Causality in the Sciences

Edited by

Phyllis McKay Illari
Research Fellow, University of Kent

Federica Russo
Research Associate, University of Kent

Jon Williamson
Professor of Reasoning, Inference and Scientific Method, University of Kent

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Chances and causes in evolutionary biology: How many chances become one chance

Roberta L. Millstein

Abstract

As a number of biologists and philosophers have emphasized, 'chance' has multiple meanings in evolutionary biology. Seven have been identified. I will argue that there is a unified concept of chance underlying these seven, which I call the UCC (Unified Chance Concept). I will argue that each is characterized by which causes are considered, ignored, or prohibited. Thus, chance in evolutionary biology can only be understood through understanding the causes at work. The UCC aids in comparing the different concepts and allows us to characterize our concepts of chance in probabilistic terms, i.e. provides a way to translate between 'chance' and 'probability'.

20.1 Introduction

In everyday English language contexts, the term 'chance' has multiple meanings.[1] For example:

I'd give that horse a 50–50 chance (degree of belief) of winning.
I hope I get the chance (i.e. opportunity) to see you.
I found this great restaurant just by chance (i.e. accident).
I'm sorry, but I just can't take the chance (i.e. risk).

As a number of biologists and philosophers have emphasized, 'chance' also has multiple meanings in *evolutionary biology* (see, e.g. Monod 1971; Beatty 1984; Eble 1999; Millstein 2000a, 2006; Gayon 2005; Lenormand *et al.* 2009; Merlin 2009). Elsewhere (Millstein 2000a, 2006), drawing on Beatty (1984) and Eble (1999), I argue that there are at least six conceptions

[1] It also has multiple synonyms, or almost synonyms, 'stochasticity' and 'randomness' in particular. However, for the most part I will restrict myself to the broader term 'chance', since both stochasticity and randomness often have particular mathematical connotations that not all concepts of chance have.

of chance that are potentially relevant to evolutionary theory. To that list, I add a seventh, chance as contingency (Gould 1989; Beatty 1995, 2006a), as follows:

1. indeterministic chance ('pure' chance)
2. chance as ignorance of the real underlying causes
3. chance as not designed
4. chance as sampling (both discriminate and indiscriminate)
5. chance as coincidence
6. evolutionary chance (independent of the generally adaptive direction of natural selection)
7. chance as contingency.

This list may still not be exhaustive; however, I will limit my comments here to these seven. As I will show, each of these seven concepts of chance has a distinct meaning, and each plays a role[2] within evolutionary biology (although some play a greater role than others).[3]

The question of the nature of chance, and related questions of determinism and indeterminism, are longstanding philosophical problems that have occupied philosophers for centuries. More recently, philosophers of science in general and philosophers of physics in particular have looked to quantum mechanics to settle issues concerning the nature of chance and to settle questions concerning the fundamentally probabilistic nature of the universe. However, evolutionary theory itself has a decidedly probabilistic character (indeed, probabilities are ubiquitous in evolutionary theory), one which in some sense does not seem to rest on any new discoveries in quantum mechanics; evolutionary biology was given a probabilistic formulation prior to and independently of the development of quantum mechanics. And as will be discussed below, chance played a role in Darwin's evolutionary thinking prior to evolutionary theory's twentieth-century probabilistic formulations. Thus, the study of the various concepts of chance in evolutionary biology may shed light on the study of chance in quantum mechanics and in other areas of science and philosophy.

The fact that there are many concepts of chance within evolutionary biology raises the following questions: Is there something that all of the concepts

[2] Possible roles include explanatory, instrumental, representational, and/or justificatory (see Millstein 2006 for discussion).

[3] One possible exception here is indeterministic chance. I myself don't think that it plays a direct role in evolutionary theory, in part for philosophical reasons I have discussed elsewhere (Millstein 2000b) and in part because it is simply my impression that it is not what biologists usually *mean* when they invoke chance and probability. However, as we shall see below, others do think that indeterminism plays a role in evolution. Moreover, it at least plays an indirect role in the sense that it is often explicitly rejected in order to begin to clarify which sense of chance *is* being used in a particular context.

have in common that can serve as a unified concept of chance? Or is this a heterogeneous collection? If there is a unified conception of chance, what is it? What makes all the chance concepts 'chance'? And what can a unified concept of chance be used for?

