdot 0 + \frac{1}{2} \cdot 2 = \frac{2}{2} = 1$. The original definition of the propensity interpretation of fitness (PIF) then states that the fitness of organism O_1 in environment E is its expected offspring value, namely, in this case, one.

Yet, this definition has come under heavy criticism ever since originally expressed (Abrams, 2009; Mills & Beatty, 1979; Sober, 2001 and 2013; etc). Many of the objections rely upon what may be called the *underdetermination of statistical distributions*, the well-known fact in statistics that an indefinite number of different probability distributions may have the same expected value, i.e., yield the same expectation over a range of outcomes.⁹ As an illustration, consider another organism O_2 in the same environment E with a distinct statistical distribution over its offspring, defined by a different probability function: $\text{Prob}_{O_2 \& E}(Q_i)$. This organism can only have exactly one offspring with certainty, i.e., with probability one. Nevertheless, the expected value of O_2 's offspring is the same as O_1 's, since $\sum_i \text{Prob}_{O_2 \& E}(Q_i) \cdot Q_i = 1 \cdot 1 = 1$.

It stands to reason, however, that these two organisms, O_1 and O_2 , are constitutionally distinct, and they differ in their capacities or propensities to reproduce in the given environment. Hence, there should be significant differences in fitness relative to one another, contrary to the definition provided by the original (PIF). This is borne out when considering the higher moments of the respective statistical distributions. The *second moment about the mean* of a distribution is the statistic known as the *dispersion* parameter σ^2 of the distribution: $\sigma_{O_1 \& E}^2 = \text{Exp} \left\{ (Q_i - \mu_{O_1 \& E})^2 \right\} = \sum_i \text{Prob}_{O_1 \& E}(Q_i) \cdot (Q_i - \mu_{O_1 \& E})^2$. This is a representation of what is known as the *variance about the mean* in a population (roughly: how large on average the spread of values is about the mean). The variance is always positive – since it is a squared quantity – and it is sometimes replaced by another quantity, the *standard deviation* σ , which is simply its square root. The larger a variance about a mean, the larger the spread of values exhibited by the random variable. A zero standard deviation or variance signals a distribution in which all values coincide with the mean.

The most common empirical models for fitness show that variance in offspring statistical distributions with identical expectations can have considerable differential effects on reproductive success (Beatty & Finsen, 1989, pp. 24ff.; Sober, 2001, pp. 30-34; see also Millstein, 2009, p.609ff. for an excellent review; many of the examples discussed originate in Gillespie, 1974, 1977). In these examples two organisms O_1 and O_2 have distinct offspring distribution functions with the same expectation:

⁹ Although the objections ride upon such mathematical facts, they are not essentially mathematical but biological, and aim to show that the predictive and explanatory power of fitness differences would be left unaccounted for (Sober, 2013). They thus take the form: 'Given such mathematical facts, if fitness were associated with expected value, differences in fitness would not be explanatory or predictive since they would miss out other relevant statistics of the distribution'.

$\mu_{O_1 \& E} = \mu_{O_2 \& E}$, because $\sum_i Prob_{O_1 \& E}(Q_i) \cdot Q_i = \sum_i Prob_{O_2 \& E}(Q_i) \cdot Q_i$. Yet, the variance in O_1 's offspring distribution is larger than that in O_2 's, pointing to the fact that the first distribution is more widely spread about the mean: $\sigma_{O_1 \& E}^2 > \sigma_{O_2 \& E}^2$, because $\sum_i Prob_{O_1 \& E}(Q_i) \cdot (Q_i - \mu_{O_1 \& E})^2 > \sum_i Prob_{O_2 \& E}(Q_i) \cdot (Q_i - \mu_{O_2 \& E})^2$. The generic difference in variance between two distributions with the same mean is illustrated by the two curves (with equal expected mean value $\mu = 6,5$ in both cases, yet differing considerably in variance) in Fig. 1 below.

The mode of both distributions (the 'peak') is at the mean value of 6,5, but in the interval of integer numbers one of the curves only ranges from having three offspring to having nine, while the other ranges all the way from having one to twelve and has a standard deviation twice as large. It is by now well known that there is often greater reproductive advantage for those organisms (or traits, or genotypes) that have the narrower spread, i.e., the smaller variance or standard deviation. Intuitively, a more regular reproductive pattern, or a spatially or temporally denser reproductive strategy is superior because the advantage brought about by high offspring in any given location (or period, say on a given year) does not balance out the disadvantage incurred in the lower reproductive success in other locations (or over longer periods). Thus a "lowering in the variance in the offspring number [...] can only raise the probability of leaving offspring behind" (Gillespie, 1974, p. 605). Elliott Sober (2001, pp. 33-34) explains these cases as failures of the commutativity of expectations, on the one hand, and quotients or ratios on the other. Quite generally, the expectation of a ratio of two quantities is not the same as the ratio of the expectations of such quantities. Since frequencies are ratios, or proportions of attributes in populations, the expectation of a certain frequency in the population is not identical to the ratio of the expectations (of attribute, and overall population). This is helpful as an illustration of the general phenomenon, particularly for trait fitness. It shows that the phenomenon of variance-dependence of fitness is general, and it does not demand any interpretation of the probabilities at stake. Rather, as I shall argue, the phenomenon calls for an explicit distinction between propensities and their probabilistic manifestations in single case chances, regardless of how we interpret those chances.¹⁰

In fact, the phenomena are more complex still since the effects of variance (in distributions with identical expectations) on reproductive success are often confounded by even higher moments of the statistical distribution. The third moment about the mean of a distribution is its *skewness*, referred to as γ , which serves to pick out asymmetries in the tails of the distribution either side of the mean. Formally, the third moment of the statistical offspring distribution for organism O_1 is expressed as (Krzanowski, 1998, p. 16-17): $\gamma_{O_1 \& E} = Exp \left\{ (Q_i - \mu_{O_1 \& E})^3 \right\} = \sum_i Prob_{O_1 \& E}(Q_i) \cdot (Q_i - \mu_{O_1 \& E})^3$. A distribution with $\gamma = 0$ is symmetrical about the mean; one with $\gamma > 0$ will exhibit a long tail of high values and a bunched-up tail of low values; another one with $\gamma < 0$, will be bunched in the high values with a longer tail in the low values (see fig. 2). Yet both variance and expectation (mean) can remain the same in all three.

