Natural Selection With Objective Imprecise Probability

Marshall Abrams　　　　　　　　　　　　　　　　　　　　　　　　　　　　　MABRAMS@UAB.EDU
Philosophy, University of Alabama at Birmingham

Abstract

I argue that natural selection sometimes depends on objective imprecise probabilities. I give a general argument for the existence of objective imprecise probabilities. I then argue that natural selection, whether involving objective imprecise probabilities or not, would give rise to organisms whose behavior was imprecisely probabilistic, and that this would mean that other organisms' environments were imprecisely probabilistic. Since natural selection can be influenced by the environment, it therefore sometimes depends on objective imprecise probability. I explain why the absence of reports of objective imprecise probability in evolution is nevertheless unsurprising, and provide illustrations of ways to model natural selection with objective imprecise probabilities.

Keywords: objective imprecise probability, biological fitness, natural selection, set-chain, hi-lo method

1. Introduction

Natural selection occurs when there are differences in biological fitness. A common view, which I adopt as my starting point, is that biological fitness depends on objective probabilities for outcomes such as organisms having particular numbers of offspring. Such probabilities depend not only on organisms' traits, but also on the character of the environments in which they live. For example, consider rabbits living in a dense forest in a warm climate, with predators that hunt rabbits by sight. In this environment rabbits with brown fur rather than white fur may have greater fitness in the sense of having a higher probability of survival and reproduction. This relationship between fur colors might be reversed in an environment with a great deal of snow and ice.

I argue that some biological outcomes have objective imprecise probabilities—imprecise analogues of real-valued objective probabilities—in such a way that fitness, and hence natural selection, can be expected to depend on objective imprecise probabilities. I first give a general argument for the existence of objective imprecise probabilities. I then argue that natural selection, whether involving objective imprecise probabilities or not, would give rise to organisms whose behavior was imprecisely probabilistic. This behavior would then be part of the environment of other organisms in ways that would make their fitnesses imprecisely probabilistic. As a result, natural selection should some-

times depend on objective imprecise probability. I explain why the absence of reports of objective imprecise probability in evolution is unsurprising, and outline approaches to modeling imprecisely probabilistic evolution.

2. Objective Imprecise Probability

Several authors have argued for the existence of objective imprecise probabilities of particular kinds (e.g. [14, 19, 23, 22, 29, 32, 33, 35, 45, 61, 63, 70]). Here I present a general argument for the existence of objective imprecise probabilities.

2.1. Erraticity

An objective probability is a probability of an outcome in a space of alternatives, where an outcome is a set of physical occurrences (token events), or the realization of a type by an occurrence, or the fact that a proposition would be true. Objective probabilities that are of the most interest in science are often those that Abrams [2015] calls *causal probabilities*. These are probabilities realized by physical factors that can be used to manipulate frequencies in experiments or natural conditions. For example, one can often manipulate dice outcome frequencies by changing the distribution of weight within the dice that are tossed. My discussion of (precise) objective probabilities below is restricted to this variety.[1] That there is a precise objective probability r that an outcome A will occur does not guarantee that the relative frequency of A will remain close to r in a large number of trials, but that is (at least) what usually happens.[2] Objective *imprecise* probabilities will allow manipulation of frequencies in a looser sense. That there is an objective imprecise probability of A, for example with its value the interval $[r_1, r_2]$, does not guarantee that the relative frequencies of A will remain in or near the interval $[r_1, r_2]$, but that should be what usually happens.

Now consider mutually exclusive occurrences or token events e_1 and e_2. If these two occurrences have objective

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1. I assume that outcomes realized only by effects of deterministic processes can have objective probabilities other than 0 and 1, perhaps as long-run propensities [27, 12], or perhaps as what have been called "natural range", "Spielraum", microconstant, or mechanistic probabilities [3, 4, 11, 53, 54, 55, 56, 62].

2. Talk of "what usually" happens is incredibly vague, but reflects scientists' intuitions about finite numbers of outcomes in systems they model, and is difficult to eliminate without circularity.

probabilities, they do so "under some description": It is as realizations of properties that e_1 and e_2 have objective probabilities. However, even if every occurrence has an objective probability as a realizer of *some* property, that doesn't imply that every algebra over a set of possible, mutually exclusive occurrences defines a space of outcomes with a common objective probability distribution. For example, suppose I define a space of outcomes by partitioning into three sets (A, B, C) the possible percentages of ink (by mass) in pieces of paper. Consider the "chance setup" [31] that consists of *averaging the densities of ink in pieces of paper in the pockets of the next 10 people that any reader of this article happens to meet after finishing it, and determining whether that average falls into A, B, or C*. Must C, for example, have an objective probability? I suspect not. Of course, the outcome C will either occur or not, because the particular circumstances in which the current reader (let's say) finds herself or himself after reading this paper is one in which processes in the world lead to meeting particular people with particular things in their pockets. It may be that these processes are merely deterministic, or not. However the setup described by the italicized text need not describe a process with outcomes that have a particular objective probability distribution common to every case in which the setup is realized.