I will argue that there *is* a unified concept of chance, which I call the UCC (Unified Chance Concept). However, it will turn out to be quite general, almost trivial; indeed, like many unifications, it is achieved only through a loss of content.[4] Because of this loss of content, it cannot replace the other concepts of chance. In other words, though I seek one concept of chance, the end result is not monism, but pluralism.

Nonetheless, I will argue, the UCC is not without utility: It tells us that the seven different concepts do have something in common, and identifies that common core, perhaps aiding in identifying future concepts both within and outside of evolutionary biology. It can be used to aid in comparisons among the different concepts. And perhaps most importantly, it will allow us to characterize our concepts of chance in probabilistic terms (i.e. provide a way to translate between 'chance' and 'probability').

20.2 Characterization of the Unified Chance Concept (UCC)

We will see each of the seven concepts of chance has a somewhat different meaning (although they can be hard to differentiate because a particular biological phenomenon might manifest more than one concept simultaneously). However, one striking commonality between them, as will become clearer below, is that there are all described in the negative, in contrast to various causes. What is interesting about this is that *indeterminism* is – though a bit misleadingly, I think – sometimes characterized as meaning 'uncaused'.

To see why 'uncaused' is a misleading definition of indeterminism, consider, for example, radioactive decay under the assumption that it is an indeterministic phenomenon.[5] When one compares the half-lives of two elements (e.g. carbon-14 and uranium-238), it is their different structures that give rise to (cause) their different half-lives. Even a particular decay event is caused by the structure of the particular atom. It may be, however, that two identical atoms in identical environments may not (indeed, are likely not to) decay at the same time. This is the intuition behind the idea that indeterministic events are 'uncaused', but again, that overlooks the causal role played by the structure of the atom.

[4] My favourite example: All scientific theories could be unified under the assertion that 'things happen'. (Slightly modified from a version suggested to me by Frédéric Bouchard.) This would be true, but so general as to be completely uninformative.

[5] See Earman (1986) for a far more detailed and sophisticated discussion for why 'uncaused' is an inaccurate description of the sort of indeterminism suggested by quantum mechanics.

Thus, even as indeterministic events are not fully caused, they are still (to an extent) caused. Similarly, it will turn out that 'chance' is defined both by what causes are left out and what causes are included (this will be explained further below).

Another commonality (again, as will become clearer below), is that both indeterminism and the various concepts of chance imply more than one possible outcome. These commonalities suggest that an analogy between indeterminism, as an empirical claim about the world, might prove fruitful for understanding the various concepts of chance. That is, examining the commonalities between each concept of chance and indeterminism gives rise to a set of characteristics that are common to all of the concepts of chance and also helps illuminate why they are considered to be concepts of chance (i.e. because they are similar to indeterminism). I won't walk the reader through that particular exercise, but rather, describe the analogy and the UCC and then in subsequent sections show how each concept of chance fits.

But we need a new definition of indeterminism. Here is a slightly better[6] one: Given the *complete state* of the world at one point in time, the state of the world at every future point in time is not uniquely determined; for a given point of time in the future, more than one state is possible.[7] Now suppose that the UCC were analogous – but not identical – to the definition of indeterminism. In particular, suppose we consider *not the complete state* of the world, but rather, some *subset* of it. This yields, I will argue, the UCC:

> UCC: Given a specified subset of causes, more than one future state is possible.

This might seem trivial. But the key will be to identify the subset of causes for each type of chance. Identifying the subset of causes involves identifying, for each concept of chance, which causes are taken into account (what I will call the *considered* causes), which causes are operating but *ignored*,[8] and which causes are *prohibited* from operating altogether if the particular concept of chance is to be manifested (if any). The particular chance concepts differ in the types of causes that are considered, ignored, and prohibited; they also differ in the relevant types of *possible outcomes*. Figure 20.1 will serve as a basic template for the UCC, to be filled in with specifics for each concept of chance.

[6] Most importantly, the definition is an ontological one (and thus is a claim about the world), rather than an epistemological one (which would be a claim about our, or a Laplacean demon's, ability to make predictions about the future).

[7] That is, *physically* possible. Here, I leave the characterization of physical possibility open; for example, one may do so in terms of laws if one is convinced that laws will clarify the notion. I am not so convinced.

[8] As should become clear below, the fact that we *ignore* certain causes does not necessarily imply that we are *ignorant* of them.