¹⁰ I have in the past defended a Sober (2010) style no-theory theory of single case chances, but my claims are more generally compatible with any sufficiently deflationary account of objective probability (Suárez, 2020, chapter 10).

It turns out that those distributions with larger skewness tend to correspond to organisms with greater reproductive success (Beatty & Finsen, 1989; see also the informed discussion in Millstein, 2016, pp. 609ff). There are even cases where larger skewness trumps lower variance, which in turn may trump higher expectation. In other words, lower variance and higher skewness can indicate greater reproductive success, and hence greater fitness, regardless of the expectations. The intuitive way around such difficulties is to relinquish the identification of fitness with the expected value of the statistical distribution for offspring. Instead, one may suppose that fitness ought to be identified with the distribution as a whole – not any one statistic thereof. And this is moreover a natural move in thinking of the fitness of an organism (or a trait, or a genotype) along the lines of a propensity interpretation of probability. Most current versions of the propensity interpretation of fitness (PIF) decisively move in this direction, and away from identifying fitness with expectation (Beatty & Finsen, 1989; Brandon, 1990; Pence & Ramsey, 2013; Sober, 2001, 2011, 2013). This move away from the identity with frequencies is, of course, entirely natural within the CNF – it is in fact a requirement for any application of the CNF to fitness.

The next section raises more general issues and difficulties with current propensity interpretations of the entire statistical distribution for offspring. But it is worth noting already that it is compromised by even more complex phenomena regarding the higher moments of the distribution. Not only do higher moments determine fitness for otherwise statistically identical distributions of reproductive offspring. More remarkable still is that the higher moments can occasionally trump the lower ones. Thus, a smaller variance can compensate for a smaller expectation, as the organism with the lowest expected value turns out to be more reproductively successful if its variance is considerably smaller; similarly higher skewness can occasionally trump larger variance in distributions with identical expectation (Beatty & Finsen, 1989, p. 24; Millstein, 2016, p. 609-10). In none of these cases is the expected value of a distribution a good measure of fitness. Rather the fact that larger skewness can trump lower variance, which in turn can trump higher expectation, suggests instead a certain ‘trumping’ hierarchy, with expected value at the lowest level, as it were: expected value \rightarrow variance \rightarrow skewness.

In other words, whether expected value is or not correlated with fitness will in fact depend on the context. Within some environments, as just noted, for some systems, expected value may even be negatively correlated with fitness. This entails that taking the entire distribution, without further qualification, as the propensity fitness of the organism is a mistake; the fitness of an organism, for instance, seems always relative to a context, since it reflects the effect of the environment on the delicate balance of the diverse statistical moments.¹¹ No pre-determined hierarchy of the

¹¹ The point is, if anything, more acute if we consider fitness to be a property of traits, not single individual organisms, as in Sober (2013, 2020) – an option discussed later in the paper. In that case, rather than thinking of propensities as the underlying physical and biological properties of an organism, one ought to think of fitness propensities as the underlying physical and biological properties of a trait, and as long as traits are not defined merely extensionally, the CNF follows: the propensities give rise to probabilities (single case chances) for particular traits to reproduce and survive within given environments; and such propensities are tested by the usual means by comparison with observed trait frequencies. On a CNF account there is no need to reject the view that trait fitness is a propensity.

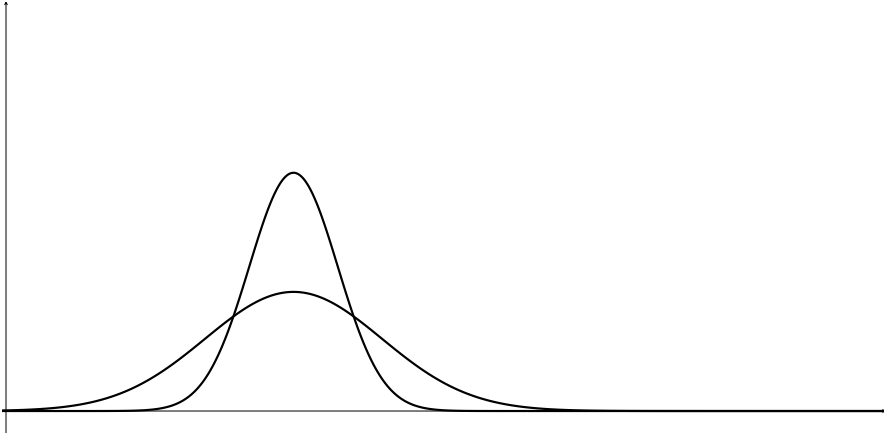


Fig. 1 Distributions with different variance but equal mean (© The author)

features or functions of the offspring distribution, taken by themselves, seems sufficient as a reliable indicator of fitness. Thus, something more complex and context dependent will be required in the relation between probability distributions and the underlying propensities. And that is just what CNF can offer.¹²

On a complex nexus of fitness (CNF) view this sort of radical dependence upon extrinsic environmental factors, as well as the intrinsic features of the mechanisms of reproduction, is only natural.¹³ The key is, recall, in the distinction between the underlying propensities and the various probability

¹² I do not claim priority: Others, such as Brandon (1990), have offered similar solutions, and Millstein (2016) endorses Brandon's approach to distinguish the mathematical representation of fitness from its ontology. But the CNF systematises such solutions, which follow naturally from a conception of propensities as clearly distinct from the single-case chances they give rise to. The former are properties of systems, -- relational or otherwise --, while the latter are mathematically representable as probabilities, by definition -- and no further distinctions are called for.

¹³ There has been an attempt, by Peter Godfrey-Smith, to revive the 'extrinsic' / 'intrinsic' distinction in evolutionary biology, albeit without any substantive ontological implications (Godfrey Smith, 2009, p. 53). Intrinsic biological features or organisms (or traits, or genotypes) are those that "do not depend on the existence and arrangement of others". While they are not more real than extrinsic features, Godfrey Smith claims that intrinsic features are indicative of more paradigmatically Darwinian evolutions by natural selection. He even introduces a measure *S* of supervenience upon intrinsic properties. A high *S* is indicative of a high degree of supervenience of reproductive success upon the intrinsic propensities of organisms (traits or genotypes); a low *S* indicates that reproductive success rather depends on extrinsic features, whether they be relational propensities of the environment, including entire ecosystems, or the conditions required for the manifestation of the underlying propensities. On the CNF view, biological propensities may be intrinsic or extrinsic, in this terminology, depending on the system and nature of the case, but there is no sense in which they are more or less 'Darwinian'. By contrast, the single case chances that manifest those propensities are always necessarily 'extrinsic', since they are reliant on the environmental context and other 'triggering' factors.