I'll therefore assume that for some setups, outcomes have no objective probabilities. We can refer these outcomes as occurring *erratically* [33], or with *erraticity*. I emphasize that the fact that a set of outcomes occur erratically does not mean that the token events that realize these outcomes happen for no reason. Such occurrences are caused, either deterministically, or indeterministically in the way that quantum mechanical events are thought to occur. Moreover, erratically occurring outcomes have relative frequencies in practice. However, there is no predictability to their frequencies from the fact that they are outcomes of the setup in question. Particular occurrences that realize the outcomes may be predictable, and frequencies for outcomes of *particular* set of realizations of the setup may be predictable from *other* circumstances than those that define the setup. However, another set of occurrences that realize outcomes in the same space from the same setup type might routinely have radically different frequencies.

2.2. Objective Imprecise Probability

Suppose we have two alternative chance setups for the same outcomes, but each setup gives these outcomes different (precise) objective probabilities. We can embed these chance setups in what I'll call a complex setup, in which one of the preceding setups is chosen by an outcome of a third setup. For example, suppose that one of two pairs of loaded dice is chosen by the result of a fair coin toss, and then the chosen pair is tossed. Let one pair of dice, d_{30}, give "ones" (i.e. two ones) an objective probability of 1/30,

while the other pair, d_{40}, gives it an objective probability of 1/40. In this case the objective probability of ones as an outcome of the complex setup would clearly have a precise value: $(1/2 \times 1/30) + (1/2 \times 1/40) \simeq 0.029$.

Suppose instead that we choose the dice to toss using something like the ink setup above, in which the outcome is determined erratically. Then what is the objective probability of ones on the new complex setup? It is neither 1/30, nor 1/40, nor a weighted average of the two: There is no probability with which to weight the alternative dice pairs d_{30}, d_{40}. Note that in sequences of repeated trials of this complex chance setup, the frequency of ones among large numbers of tosses of the d_{30} pair would usually be near 1/30, and the corresponding frequency among tosses of d_{40} would usually be near 1/40. However, there would be no particular overall frequency of ones that would usually occur, since no particular frequencies for d_{30} and d_{40} should often occur. It seems most reasonable to hold that ones would have no (precise) objective probability as an outcome of the new complex setup. Nevertheless, it doesn't seem appropriate to say that the ones outcome occurs erratically in the way that the choice of dice pairs was. For example, in long sequences of trials of the complex setup, frequencies of ones would usually be found in or near the interval [1/40, 1/30]. It seems that ones occurs as a sort of erratic mixture of the precise probabilities determined by the two biased pairs of dice. We should say that the occurrence of ones has an an objective imprecise probability.[3] I don't assume that objective imprecise probability can only arise as an erratic mixture of precise objective probabilities, but such mixtures provide a simple illustration.

3. Objective Imprecise Probability in Evolution Is Possible

In this section of the paper, I argue that natural selection can depend on imprecise probabilities.

3.1. Fitness and Environmental Variation

Natural selection is always relative to an environment: Were a population of organisms placed in a different environment (a cold rather than warm one, for example), the naturally selected traits might differ. Biologists sometimes extend this idea to smaller "environments" (habitats, patches, subenvironments) within an overall environment. These variant environments may be arranged spatially within the overall environment, or they may occur at different times, or both. Consider a toy example like ones in [1] or [71]: In a population of animals of small mammals, one genetically influenced trait, *deep*, leads its bearers to dig deep burrows,

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3. Combining erraticity with precise probabilities in this sort of way is related to some other schemes for generating objective imprecise probabilities in which the role played by erraticity above is restricted to narrower ranges of cases [20, 70, 19, 23, 61].

while the other, *shallow*, leads its bearers to dig shallow burrows. The *deep* trait makes drowning more likely during periods of torrential rain, but it is better than *shallow* during hot, dry periods, because cool burrows are advantageous. Suppose *deep* animals have an average of 1 offspring during *wet* (rainy) periods and 2 offspring during *dry* periods, while *shallow* animals have an average of 2 offspring during *wet* periods and 1 offspring when during *dry*. (Take these averages to be sum of numbers of offspring, weighted by their objective probabilities conditional on the *wet* or *dry* environment.[4]) Which trait will natural selection most likely favor? If the *wet* and *dry* environments have equal objective probabilities, and so are likely to occur roughly with equal frequency over a long period of time, it's likely that animals with either *deep* or *shallow* will have 1 offspring on average roughly half of the time, and 2 offspring on average the rest of the time. In that case natural selection doesn't favor one trait over the other. However, if the *wet* environment has a greater objective probability, then *shallow* will be more likely to increase in frequency, because *shallow* animals have two offspring on average in *wet* environments, while *deep* animals have only one offspring on average. Similarly, if *dry* has a greater objective probability, then *deep* is more likely to increase in frequency. Thus the overall probability of evolutionary success depends on the overall environment—defined, in part, by the objective probabilities of the *wet* and *dry* environments.

3.2. Environmental Erraticity

It's often assumed that that there are determinate probabilities of environmental fluctuations, or of organisms finding themselves in different environments (e.g. [42, 17, 26, 48, 1]). but this assumption doesn't seem required. Perhaps there are cases in which some environmental changes obey no probabilities: Though in any particular period of time, organisms would encounter some environments more often than others, there would be no reason for this pattern to be likely to continue over many generations. Given the complexity and variety of environmental variation in nature, it doesn't seem implausible that such cases might exist. This would make the determination of environments analogous to the erratically-chosen dice setup. Such erratically determined environmental conditions could make traits' fitnesses, and natural selection, depend on objective imprecise probabilities.