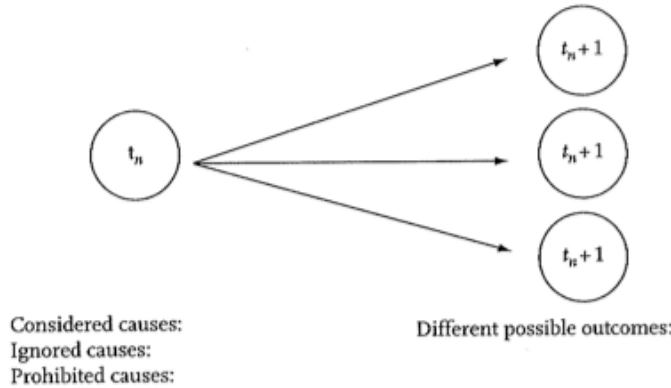

Fig. 20.1. The unified conception of chance.

20.3 The seven chance concepts

Now I need to show that the UCC genuinely unifies the seven concepts of chance. I will explain each concept, give examples from evolutionary biology, and then show how the concept fits the UCC.

20.3.1 Indeterministic chance ('pure' chance)

Above, I discussed indeterminism as a thesis about the world in general. Here I focus more locally, on the indeterminism of particular processes or types of processes. Indeterminism is said to be a true description of microlevel processes by, e.g. those who argue for the Copenhagen interpretation of quantum mechanics. A typical example of a such a process is radioactive decay. But what about macrolevel processes, and evolutionary processes in particular – are they indeterministic? For example, if cloned plants grown under (purportedly) identical conditions nonetheless differ considerably in height, weight, etc., is this an example of an indeterministic macrolevel process? Brandon and Carson (1996) argue, on the basis of examples such as these, that a scientific realist ought to conclude that the evolutionary process is indeterministic.[9]

Of course, if it were the case that the height of a cloned plant were due to indeterministic chance, it would not follow that the plant could be any height at all. A California poppy, which typically grows to a height of about 5–60 centimeters, would not grow to a height of 1 meter. Rather, the claim

[9] As will become clearer below, I do not find these arguments persuasive; my reason for including this example is to incorporate the full range of the types of claims that have been made about chance in evolution. Indeed, I think it is rare – if ever – that indeterministic chance is invoked in evolutionary contexts. However, it is important to leave open the conceptual possibility, as well as to emphasize that the other concepts of chance do *not* assume indeterministic chance.

is that given certain physical characteristics of the plant and the conditions in which it grows, there is a range of possible heights that it can achieve. If the plant's height really is due to indeterministic chance, then identical conditions can yield more than one possible height, with nothing further to be said (there are no 'hidden variables' to distinguish one case from another). Thus, indeterministic chance, unsurprisingly, fits the UCC quite cleanly: all the causes at a given point in time are considered, yielding a range of possible future outcomes with respect to the phenomenon of interest. No causes are ignored or prohibited.

However, one might reasonably ask just how relevant this notion of chance is for evolutionary biology, a point that Richardson (2006) has emphasized. Indeed, a recent exploration by three biologists of the meanings of chance in evolution states very clearly that describing evolution as a stochastic process 'has nothing to do with the claim that the natural world is, *in fine*, deterministic or not' (Lenormand *et al.* 2009, 158). Moreover, Brandon and Carson (1996) arguments for the indeterminism of evolution are not by any means universally accepted. Graves, Horan, and Rosenberg (1999) argue that at the macrolevel of evolutionary processes, there is '*asymptotic determinism*'. And as I argue (Millstein 2000b), given our current state of knowledge, even a scientific realist ought to be an agnostic on debate between the indeterminists and the 'asymptotic determinists'; most discussions end up trading one philosophical intuition for another rather than engaging in the painstaking task of tracing uncontroversially indeterministic microlevel phenomena to widespread macrolevel evolutionary processes (see Millstein 2003a for further discussion).

Even if evolutionary processes are to some extent indeterministic (as is likely to be the case if there is indeterminism at the microlevel – even the determinists concede that microlevel phenomena could occasionally 'percolate up' to the macrolevel), it does not seem plausible that observed statistical outcomes of evolutionary processes (such as variations in cloned plants given purportedly identical treatment) could be *fully* explained by indeterminism (Weber 2001). It is unlikely that in either our models or in any particular case we know all of the relevant causes; surely *some* of the observed statistical outcomes are due to these unknown causes. Thus, for the remainder of this paper, I will remain neutral on the indeterminism question, i.e. the rest of the chance concepts assume neither determinism nor indeterminism. Some might think that the indeterministic chance concept is the only 'real' chance concept; the subsequent discussion will show that the other meanings of chance in evolutionary biology are equally 'real' and equally useful, just different in meaning. That is, each chance concept describes a particular way that the world could be, and when a concept of chance is ascribed to a particular phenomenon, it is an empirical matter whether or not the phenomenon in fact manifests that description.