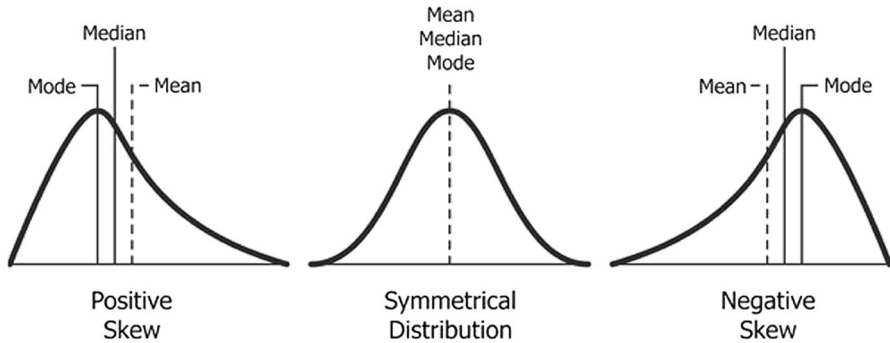


Fig. 2 Distributions with different skewness and median but equal mean (© Diva Jain under a CC BY-SA 4.0 license)

distributions that these may give rise to in different contexts. The probability distribution that emerges in each context is as responsive to the environmental conditions as to the system's propensities.¹⁴ Note in addition that the propensities themselves may be more or less intrinsic to a particular organism or population – there are also environmental systems, for instance in ecology, which possess holistic propensities of their own – nothing in the account rules out such holobionts, or any other complex holistic systems. At any rate, the critical point is that the underlying propensities first determine the space of possible outcomes, and then define the probability distributions over such outcomes.¹⁵ On this picture, it is not surprising that the environment will often influence how the higher moments of a distribution relate to the lower ones in effecting changes in the reproductive success of organisms. In a different environmental context, there may be different extrinsic propensities, and those that are intrinsic may manifest themselves in different probability distributions. This is certainly so for long term reproductive success, but often also in very short generational terms.

¹⁴ Note that this is not the usual claim about the variety of fitnesses (for which see e.g., Millstein, 2016, p. 612). It rather states that even with the same underlying propensities, an organism would exhibit different offspring distribution in different environments. The propensities do not vary with the probabilities here, because, as already pointed out, the CNF keeps propensities and probabilities (single case chances) distinct. So, the regimentation of the language is novel, and the concepts employed are filled in differently.

¹⁵ See Suárez (2018), which also suggests an indexical formulation of the probability distributions to keep out any variables representing the propensities out of the chance functions, thus avoiding Humphreys' like paradoxes. The propensities set up the probabilities and their outcome spaces, thus delimiting the regime of the possible - not the other way around.

5 Varieties of Propensity and Fitness: The Long Term and the Long Run

The literature on propensities distinguishes long run and single case varieties of the propensity interpretation of probability (Hacking, 1965). Long run views are inspired by empiricist accounts of evidence, concept formation, and belief (Gillies, 2000), and stay as close as possible to frequency interpretations such as Von Mises' (Von Mises, 1928). In a long run version, propensities generate stable frequencies in long, limiting, or infinite sequences of outcomes (depending on the type of long run propensity interpretation). The standard illustration employs the tossing of a fair coin: A long run theory ascribes propensities to the conditions that generate a 50-50 frequency in a long, limiting, or infinite sequence of outcomes of the coin toss. While long-run propensities are ostensibly identified with the conditions that generate sequences and not with the sequences themselves, the sequences must be a version of what Von Mises called a 'collective': A random sequence with a well-defined limit and no possible selection function picking out any subsequence within it with a different limit. It can thus be argued that long run propensities are indistinguishable in practice from frequencies (Suárez, 2014, p. 219).

A single case interpretation, by contrast, identifies propensities with conditions that uniquely generate the probabilities that obtain in every single experimental trial, regardless of whether they are actualised in any actual or imaginary sequence of outcomes. In the coin toss example, propensities are identified with the conditions required to generate a probability distribution over the possible outcomes of any given single experimental trial on a chance setup. In any given coin toss, if the coin is fair, the probability of heads / tails is $\frac{1}{2}$. The propensity in this case is the set of those properties of the chance setup (including the coin) that make it the case that the probability is indeed $\frac{1}{2}$ for any given toss. Whether or not this is a random sequence (or a Von Mises' *collective*) is immaterial to both propensity and probability.

In other words, in a coherent single case theory propensities and probabilities are distinct – the propensities give rise to the probabilities, and both concepts are required to make sense of objectively chancy phenomena. Moreover, testing a single case propensity requires displaying some experimental frequency that may support or contradict the probability distribution that it prescribes. Hence single case propensities, if they are in principle to have empirical manifestations and be subject to test – as surely most if not all scientific propensities must be – need recourse to empirical finite frequencies as the result of experimental trials. In other words, adopting a single case propensity theory makes it possible to appreciate the three distinct ingredients in any meaningful ascription of objective chance in scientific modelling, namely: propensities, probabilities, and frequencies. I refer to this tripartite conception together with their inter-relations, as the 'complex nexus of chance',

and advocate employing it as an appropriate tool for the analysis of biological fitness.¹⁶

The rejection of long run varieties of the propensity theory, in favour of the single case variety, does not necessarily conflict or contradict the view that biological fitness is best understood as ‘long term’ as opposed to ‘short term’. A long-term view of fitness is not just compatible with a single case propensity interpretation of fitness but, I urge, it is best understood in its light: *Long-term fitness is not long run propensity*.

Fitness is viewed as a short-term property of an organism (or a population or a trait – more about the differences later), when it entails reproductive success in the short term, and possibly in the next generation only. Thus, two organisms O_1 and O_2 have different relative fitness if their expected (next generation) reproductive success is different. This is straightforward only *post facto*, and in fact only under substantial assumptions. Suppose that throughout their existence O_1 has two offspring, and O_2 only one offspring; and suppose only natural selection was acting (no drift, mutation, migration): On a short-term view of fitness, O_1 is then necessarily fitter than O_2 .