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4. Defining fitness as an expectation of numbers of offspring has a long history in philosophy of biology beginning with [43, 16]; similar ideas can be found in some biological publications (e.g. [60]). However, what's important in this part of the paper is just that fitnesses and hence natural selection be treated as functions of objective probabilities of outcomes for organisms.

4. Objective Imprecise Probability in Evolution Is Actual

The preceding section suggested that objective imprecise probability could play a role in evolution by natural selection. I'll argue next that a role for objective imprecise probability in evolution is no mere a possibility; it's likely that objective imprecise probability often plays a role in evolution by natural selection.

4.1. Behavioral Imprecision

If mechanisms that influence behaviors of an organism have effects whose objective probabilities are imprecise, the imprecision could affect the determination of behaviors.

Here is a well-known example. In humans, behavior may be determined in large part by interactions between beliefs and desires, which I will suppose are realized as brain states that have degree properties, epistemic probabilities and utilities, that affect behavior. It would be possible, then, that people acted in ways that more or less approximate some proposed decision theory (e.g. [50, 38]). However, it's widely thought that human behaviors routinely fail to satisfy the traditional decision theoretic requirements (e.g. [28, 51]). It seems more plausible to say that we instead act as if our epistemic probabilities or utilities are imprecise. That is, it may well be that our behaviors fluctuate in ways that are best explained by internal cognitive mechanisms that reflect imprecise epistemic probabilities or imprecise utilities. These imprecise epistemic probabilities and utilities need not be realized in a way that makes them into objective imprecise probabilities (although I think that is one possibility). Nevertheless, the result would be fluctuations in behavior under similar conditions that was as if it were the result of objective imprecise probabilities and imprecise utilities. Behavior would then be imprecisely probabilistic, whether or not its causes were.

A similar point applies to organisms' behaviors more generally. First note that organisms' behaviors would sometimes come to be tuned to precise objective probabilities of various environmental conditions. For example, small birds such as house sparrows have to make a choice about whether and when to eat from a food source (e.g. a clump of plants) that is not sheltered from the sky. Incautiously eating from such sources might be selected against if eating in the open increased the risk of predation. On the other hand, completely forgoing food from sources open to the sky could be selected against if the result was inadequate nutrition. In practice, birds often interrupt eating to scan the sky to see if raptors (e.g. merlins) are present, and some birds may wait for other small birds to arrive so that these sky-scanning responsibilities can be shared [18, 7].

The optimal behavioral tendencies for such potential prey birds then depend on probabilities of raptors seeing a prey bird given where food is located, the probability

that a raptor will be noticed by the prey birds, the overall influence on fitness (or utility) of various food sources, etc. Natural selection should then favor mechanisms that alter behavior in ways that are sensitive to objective probabilities of conditions in an organism's environment. However, that doesn't mean that the mechanisms that produce such behavioral variation will do so perfectly. Human behaviors aren't precisely tuned to what's adaptive; it's implausible that other organisms' behaviors are, either, as I'll explain.

4.2. Behavioral Precision Is Expensive

Organisms' environments are complex, cellular processes are complex, physiological processes are complex, and nervous systems are complex. Moreover, there are tradeoffs involved in the energy required for construction and maintenance of nervous systems. More elaborate nervous systems that might be capable of more accurate assessment and rapid decision making may require more energy, special nutrients, etc. Genetic variation in populations also constrains how they can evolve, and even where some adaptive genetic variants exist in a population, adaptation through natural selection can take many generations. All of these factors make it unlikely that natural selection will always produce organisms whose behavioral choices are precisely and optimally tuned to probabilities in their environments. Natural selection will favor organisms with behavioral strategies that are better tuned to environmental probabilities and costs and benefits than other strategies that had been present in the same population, but it will also favor organisms that can make choices that are good enough, quick enough, and that don't require inordinate time or resources compared to alternative behavioral strategies. present in the population. To use Herbert Simon's term, natural selection "satisfices" [59].

One way that an organism's behaviors might be poorly tuned to the environment could involve producing behaviors that *would* be appropriately tuned if the environment were different. Such a behavior might be (precisely) probabilistic. That is, it could be that for some environmental contexts s_i, an organism exhibited a range of behaviors $\{b_1, \ldots, b_i, \ldots b_r\}$ with probability $P(b_i|s_j)$, even though behaving according to some other, similar pattern would have greater fitness. However, maintaining behavior in this way—producing exactly the same pattern of behavior in identical situations—could itself be expensive, requiring insensitivity to irrelevant environmental variation, physiological variation, tiredness, illness, or intrinsic variation in a nervous system. Thus it seems likely that a common kind of failure of precise behavioral calibration to the environment would involve variation in patterns of behaviors, even in the same external circumstances. There would be no need, in any event, for selection to favor maintenance of a precise objective probability distribution over behaviors if all of the behaviors b_i that might be chosen given condition s_j

are more or less good enough—in the sense that they produce fitness that is greater than that of any competitors in the same population. Thus it seems likely that often organisms' behaviors would exhibit patterns that, even if close to optimal patterns, would exhibit erratic or imprecisely probabilistic variation, even in identical situations, because of complex cost-benefit tradeoffs.

4.3. Imprecise Behavior as an Environmental Factor

However, in general, the behaviors of members of a population of one species will be part of the environment of members of other species in ways that are relevant to survival and reproduction of those other species. For example, consider choices made by house sparrows in the presence of their food sources, as described above. The patterns of their choices might affect the survival and reproduction of raptors such as merlins that eat them. If this sort of behavior by the house sparrows were *precisely* probabilistic, then to the extent that the survival of raptors depended on that behavior, there would be selection for merlin behaviors that reflected the precise probabilities that characterize house sparrow behavior. On the other hand, if the house sparrow behaviors were imprecisely probabilistic, that would introduce objective imprecise probability into merlins' environment in ways that could be relevant to their survival, and thus to natural selection.[5] Here objective imprecise probabilities in prey behaviors plays a role analogous to objective imprecise probabilities due to wet and dry environmental conditions in section 3.2.

To summarize the argument: It's likely that in response to evolutionary tradeoffs, natural selection will often make some organism behaviors imprecisely probabilistic, and this will often have an impact on other organisms' evolution. Thus it's likely that environments often involve objective imprecise probabilities in ways that make evolution depend on them. Whether we begin by assuming that environmental factors are precisely or imprecisely probabilistic, we end up seeing that they are often likely to be imprecisely probabilistic.[6]

4.4. Where's the Empirical Evidence?

If, as I claim, natural selection is affected by imprecise objective probabilities, why don't evolutionary biologists

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5. It's likely that there is sometimes selection for robustness to environmental variation (cf. [68]; [73]; [24]). This could mean that some behavioral imprecision in, say house sparrows, might have no effect on natural selection for merlins. Nevertheless, robustness to *all* environmental variation would be very costly, so it seems likely that there are cases in which behavioral imprecision in one species affects selection on another.

6. What would imprecisely probabilistic environmental variation look like? This is topic for a future work. It requires more discussion than is appropriate here, in part because of the difficulty of answering the corresponding question for precisely probabilistic variation in nature in some systematic way.

notice this? The answer, in part, is that imprecise probability concepts are not part of most biologists' or statisticians' thinking.[7] It's unclear how one would notice evidence of imprecise objective probabilities without first having relevant concepts to guide research. Further, statistical methods and modeling strategies for imprecise probability are relatively immature compared to those based on precise probability [9].

But if objective imprecise probabilities were common in evolutionary processes, wouldn't that interfere with the application of traditional statistical methods? Not necessarily. All that's needed for traditional statistical methods to be successful is that whatever imprecision there is to objective probabilities involve narrow ranges of environmental fluctuations that can easily be modeled using precise probabilities. The fact that precise probability-based methods are successful, where that success depends on a match between modeled probabilities and the world, at best supports the claim that the relevant aspects of the world are either precisely probabilistic or imprecisely probabilistic with narrow imprecision. The latter is in fact a weaker assumption. There might also be cases in which precise probabilities are insufficient for modeling objective imprecise probabilities that affect evolution. Such cases would not be reflected in the biological literature ether because researchers would search to understand the evolutionary processes in terms of *additional* causal factors (cf. §2.1), or they would simply choose another subject to study in the same same research area. (Scientists abandoning projects doesn't cause cause the projects to depend on objective imprecise probabilities; rather, the dependence on objective imprecise probabilities causes scientists to abandon their projects.) The result of this pattern of research would be a lack of evidence for objective imprecise probability in the research literature, even if it exists.

5. Modeling Evolution with Imprecise Probability

One might want further details. What is fitness in an objective imprecise probability context? How should we model evolution? I can offer some preliminary illustrations at this point. It's not clear whether the concepts and methods described below will lead to practical applications, and my remarks above suggest, for many practical cases, modeling with precise probabilities will be appropriate even when what is modeled is somewhat imprecise. The concepts and methods below at least serve to refine and clarify implications of my arguments above. Refinements and elaborations must wait for future work.

5.1. Imprecise Fitness Comparisons

What is biological fitness given objective imprecise probability? I'll modify a very simple model of fitness as expected number of offspring with erratically determined environmental variation, without considering long-term changes in a population.

When there are no probabilities that organisms will encounter particular environments, can we ever say that one trait is fitter than another? Yes. For example, if the expected numbers of offspring for *deep* in both *wet* and *dry* is greater than that of *shallow* in either environment, then whatever the frequency with which *wet* and *dry* alternate, *deep* will have a higher average number of offspring. Suppose, for example, that the expected numbers of offspring for *deep* are 1.5 and 1.7 in *wet* and *dry* environments, respectively, and the corresponding numbers for *shallow* are 1.2 and 0.9. No matter what environmental state occurs, *deep* should usually have a greater number of offspring on average than *shallow*.

Such cases can be represented by treating fitness of a trait A as a pair of numbers representing the minimum $\underline{w}(A)$ and maximum $\overline{w}(A)$ precise fitnesses, understood as expectations over per-trait number of offspring in each environment that organisms erratically encounter. (The symbol w is a traditional, widely used notation for fitness, as in e.g. [21].) Here the *lower fitness $\underline{w}$* and *upper fitness $\overline{w}$* functions are lower prevision and upper prevision operators, respectively [69, 65, 8].[8] If organisms in the population always found themselves in just one of the two environments, then the expected number of offspring for trait A would be either $\underline{w}(A)$ or $\overline{w}(A)$ Otherwise, the result would be a weighted average of these values, but this average would depend on what environments were actually encountered (erratically) by organisms in the population. I'll refer to such a pair of minimum and maximum fitnesses—the values of particular lower prevision and upper prevision operators applied to a trait—as a "fitness interval", represented by the notation $[\underline{w}(A), \overline{w}(A)]$. In the *wet/dry* example, it's reasonable to model the pair of fitness values for a trait as an interval when the population is large, since what happens in the world will involve some combination of the two environmental states. In a large population that is distributed erratically among *wet* and *dry* environments at one time, the different ways in which these can be combined will approximate a convex set between the two extremes.