However, it is well known that the short-term definition of fitness has several paradoxical or counterintuitive consequences (Abrams, 2009; Beatty & Finsen, 1989; Sober, 2001). There are certain scenarios and environments where short-term reproductive success leads to long term failure and vice-versa (Gillespie, 1977; Pence and Ramsey (Pence & Ramsey, 2013, p. 857) refer to this as the *delayed selection problem*). The initially least successful organism may enjoy greater reproductive success down the road, and go on to gain selective advantage, if there are environmental reasons why an early overpopulation may turn out to be deleterious in the long term. Thus, suppose that resources suddenly and temporarily become very scarce at the next generation. Having to feed and protect equally for two offspring may become more costly, to the point perhaps that it may lead to the early extinction of both. In this scenario, and environment, having only one offspring at an earlier point in time may lead to greater reproductive success down the generations, when resources recover.

Even in a two-generation model, with scant environmental variation, it is possible for O_1 to have greater reproductive success in the short term, as above, while having less reproductive success in the slightly longer two-generation term. The classic case is the mutation found in some species of drosophila (Crow & Kimura, 1956). If both of O_1 's offspring die before reproducing, but O_2 's sole offspring survives and goes on to reproduce, O_2 already has reproductive advantage over O_1 within two generations. It is obvious that such reversals are more likely the larger the number of generations envisaged, in whatever complex scenarios or environments, particularly if overlapping generations are allowed.¹⁷

¹⁶ See Mellor (2005) for an exposition of single case propensities, and Suárez (2017, 2020) for a defence of the tripartite conception in statistical modelling.

¹⁷ In as much as an entire lineage may be wiped out if the organism reproduces early in what Godfrey-Smith (2009, p. 51) calls a ‘strongly competitive’ intergenerational environment.

Fitness is therefore often best understood to be long term. But how long is 'long'? The phenomenon of later (i.e., two or more generations down the road) reversals in reproductive success is well established (Sober, 2001), and it is hard to see what would constitute an insurmountable number of generations, or generational threshold, beyond which no reversals are biologically possible.¹⁸ For this reason, some defenders of long-term fitness define it in an infinite limit. For example, Pence and Ramsey (Pence & Ramsey, 2013, p. 862) define it in terms of Tuljapurkar's (1990) asymptotic sequences of random, non-negative matrices:

$$F = \exp\left(\lim_{t \rightarrow \infty} \frac{1}{t} \int_{w \in \Omega} \Pr(\phi(w)) \cdot \ln \phi(w, t) dw\right) \quad (\text{Infinite Fitness})$$

Nonetheless, such limits only obtain under stringent conditions. For instance, Pence and Ramsey's (Infinite Fitness) equation above demands: i) weak ergodicity, ii) that the logarithmic moment of the growth rate be bounded and, most importantly for our purposes, iii) that the probability function be generated by a stationary random process. Roughly, a random process, i.e., Brownian motion, is one where the values of the dynamical variables at a given time do not determine the next values; it is stationary if it converges towards its mean or average value. The assumption therefore entails that while no daughter population determines any of its direct descendant populations, the series converges towards its mean or average. While this does not amount to (PIF), as usually expressed, it does impose a requirement on the evolution of populations that may not always be satisfied in stochastic dynamics.

It has in addition been argued (Abrams, 2009; Sober, 2001) that short-term fitnesses also have their uses, and can claim legitimately to be real too. It stands to reason that the knowledge that O_1 's short-term fitness is greater than O_2 's, even if only for the next generation, may be very useful for purposes of both prediction and explanation regardless of whether in the longer term O_1 's reproductive success continues to be greater. Or, to take a more extreme example, suppose that the environment is such as to generate mass extinction within two generations, anyway; it follows that the only concept that is explanatory and predictive in that environment is short-term fitness. The pluralist would be able to accept both short-term and long-term fitness. This strikes me as correct: It is not sound scientific methodology, and certainly not sensible pragmatic policy, to do away with a concept that has its uses – however limited. And there is no better hallmark of reality for any concept than finding use within scientific practice.

Yet, if fitness is identified with long run propensity, in accordance with the *propensity identity*, there could be no such uses of short-term fitness: nothing short of the long run would have any reliable expectation value. So, anyone who accepts Sober's and Abrams' point regarding the uses of short-term fitness is bound to reject long run propensity accounts of fitness. There are yet more general reasons to reject them, and most importantly, the tripartite conception at the heart of CNF is perfectly

¹⁸ Biologists tend to define fitness in the long but finite term and remain uncommitted about how long that is, which is fine empiricist methodology, but leaves the conceptual questions unanswered.

compatible with *both* long-term and short-term fitness. For, recall, the propensities that are employed by the CNF, and the related CNC account of chance, are not identified with probabilities. Instead, propensities are employed to partly explain the probabilities that emerge in those contexts in which chance setups operate. While such a distinction (between the probabilities for reproductive success and the propensities of the chance setup that generate them) makes no sense in a frequency or long run propensity interpretation of probability, it makes perfect sense in a CNC. This means that the propensities, or probabilistic dispositions, of the organism within its environment may ground all the expected values for its reproductive successes – whether short or long term. In cases where the limiting value of fitness can be calculated – as in the equation (Infinite fitness) above, whenever all its three assumptions apply –, the probability distribution that obtains in each generational ‘trial’ is indeed given by (Infinite fitness), and the values of reproductive success at each generation are simply the random outcomes at each single trial that are consistent with that probability in the limit. The phenomenon does not then differ in any significant way from the case of a fair coin, i.e., one whose propensities display a single case chance to land heads and tails with equal probability $\frac{1}{2}$ in each trial – even though obviously in every trial either heads or tails obtains.¹⁹

The tripartite conception within the CNF thus resolves the conundrum between short-term and long-term fitness by making it clear that fitness is a complex notion, that includes propensities *and* expected values of all statistical distributions for offspring, whether short or long term. On this view the fitness of an organism (or a trait, or a genotype) is not identified with any of the distribution functions. Neither is it identified with the propensities that give rise to the distributions; fitness is rather the combination of both within each context. Now, this sort of pluralism regarding short versus long term fitness is, of course, not entirely new. It is in fact in line with similar views espoused by Beatty and Finsen (1989, p. 20), Sober (2001, pp. 29ff), Abrams (2009, pp. 754ff), and Millstein (2016, pp. 612ff.). Yet, there are some significant differences. While all these authors emphasise the plurality of expectations, and how fitness cannot be reduced to either short or long term, the CNF emphasises the plurality of chance itself, and how a set of propensities in a chance setup may give rise to different probabilities in different environments, both short and long term.²⁰ An issue undoubtedly remains regarding the explanatory nature of the relation between the underlying propensities, on the one hand, and the probabilities of reproductive success that they give rise to, on the other. But nothing particularly hinges on whether success is short or long term, as both can be accommodated within CNF.