Interval Dominance   The example above in which the fitness of *deep* is $[1.5, 1.7]$ and that of *shallow* is $[0.9, 1.2]$ illustrates a general claim that can expressed in terms of

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7. Samuels' [58, 57] application to ecological data of methods [34] to model objective imprecise probability is an exception. Other biological research, such as [49, 52, 66], has used imprecise probability concepts as part of inference and modeling without treating anything in the world as if it involved objective imprecise probability.

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8. So defined, the $\underline{w}$ and $\overline{w}$ functions are coherent lower and upper previsions, by the lower envelope theorem [65, Theorem 4.38, p. 71].

the *interval dominance* relation, $\sqsupset$ [64, 37, 13]:[9]

$$A_1 \sqsupset A_2 \quad \text{iff} \quad \underline{w}(A_1) > \overline{w}(A_2). \qquad (1)$$

That is, $A_1 \sqsupset A_2$ iff A_1's *lower fitness* $\underline{w}(A_1)$ is greater than A_2's *upper fitness* $\overline{w}(A_2)$. In the sense of interval dominance,

A_1 is fitter$_{id}$ than A_2 if $A_1 \sqsupset A_2$.
A_1 is fittest$_{id}$ if $A_1 \sqsupset A_j$ for all competing traits A_j.

(Here *id* stands for "interval dominance".) The fitness$_{id}$ relation provides only a partial ordering of traits, since it may be that neither A_1 or A_2 is fitter$_{id}$ than the other.

Dominance Across Population-Wide Environments
There is at least one kind of case in which a trait can be considered fitter than another though they have overlapping fitness intervals. Suppose that trait A_1 dominates trait A_2 in the sense that in every environment e, the precise fitness $w_e(A_1)$ of A_1 relative to that environment is greater the corresponding precise fitness $w_e(A_2)$ for A_2 (cf. [13]). It's then probable that the instances of trait A_1 will have a higher average number of offspring than instances of A_2 *if* the environmental variation is such that all members of the population experience the same environment at any given time, as in the case of population-wide temporal variation in environments. Suppose that generations don't overlap, as when organisms lay eggs and then die, and suppose that environments change erratically only between generations. In such cases we can say that A_1 *dominates A_2 across population-wide environments*. Then,

If environments e vary erratically in such a way that any time, the entire population experiences the same environment, then:
A_1 is fitter$_{dp}$ than A_2 if $(\forall e) w_e(A_1) > w_e(A_2)$.
A_1 is fittest$_{dp}$ if $(\forall e) w_e(A_1) > w_e(A_j)$ for all competing traits A_j.[10]

(Here *dp* stands for "*d*ominates across *p*opulation-wide environments".) Note that if we change the strict strict inequality to $\geq$, we can replace "fitter$_{dp}$" and "fittest$_{dp}$" with "is at least as fit$_{dp}$ as" and "is among the fittest$_{dp}$", respectively. (An analogous generalization of interval dominance is not so straightforward.)

For other kinds of environmental variation, that trait A_1 dominates trait A_2 in every environment need not imply that A_1 will probably increase in frequency. For example, suppose that the environment of A_1 and A_2 is composed of two spatially varying environments e_1 and e_2, and that

whether a given organism ends up in one environment or the other is merely erratic. Assume that A_1 has precise fitness $w_{e_1}(A_1) = 1.5$ in environment e_1, and fitness $w_{e_2}(A_1) = 2.5$ in environment e_2, while corresponding fitnesses for A_2 are $w_{e_1}(A_2) = 1$ and $w_{e_1}(A_2) = 2$. Thus A_1 dominates A_2 in every environment. However, since it's erratic which tokens of A_1 or A_2 are to be found in either environment, it may turn out that most of the A_2's end up in e_2 where they have a fitness of 2, while most of the A_1's end up in e_1, where their fitness is 1.5. Given that actual distribution of A_1's and A_2's it would be probable that A_2 would increase in frequency, even though A_1 dominated A_2.

We can summarize the implications of the two kinds of fitness relation described above as: A_1 is fitter than A_2 iff either A_1 is fitter$_{id}$ than A_2, or A_1 is fitter$_{dp}$ than A_2. That is:

A_1 is fitter than A_2 iff either $A_1 \sqsupset A_2$, or all organisms experience the same environment e at the same time and $(\forall e) w_e(A_1) > w_e(A_2)$.

This generalizes traditional meaning of "fitter than" for fitnesses that are expected numbers of offspring. Note that it may be that there is a set $\mathscr{A}$ of traits A_i such that each A_i is fitter than all traits not in in $\mathscr{A}$, but that no trait in $\mathscr{A}$ is fitter than any other in $\mathscr{A}$.

If A_1 is not fitter than A_2 in either of the preceding senses, it would be misleading to say that they are equal in imprecise fitness, since that would suggest that the traits' evolutionary successes would usually be similar, at least in the short run when there are many organisms with those traits. I would prefer to say that when neither A_1 nor A_2 is (imprecisely) fitter than the other, the two traits are *incomparable* (cf. Rinard's [51] "indeterminate").

Choice Functions The literature on decision making with imprecise probabilities often focuses on choice functions that specify sets of gambles (or actions) from which it might be rational to choose one gamble (e.g. [41, 64, 37, 51, 44, 15]). Some of the commonly discussed choice functions, which may be prudent guides for decision makers who want avoid certain kinds of losses, turn out to be irrelevant to understanding biological fitness and natural selection. I'll give a very brief argument for this point, considering three prominent choice functions expressed in terms of expectation operators E_e, E_f for numbers of offspring in environments e, f. Each of these choice functions specifies a set of traits A_i for which no traits have higher precise fitnesses in certain environments. The choice functions differ in how the environments are specified in relation to the alternative traits.[11]

E-Admissibility: $\{A_i : (\exists e)(\forall A_j)\ \mathsf{E}_e(A_i) \geq \mathsf{E}_e(A_j)\}$
This specifies the traits such that there is some partic-

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9. The interval dominance relation is used in [64, 37] to define a somewhat different rule for choosing gambles, also called "interval dominance".

10. Cf. [17, chapter 2] and [5] on "selective environments", Joyce's [2010] choice function 4I, and Rinard's [2015] Moderate choice function.

11. See [37] for this way of formulating these choice functions. One might think of them as ways of specifying traits on whose proliferation it would not be irrational to bet.

ular environment that makes all of them at least as fit as all other traits.[12]

Maximality: $\{A_i : (\forall A_j)(\exists e) \; \mathsf{E}_e(A_i) \geq \mathsf{E}_e(A_j)\}$

This specifies the traits such that for each, there is some environment in which the trait is at least as fit as all other traits.

Interval Dominance:

$\{A_i : (\exists e)(\forall A_j)(\exists f) \; \mathsf{E}_e(A_i) \geq \mathsf{E}_f(A_j)\}$

This specifies the traits such that there is some environment that makes all of them at least as fit as other traits are in some (perhaps different) environment.[13]

None of these ways of specifying the "fittest" traits implies that the chosen traits A_i are likely to be more successful in terms of survival and reproduction than those not chosen. In each case, in order for the A_i's to be more likely to be successful, environments would have to vary in ways that were probabilistic, but we are assuming that environments vary erratically. For example, consider the claim that the E-admissible traits should be treated as fittest. Certainly, if organisms with E-admissible traits A_i, and organisms non-E-admissible traits all experience an environment in which A_i's precise fitness is greater, it's likely that those with A_i will have more offspring, on average, than the others. The problem is that if the environments encountered by organisms are determined erratically, there's no reason that organisms of both kinds would encounter such an environment often—or ever. Thus the E-admissibility of traits provides no information about evolutionary success. A similar point can be made about the Maximal traits and those that are Interval dominant in the immediately preceding sense.

It's not clear to me that much more can be said about fitness inequalities for imprecise fitness, at least for the simple model of fitness as expected number of offspring.

5.2. An Imprecise Probability Wright-Fisher Model

Fitness is usually supposed to provide a way of summarizing the probable future evolution of a population. However, if the fact that A is fitter than B is supposed to imply that it's probable that over a large number of generations, the relative frequency of A in the population will increase at the expense of B's relative frequency, then definitions of fitness other than expected number of offspring can be more accurate (e.g. [42, 25, 47, 30]). For example, in some contexts, a trait with a higher arithmetic mean number of offspring will have more descendants. Some authors (e.g. [10, 17, 46]) have sought a single general measure of fitness; I argue elsewhere that no one measure of fitness is suitable for all

evolutionary studies [2]. On this view, any attempt to summarize multigenerational objective imprecise probabilities of outcomes faces an additional challenge of determining the appropriateness of different independence relations (cf. [36]). I won't attempt to construct a general conception of fitness using objective imprecise probabilities. It may be better to simply model the evolution of a population over time based on empirical conditions that motivate a choice of independence relations. I illustrate that possibility here using Hartfiel's [34] set-chain framework.

It will be easier to understand how set-chain framework can be used to model imprecise evolution if we start by looking at a standard evolutionary model that assumes precise probabilities. A (precise) diploid Wright-Fisher model with random mating is a Markov chain model determining probabilities of changes in frequencies over time of two competing alleles (genes) at the same genetic locus on two chromosomes per organism (e.g. [21]). The alleles in the next generation are distributed binomially, conditional on frequencies in the current generation. Elements of the transition matrix for a Wright-Fisher model have the following form; each element is a probability for the shift from a population state with allele A having frequency i to it having frequency j:

$$p_{ij} = \binom{2N}{j} \eta_i^j (1 - \eta_i)^{2N-j} , \tag{2}$$

where p_{ij} is the probability that the population will contain exactly j A alleles in the next generation given that there are i A alleles in the current generation. If there is no natural selection, $\eta_i = i/2N$ is the probability that an A allele will be included in one of the N organisms in the next generation.[14] With natural selection, organisms differ in their probability of contributing to the next generation depending on which alleles they have. In this case,

$$\eta_i = \frac{w_{AA}i^2 + w_{AB}i(2N-i)}{w_{AA}i^2 + 2w_{AB}i(2N-i) + w_{BB}(2N-i)^2} . \tag{3}$$

Here w_{AA}, w_{AB}, w_{BB} are constants representing the fitnesses of organisms with, respectively, two A alleles (one on each chromosome), an A allele and a B allele, and two B alleles, respectively.