¹⁹ Defenders of the most sophisticated recent versions of (PIF) are not always entirely clear whether they mean to identify fitness with a long run propensities or single-case ones. One may take my argument above as confirming that they must mean the single case.

²⁰ Sober comes perhaps close to this view when he asserts (2013, p. 337): “Mixing is routine in models of evolution where some probabilities represent actual frequencies and others do not”. While agreeing with the need to mix different probabilities, CNF would nonetheless go beyond it in explicitly distinguishing the propensities (dispositional properties) from probabilities (single case chances).

6 The Explanatory Role of Fitness

The generic CNC account takes propensities to be dispositional properties of systems or chance setups with probabilistic manifestations that can be tested against frequency data. The possession conditions for propensities are thus not the same as those for the properties that manifest them, as is more generally the case for any dispositional property (think of the possession conditions for the fragility of an object, typically describing its internal composition and architecture, which do not coincide with the conditions, typically including environmental factors, for the breaking of the object). But, in addition, propensities – unlike sure-fire dispositions—, manifest themselves only probabilistically. It is then possible to test the probabilities manifested against frequency data – and this provides reasons, typically of an abductive sort, as is common for theoretical properties, for or against the ascription of the propensities.

The CNC account fits in better with the practice of statistical modelling, including in biology, where parametrization of the phenomena plays a critical role.²¹ It is easier to see the practice of parametrization as reliant upon propensities understood as dispositional properties; the probability distributions as the emergent properties that get modelled by means of the probability distributions; and the experimental outcomes as the frequency data that can be used to test them (Suárez, 2017, 2020).²² The sorts of model explanations that are typical in statistical modelling fall out as applications of the parametrizations of the probability distributions to the frequency data. It is a plausible conjecture that all explanatory uses of evolutionary fitness in practice can be understood in this way, as cases of statistical model explanations. If so, I suggest that fitness properly speaking is not merely propensity, but it is rather to be identified with the whole complex nexus of chance, involving fully the tripartite distinction between propensities, probability distributions, and frequency data.

It would be beyond the scope of this paper to attempt a complete analysis and study of the modelling methodologies in evolutionary biology that bear the conjecture out. I will more modestly explore some of the relative advantages of the conception of propensities within the CNF as regards some of the recent controversies in the philosophical literature. CNF accepts that dispositional properties play a role, so it bears superficial similarities with causal dispositional accounts of fitness. The critical difference is that CNF rejects any reduction of fitness to dispositions, embracing instead a tripartite conception of fitness.²³ More generally, ‘causal dispositionalism’

²¹ Abrams (2012, forthcoming), while not necessarily endorsing the CNF, are excellent accounts of the practice of parametrization in evolutionary biology. Rice (2008) puts parametrization to work in the development of a stochastic version of Price’s equation.

²² The idea again finds a correlate in evolutionary biology modelling practice, for instance, explicitly in the calculation of relative and marginal fitnesses (Rice, 2004, pp. 7ff), which assumes a primitive probability for an allele to be found in a certain genotype. As noted above, the present paper is devoted to introducing the CNF framework, and to placing it within the philosophy of probability literature. And while the paper is a call for further study of the modelling practice, any more detailed application must await subsequent publications.

²³ Triviño and de la Rosa (2016) defend causal dispositionalism, which Drouet and Merlin (2015) rightly reject. Sober (1984, 2013) is implicitly a defence of propensities as distinct from frequencies, hence incompatible with causal dispositionalism, yet closest to my views.

(Mumford & Anjum, 2011) is a monistic doctrine about the metaphysics of dispositions, which attempts to reduce probability to causal dispositions. By contrast, the complex nexus of chance (CNC) and its application to fitness (CNF) take a pluralistic view of chancy phenomena, attempting no reduction of either fitness to probability, or of probability to dispositions (or propensities).

CNF instead recommends considering fitness a generalisation over all those physical and biological properties that make some organisms ‘fitter’. The probability distributions over offspring – and their statistical moments – supervene upon those dispositional properties, or propensities.²⁴ But, as noted earlier, the properties are not the cause of the probability distributions, which are merely the grounded representations of the overall expectation of reproductive success. What the properties of organisms do cause (at least partly) is of course further properties in themselves and other organisms as they evolve (they can also influence their environments, as is nowadays accepted to be the norm in niche construction). There has been a tendency in the literature to identify fitness with either the frequencies of observed reproductive success (as in early circular conceptions of fitness); the probability distributions or their expectations (as in the PIF we just reviewed in previous sections), or the underlying properties in the supervenience base (as is the case amongst defenders of causal dispositionalism). I urge the view that fitness properly understood is all of these taken together – and moreover taken in their very productive connection in the practice of modelling the phenomena.²⁵

I have argued that the pluralism inherent in CNF is the key to its distinct way of answering some recalcitrant objections to PIF. CNF recommends explicitly embracing propensities not as an *interpretation* of evolutionary probabilities, but an *explanation* of how they come about. The best way to illustrate the explanatory power of fitness on the CNF account is then precisely to run through its way of responding to some of these issues. I will consider here only two issues, but the conjecture is that other discussions and issues in the field may take a different form in view of CNF, thus casting the approaches that have been proposed in response in an interesting new light. I first consider the argument that the PIF does not capture the proper objects of fitness (whether they are token organisms or genes, or token traits or populations). Then I move to the objection that

²⁴ For overall fitness as a supervenient property, see Sober (1984, Ch.3). Peter Godfrey-Smith (2009, p. 30) also recommends thinking of fitness as “a compression of a full specification of causal factors”.

²⁵ CNF chimes in with a number of recent accounts in the philosophy of biology literature that there is no space here to discuss in full. Besides being on board with Elliott Sober’s pluralism regarding probabilities (Sober, 2013) and sympathetic to his minimalism about single case chances (Sober, 2010), CNF was noted to chime in well with the pluralism in Beatty and Finsen (1989), and Millstein (2003, 2016). True, it does not restrict it to propensities in the way they do (one could say that Beatty and Finsen, and Millstein, embrace horizontal pluralism only as regards different probability distributions; while CNF pluralism is in addition vertical, since it distinguishes three layers in one complex notion of fitness). Still, as we shall see, the CNF echoes Millstein’s (2006) prising apart of ‘causalist’ and ‘statisticalist’ claims. I also believe that Marshall Abrams’ (2012, 2014, 2015) nuanced distinctions between tendential / parametric fitness, mathematical / statistical fitness, and measurable fitness can be subsumed under the tripartite conception in the CNF. Finally, CNF is also evidently in line with Peter Godfrey Smith’s (2009) emphasis on the plural practices of modelling fitness.

population level properties affect reproductive success rates, yet cannot be said to cause them, which would see PIF fail too.²⁶ In neither case do I claim priority for the way the CNF resolves the issues, but I do urge that casting proposed solutions to these issues in terms of the CNF has the promise to resolve tensions, answer objections, and provide greater detail regarding the explanatory role of propensities in fitness.