Figures 1 and 2 illustrate how the probability distribution over the frequency of the A allele changes over eight generations for a (standard, precise) Wright-Fisher model. (Note that the vertical axis scale changes.) The data for these plots is generated from an initial vector of possible frequencies for A in which a single element has probability 1. This vector is multiplied by the transition matrix defined by (2) and (3) to produce a vector of probabilities of relative frequencies for generation 1. This vector is multiplied by

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12. [44] calls this rule "permissive"; [72] and [51] call it "Liberal".
13. The interval dominance choice function is so called because it can be expressed using the interval dominance ordering relation.

14. The standard Wright-Fisher model idealizes by assuming a large pool of offspring, so the the process of "choosing" alleles for the next generation will be approximated by sampling with replacement.
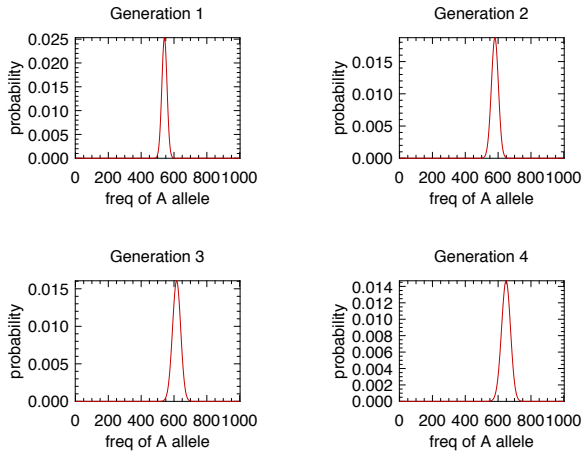
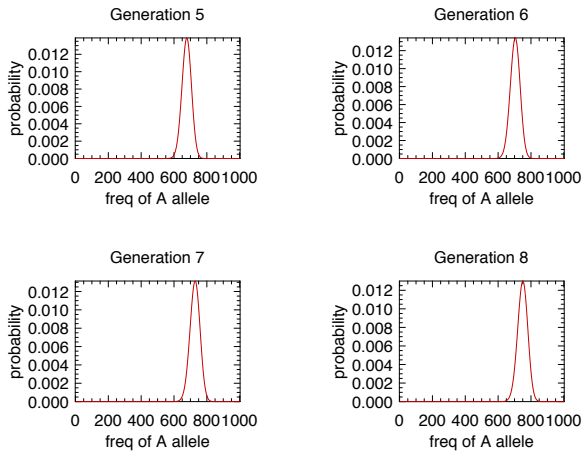Figure 1: Precise Wright-Fisher model, generations 1 through 4. See text for details.

Figure 2: Precise Wright-Fisher model, generations 5 through 8. See text for details.

the same matrix to produce the generation 2 data, and so on. The fitness values used to define η_i in equation (3) for figures 1 and 2 were: $w_{AA} = 1.0$, $w_{AB} = 0.95$, and $w_{BB} = 0.7$; the population size N was 1000, and the initial frequency of A was 500. We can see in 1 and 2 that because the AA genotype is fitter than the other two genotypes, and the AB genotype is fitter than the BB genotype, the probability distribution over possible frequencies of the A allele shifts to the right—i.e. toward higher frequencies.

An objective imprecise probability Wright-Fisher model would be one in which there were multiple transition matrices representing different allowed transition probability

distributions corresponding, perhaps, to different erratically determined environments. Suppose that future states of the population are determined by a convex set of environmental conditions that vary erratically over time, and that all organisms experience the same environment at t. Then the objective imprecise probabilities can be represented by convex intervals of transition matrices with separately specifiable rows [36].[15] Such an "interval" can be specified by a pair of (non-stochastic) matrices. Each element in the "upper" matrix represents the supremum of values for corresponding elements in all of the transition matrices in the interval; each element in the "lower" matrix is the infimum for corresponding elements in the same set of matrices. Similarly, at each time t, we upper and lower vectors will represent suprema and infima for each element in a set of vectors of probabilities of frequencies of the A allele. This is a Markov set-chain model [34].

Computing the interval of vectors of probabilities of possible allele frequencies at $t + 1$ requires multiplying every vector in the interval at t with every matrix in the transition matrix interval. It's possible to compute only a set of extreme points of the vector intervals, but the number of points involved grows very quickly [34]. Fortunately, Hartfiel's [34] hi-lo algorithm can be used to compute close upper and lower bounds for these vector intervals in constant time. That is, at each step, it estimates bounds for the suprema and infima of probabilities of possible frequencies of the A allele, using an analog of matrix multiplication, for intervals of transition matrices. Note that this is not an imprecise version of a Monte Carlo simulation. The model represents erratically determined environments as a set of possible transition matrices, and the computations using them are purely mathematical.

Figures 3–5[16] show the upper and lower bounds of possible probabilities of allele frequencies for a population of size 1000, with an initial frequency of allele A of ten, and with the interval containing the smallest set of transition matrices including those defined by these two sets of fitnesses:[17]

$$w_{AA} = 1.0, w_{AB} = 0.9, w_{BB} = 0.3$$
$$w_{AA} = 1.0, w_{AB} = 0.3, w_{BB} = 0.2$$

Iterating the hi-lo algorithm on the initial population state (probability of 1 for a frequency of 500 for A) generates the data for the upper and lower curves shown in figures 3–5. Each point on the upper curve (outlined lightly in red) of the gray region in a plot represents an estimate of the supremum probability for a particular frequency (x-axis) across all of the vectors of probabilities at that generation. There is a lower curve too, representing infima

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15. This means that the resulting imprecise Markov chain is based on strong independence [8, 67].

16. The software is available at https://github.com/mars0i/imprecise-evolution.

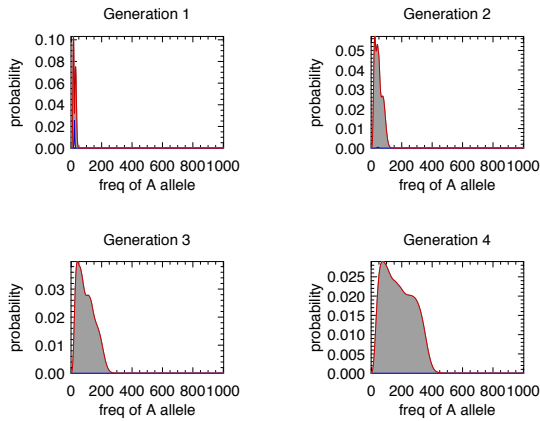17. I apply Hartfiel's [34] tight interval algorithm in the process.

Figure 3: Upper, lower bounds of probabilities for *A* allele frequencies, generations 1 through 4. See text.
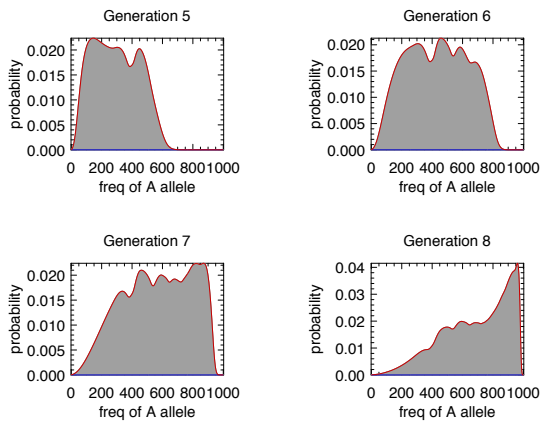

Figure 4: Generations 5 through 8; see figure 3 caption.
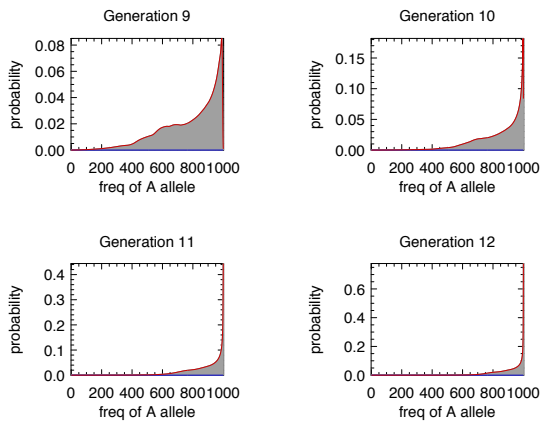

Figure 5: Generations 9 through 12; see figure 3 caption.

of probabilities across all of the state vectors, but it is near zero at most frequencies. (You may be able to see the narrow, blue outline of this lower curve in the plot for generation 1.) These upper and lower curves are not probability distributions. The point on the upper curve over a given allele frequency *x* is an estimate of the supremum probability, over all probability distributions allowed by the model at a specified generation, for allele *A* having frequency *x*. This curve cannot be a probability distribution, as long there are multiple distributions in the interval of vectors, since each point of the curve is greater than the corresponding elements of other vectors of probabilities. The integral under the upper curve is greater than 1.

Notice that although in middle generations, the range of possible probabilities for most frequencies is very large, by generation 12, all of the possible probability distributions assign high probabilities to states in which the *A* allele has a very high frequency. This shows that despite probabilities being imprecise, it may be possible to predict that evolution by natural selection will take place in some circumstances. (This is extremely rapid evolution; it results from the small population size and the large fitness differences I assumed. However, similar effects over longer times can be produced with larger populations and broader ranges of fitness assignments.)

6. Conclusion

I argued that some outcomes are determined erratically, i.e. according to no objective probabilities. When a complex setup consists of erratically determined alternative chance setups with different objective probability distributions over the same set of outcomes, these outcome have objective imprecise probabilities. I argued that environmental conditions are, probably, often imprecisely probabilistic because natural selection is likely to make some behaviors of organisms that are part of an environment to be imprecisely probabilistic. Thus evolution by natural selection probably depends on imprecise objective probability. I also illustrated some simple ways to model fitness as dependent on objective imprecise probabilities, and a ways to model evolution of a population in an imprecisely probabilistic environment.

Acknowledgments

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