6.1 The objects of fitness

Mills and Beatty (1979) distinguished between $fitness_1$ and $fitness_2$, where the former is the fitness of an organism, and the latter is the fitness of the type of organisms that share some trait. They then identified $fitness_1$ with the expectation or expected value of the organism's offspring distribution – a definition we rejected in section three (following Beatty and Finsen's (1989) own subsequent arguments). Nevertheless, if a trait T is defined extensionally as the set of organisms that share T (call this set {T}), then the $fitness_2$ of trait T is simply the average of the $fitness_1$ of the organisms in the set {T}. As Sober (2013, p. 336) puts it: “the fitness of a trait is the average fitness of the individuals that have that trait”. The full definition makes it explicit that $fitness_1$ is relative to a population P and an environment E, and therefore so is $fitness_2$ since it is built upon it. Sober (2013) then goes to argue that neither $fitness_1$ nor $fitness_2$ can be understood as propensities, but *changes* or *variations* in $fitness_2$ may be. For only the latter exhibit the required causal asymmetries, and sensitivity to population and environmental conditions. The starting point of CNF, by contrast, is that neither $fitness_1$ nor $fitness_2$ can be identified with propensities – on pain of running propensities and probabilities together in a way that conflicts with the tripartite distinctions within CNC. Rather Mills and Beatty's $fitness_1$ and $fitness_2$ are in my terminology the *displays* (or manifestations) of underlying propensities. But are they displaying the underlying propensities of organisms, sets of organisms, or traits?

The question is whether traits are just averages over the properties of the individuals that make up the set of those organisms that share the trait. If so, since a set is extensionally merely the collection of the elements that compose it, only individual organisms may be said to display propensities – the ‘propensities’ of traits would be merely epiphenomenal.²⁷ Mills and Beatty's ‘ $fitness_1$ ’ and ‘ $fitness_2$ ’ are then simply

²⁶ Amongst the many other issues that may be cast in a new light, those regarding causation in evolutionary biology naturally stand out. For instance, Walsh (2010) has recently objected that PIF entails Simpson-like paradoxes (reversals of conditional probability in subpopulations) and that fitness – and natural selection to boot – can therefore not be said to be a cause of evolution. From a CNF perspective such Simpson reversals are innocuous, since they only affect the probability distributions that emerge in distinct contexts, and not the underlying propensities and their causal effects.

²⁷ This relies on the above extensional definition of traits as *types* of organisms. Sober himself makes it clear that the mathematical models of trait fitness variation introduce selection coefficients in modeling the *strength of selection* that are not themselves functions of expectations; only the responses to selection are expected values (Sober, 2013, p. 340). So Sober does not really think of ‘traits’ extensionally, as merely the set of the organisms that share them, but rather claims that different traits may well be co-extensive.

the expectation values of the distributions for token organisms, and for sets of token organisms, respectively, and they all answer to the underlying propensities of individual organisms. The CNF would go along with this and ascribe all relevant propensities to the individual organisms. If, on the other hand, traits are alternatively defined non-extensionally to be primitive token properties, the CNF would apply the tripartite distinction directly on traits, invoking separate (emergent) propensities, their manifestations in single chances *for* those traits, and the observed frequencies *of* such traits, without attempting any further reduction.²⁸ And since we are no longer defining fitness in terms of expected value, or expectation – but rather as a complex nexus of propensities, probabilities, and frequencies, as modelled relative to a population and environment –, it no longer follows that the fitness of the trait is the average of the fitness of the member organisms.

The same argument goes through *mutatis mutandis* for genes. We can again consider fitness₁ (G) to be a property of some token allele G, and fitness₂ ({G}) to be a property of the population of organisms {G} that carry a given genotype. Since CNF no longer defines fitness₁ to be simply the expectation of the offspring distribution for G, it follows that fitness₂ is neither the arithmetic average of the expectations. Rather the fitness of an individual allele, or a genotype, when it can be defined at all, is a complex three-layered notion that includes the propensities of the token allele or genotype, the probabilities (single case chances) generated by them in their given context, and the frequency data it gives rise to when experimentally probed.²⁹

To sum up, CNF is neutral on the issue of whether fitness applies to individual organisms or traits, whether at type or token level. It can be freely applied to token organisms, and to traits regarded as types with emergent properties of their own. On the other hand, if traits are treated extensionally, as mere statistical collections, then naturally CNF ascribes propensities to the token organisms, or individual alleles, only. But that latter option seems uncalled for, since traits are better thought of non-extensionally anyway.

6.2 Properties of Populations and Reproductive Success

Ariew and Ernst (2009) argue that the Gillespie examples discussed in section three, which show sensitive dependence on higher moments of the offspring distribution, already by themselves demonstrate that evolutionary fitness cannot be understood as a

²⁸ This assumes that Beatty and Mill's definition of trait fitness as the average of the organisms' fitnesses, follows through regardless of whether traits are defined extensionally or not. Indeed, Sober (2013, p. 336) derives their definition from independent premises, namely i) the identity of an organism's fitness with the fitness of its total trait complex, and ii) that at least some of the single case chances be identical to measurable frequencies, as befits the fact that they are testable. (I thank a referee for pressing me to state this explicitly).

²⁹ Except perhaps for fitness regarded as a *property of an arbitrary population*, which by necessity must be defined as some statistical function over the arbitrary set of elements in the population. However, the concept of fitness as applied to an arbitrary population – unlike populations naturally defined by traits – is of no use in understanding evolution by natural selection.

propensity.³⁰ On their account PIF requires fitness to be “a function of the properties of individual members of the population within their local environmental conditions” (what they refer to as desiderata (C) on any viable PIF).³¹ It follows, on their account, that Darwinian natural selection (of the fittest) is not an explanatory cause, but merely a statistical phenomenon. Their reasoning is straightforward: Since variance is a population level property, which critically depends on population size, it cannot be understood to lie in any individual organism. Gillespie (1977) showed fitness w_i to rely on population size n according to what we may call *Gillespie’s equation*: $w_i = \mu_i - \sigma_i^2/n$, where μ_i is the fitness in reproductive output, and σ_i is the variance within a generation. This entails that we can increase population size – and therefore variance – by adding members even if they “do not causally interact with the existing members of the population at all” (Ariew & Ernst, 2009, p. 294). Yet variance can have a decisive role in determining reproductive success, so it follows that the explanation of natural selection involves non-causal, merely statistical features of populations at large.

The argument does not apply to CNF, which is not committed to (C). It is firstly, as just noted, not committed to only taking token organisms as the recipients or units of propensity ascriptions. But, in addition, even when applied to individual organisms as the appropriate units, CNF is not committed to identifying fitness with any one physical property of those organisms, at the expense of the probability distributions, and the frequencies observed. Rather CNF takes fitness to be the complex combination of all of them, and their interconnections.

Nevertheless, Ariew and Ernst make the additional point that even if (C) is abandoned as a desideratum, there are two other essential desiderata on PIF that cannot be jointly satisfied in any case, namely (A): “a fitness concept must be able to explain why one trait is expected to be better represented in a population under the influence of natural selection”; and (B): “a fitness concept must enable us to compare the degree to which natural selection will favour the spread of one trait over another, alternative trait” (Ariew & Ernst, 2009, p. 290). Yet, their reasons for thinking that (A) and (B) are not co-satisfiable is the fact that for any given evolutionary explanation of reproductive success, there is more than one statistic, even more than one distribution, that is appropriate in different cases, depending on the environment, the population, and the trait or type of organism considered.³² Since there

³⁰ See also Matthen and Ariew (2002, 2009) for related arguments, and Millstein (2006) for a perceptive response that emphasises natural selection at the population level. The CNF largely agrees with Millstein here, except for her claim that population-level propensities are causal, since, as explained earlier, on the tripartite conception within the CNC, generally, propensities do not *cause* but rather *ground* single case chances.

³¹ Ariew & Ernst (2009, p. 291). Okasha (2006) provides a good overview of population genetics.

³² As they write: “no single unified account of fitness that satisfies conditions A and B can be found” (Ariew & Ernst, 2009, p. 298). This is echoed in another well-known paper by Ariew and Lewontin (2004, p. 348): “any attempt to introduce a unitary analogous concept of ‘reproductive fitness’ into dynamical models as a scalar ordinal, which will explain or predict quantitative changes in the frequency of types, must fail”. If by ‘unitary’ it is meant an account that identifies fitness precisely with one and only one property of the organisms involved in each case, I agree. However, such an account of fitness would be anathema to the plural character of CNF explored here. It does not follow though that there are no propensities involved in fitness, or that they do not have an explanatory role.

can be no unique comparison, there is no univocal explanation. Ariew and Ernst are therefore reading (B) in a particular robust way, as implying that any comparative measure must be unique, at any rate for any given set of environmental conditions.

By contrast, CNF embraces pluralism for the statistical distributions that manifest underlying propensities – the tripartite conception is in fact of a piece with the thought that differences in the environmental conditions, and within populations, bring out different probabilistic manifestations of the underlying propensities. An arbitrary change in the membership of the population would not affect the underlying propensities of the organisms already included in the population, but it would alter their probabilistic manifestation in the group as well as obviously their relative frequencies in the set. Ariew and Ernst's critique relies on conflating such distinctions. If, by contrast, desideratum (B) is understood to already imply pluralism then the CNF naturally fulfils it, since it enables many different comparisons of the degrees to which natural selection favours one trait over another, depending sensitively on trait, population, environment, and underlying propensity ascriptions to either organisms, genotypes, or traits (or any of their sets). Ariew and Ernst's difficulties with the explanatory character of fitness are thus seen to be a consequence of their underlying identification of fitness with the probability distributions that make up only a part of a necessarily more complex concept.

7 Conclusions

In this paper I have defended a new approach to evolutionary fitness in terms of what I call the complex nexus of chance (CNC). The resulting complex nexus of fitness (CNF) clarifies some of the commitments of a propensity account of fitness. It does not attempt to reduce fitness to the concept of propensity, nor does it think of propensity as a mere interpretation of probability. Nevertheless, propensities play a critical explanatory role in the account, and the tripartite distinction at the heart of the CNF is in close agreement with modelling practice. I first showed that the CNF overcomes the 'momentous objection' regarding the influence of higher moments of the offspring distribution. I then argued that it renders superfluous the debate over whether fitness is properly long or short term. I finally argued that the explanatory power of fitness as a complex chancy nexus is revealed by a careful application to a range of issues and contemporary debates within the philosophy of biology; and I provided two such instances in the debates surrounding the objects of selection and the effects of population size on fitness.

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References

- Abrams, M. (2009). The unity of fitness. *Philosophy of Science*, *76*, 750–761.
- Abrams, M. (2012). Measured, Modelled, and Causal Conceptions of Fitness. *Frontiers in Genetics*, *3*(196), 1–12.
- Abrams, M. (2014). Environmental grain, organism fitness, and type fitness. In G. Barker, E. Desjardins, & T. Pearce (Eds.), *Entangled life: Organism and environment in the biological and social sciences* (pp. 127–151). Springer.
- Abrams, M. (2015). Probability and manipulation: Evolution and simulation in applied population genetics. *Erkenntnis*, *80*, 519–549.
- Abrams, M. (forthcoming). *Evolution and the machinery of chance*. University of Chicago Press.
- Ariew, A., & Lewontin, R. C. (2004). The confusion of fitness. *British Journal for the Philosophy of Science*, *55*, 347–363.
- Ariew, A., & Ernst, Z. (2009). What fitness can't be. *Erkenntnis*, *71*(3), 289–301.
- Beatty, J., & Finsen, S. (1989). Rethinking the propensity interpretation: A peek inside Pandora's box. In M. Ruse (Ed.), *What the philosophy of biology is* (pp. 17–30). Kluwer Academic Publishers.
- Brandon, R. N. (1978). Adaptation and evolutionary theory. *Studies in History and Philosophy of Science*, *9*, 181–206.
- Brandon, R. N. (1990). *Adaptation and environment*. Princeton University Press.
- Brandon, R. N., & Beatty, J. (1984). The Propensity interpretation of 'fitness' – no interpretation is no substitute. *Philosophy of Science*, *51*(2), 342–347.
- Crow, J., & Kimura, M. (1956). Some genetic problems in natural populations. *Proceedings of the Third Berkeley Symposium on Mathematical Statistics and Probability*, *4*, 1–22.
- Drouet, I., & Merlin, F. (2015). The propensity interpretation of fitness and the propensity interpretation of Probability. *Erkenntnis*, *80*, 457–468.
- Eagle, A. (2004). Twenty-one arguments against propensity analyses of probability. *Erkenntnis*, *60*, 371–416.
- Fisher, R. A. (1934). Indeterminism and natural selection. *Philosophy of Science*, *1*(1), 99–117.

- Gillespie, J. H. (1974). Natural selection for within-generation variance in offspring number. *Genetics*, 76, 601–606.
- Gillespie, J. H. (1977). Natural selection for variances in offspring numbers: A new evolutionary principle. *American Naturalist*, 111, 1010–1014.
- Gillies, D. (2000). *Philosophical theories of probability*. Routledge.
- Godfrey-Smith, P. (2009). *Darwinian populations and natural selection*. Oxford University Press.
- Grimmett, G., & Stirzaker, D. (1982). *Probability and random processes*. Oxford University Press.
- Hacking, I. (1965). *The logic of statistical inference*. Cambridge University Press.
- Hájek, A. (1997). 'Mises-Redux' - redux: Fifteen arguments against finite frequentism. *Erkenntnis*, 49, 209–227.
- Hájek, A. (2003). What conditional probability could not be. *Synthese*, 137(3), 273–323.
- Hájek, A. (2009). Fifteen arguments against hypothetical frequentism. *Erkenntnis*, 70(2), 211–235.
- Hájek, A., & Hitchcock, C. (Eds.). (2016). *The Oxford handbook of probability and philosophy*. Oxford University Press.
- Humphreys, P. (1985). Why propensities cannot be probabilities. *The Philosophical Review*, 94(4), 557–570.
- Krzanowski, W. J. (1998). *An introduction to statistical modelling*. Wiley and Sons.
- Matthen, M., & Ariew, A. (2002). Two ways of thinking about fitness and natural selection. *The Journal of Philosophy*, XCIX(2), 55–83.
- Matthen, M., & Ariew, A. (2009). Selection and causation. *Philosophy of Science*, 76, 201–224.
- Mellor, H. (2005). *Probability: A philosophical introduction*. Routledge.
- Mills, S., & Beatty, J. (1979). The propensity interpretation of fitness. *Philosophy of Science*, 46(2), 263–286.
- Millstein, R. (2003). Interpretations of probability in evolutionary theory. *Philosophy of Science*, 70(5), 1317–1328.
- Millstein, R. (2006). Natural selection as a population-level causal process. *British Journal for the Philosophy of Science*, 57, 627–653.
- Millstein, R. (2016). Probability in biology: The case of fitness. In A. Hájek & C. Hitchcock (Eds.), *The Oxford handbook of probability and philosophy* (pp. 601–622). Oxford University Press.
- Mumford, S., & Anjum, R. (2011). *Causes out of powers*. Oxford University Press.
- Okasha, S. (2006). Population genetics. *Stanford Encyclopedia of Philosophy*.
- Pence, C., & Ramsey, G. (2013). A new foundation for the propensity interpretation of fitness. *British Journal for the Philosophy of Science*, 64, 851–881.
- Popper, K. (1959). The propensity interpretation of probability. *British Journal for the Philosophy of Science*, 10(37), 25–42.
- Reichenbach, H. (1934/1949). *The theory of probability: An inquiry into the logical and mathematical foundations of the calculus of probability*. University of California Press.
- Rice, S. (2004). *Evolutionary theory: Mathematical and conceptual foundations*. Sinauer Associates Publishers.
- Rice, S. (2008). A stochastic version of the price equation reveals the interplay of deterministic and stochastic processes in evolution. *BMC Evolutionary Biology*, 8, 262ff.
- Rosenberg, A. (1982). On the propensity definition of fitness. *Philosophy of Science*, 45, 263–286.
- Sober, E. (1984). *The nature of selection*. University of Chicago Press.
- Sober, E. (2001). The two faces of fitness. In R. Singh, D. Paul, C. Krimbas, & J. Beatty (Eds.), *Thinking about evolution: historical, philosophical, and political perspectives* (pp. 309–321). Cambridge University Press.
- Sober, E. (2010). Evolutionary theory and the reality of macro-probabilities. In E. Eells & J. H. Fetzer (Eds.), *The place of probability in science* (vol. 84, pp. 133–161). Boston Studies in the Philosophy of Science.
- Sober, E. (2011). A priori causal models of natural selection. *Australasian Journal of Philosophy*, 89(4), 571–589.
- Sober, E. (2013). Trait fitness is not a propensity, but fitness variation is. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 44, 336–341.
- Sober, E. (2020). Fitness and the twins. *Philosophy, Theory, and Practice in Biology*, 12(1), 1–13.
- Suárez, M. (2011). Four theses on probabilities, causes, propensities. In M. Suárez (Ed.), *Probabilities, causes and propensities in physics*, Synthese Library (pp. 1–41) Springer.
- Suárez, M. (2013). Propensities and pragmatism. *The Journal of Philosophy*, 110(2), 61–92.

- Suárez, M. (2014). A critique of empiricist propensity theories. *European Journal for the Philosophy of Science*, 4(2), 215–231.
- Suárez, M. (2017). Propensities, probabilities and experimental statistics. In M. Massimi et al., (Eds.), *EPSA15 selected papers: European studies in the philosophy of science* (vol. 6, pp. 335–345). Springer.
- Suárez, M. (2018). The chances of propensities. *British Journal for the Philosophy of Science*, 69, 1155–1177 First published online August 2017.
- Suárez, M. (2020). *Philosophy of probability and statistical modelling*. Cambridge University Press.
- Triviño, V., & de la Rosa, L. (2016). A causal dispositional account of fitness. *History and Philosophy of Life Sciences*, 38(6), 1–18.
- Von Mises, R. (1928/1953) *Probability, statistics and truth*. Dover Publications.
- Walsh, D., Ariew, A., & Matthen, D. (2016). Four pillars of statisticalism. *Philosophy Theory and Practice in Biology*, 9(1), 1–18.
- Walsh, D. (2010). Not a sure thing: Fitness, probability and causation. *Philosophy of Science*, 77(2), 147–171.

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