20.3.2 Chance as ignorance of the real underlying causes

Sometimes, we say that a future event is a matter of chance because we are unaware of some of the causes. To use an everyday example, we think of the flip of a fair coin as having a 50% chance of turning up heads. And yet (again, barring the occasional percolation of microlevel indeterminism), we generally think that is because there are numerous unknown causes, such as the way the coin is flipped or wind resistance, that are responsible for the outcome on each toss. In other words, we might say that the our ascription of the coin's 50% chance of turning up heads is really just a reflection of our ignorance of these other causes.

In the evolutionary realm, Darwin invoked chance as ignorance when he said that new variations were due to chance (though this was not the only sense of chance that Darwin ascribed to new variations):

> I have hitherto sometimes spoken as if the variations—so common and multiform in organic beings under domestication, and in a lesser degree in those in a state of nature—had been due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation (Darwin 1859, p. 131).

And the use of this sense of chance, chance as ignorance, persists among biologists today, as Lande *et al.* make clear:

> Fluctuations in population size often appear to be stochastic, or random in time, reflecting our ignorance about the detailed causes of individual mortality, reproduction, and dispersal (Lande *et al.* 2003, p. 1).

Of course, we are not completely ignorant about the causal factors influencing fluctuations in population size. Known causal factors include the current population size, the typical life span of organisms of the species in question, and density dependent population regulation (Lande *et al.* 2003). These causal factors are the considered causes, and they determine which outcomes (in this cause, which range of fluctuations in population size) are possible. The causes we are ignorant of are ignored. No type of cause is prohibited from operating altogether.

Here one might worry that this is just the Laplacean notion of chance, and so only a deterministic notion. However, this is not the case. Even if evolution is indeterministic, we still might be ignorant of some of the underlying causes, and so, this concept of chance might still be relevant. In such a case, the range of possible outcomes is mediated both by the unknown causal factors and the inherent indeterminism.

A related worry is that determinism, combined with 'chance as ignorance', is sometimes seen as exhausting all the possible meanings of chance. In other words, some authors have written as though 'chance as ignorance' is the only concept of chance that makes sense under determinism (e.g. Rosenberg 1994;

but see Bouchard and Rosenberg 2004 for an alternate view). As Henri Poincaré noted, such a position is wrong-headed.[10] The fact that the 'laws of chance' can correctly predict phenomena such as the motions of molecules of a gas shows that ignorance does not exhaust the meaning of chance and that 'the information given us by the calculus of probabilities will not cease to be true upon the day when these phenomena shall be better known' (Poincaré 1921: p. 396). Indeed, we will see that each of the following concepts of chance is sensible in deterministic (as well as indeterministic) contexts.

20.3.3 Chance as not designed

Events that appear planned or designed, but are not in fact so, are often attributed to chance. For example, one might say that the shape of a running horse appearing in the clouds was due to chance in this sense.[11] For Darwin, new variations were chance in this sense:

> ...if we do not admit that the variations of the primeval dog were intentionally guided in order that the greyhound, for instance, that perfect image of symmetry and vigour, might be formed,—no shadow of reason can be assigned for the belief that variations, alike in nature and the result of the same general laws...were intentionally and specially guided"(Darwin 1868, pp. 431–432).

Here we see that the same phenomenon can be chance in more than one sense: in the previous section, I noted that Darwin also held that new variations were due to chance in the sense that he was ignorant of the true causes.[12] This form of chance is often not explicit in contemporary practice, but it is made explicit in responding to proponents of creationism or so-called 'Intelligent Design'. Neither the new variations nor selection itself (nor any evolutionary process, for that matter) are thought to be designed; thus, they are all due to chance in this sense, though this is not to imply the other senses of chance are relevant. One of the sources of confusion in the creationist debates is the conflation between 'chance as not designed' and the other senses of chance, but clearly, the former sense does not imply the latter, as Richard Dawkins notes:

> The argument from improbability states that complex things could not have come about by chance. But many people *define* 'come about by chance' as a synonym for 'come about in the absence of deliberate design'. Not surprisingly, therefore, they think

[10] See also Weber (2001) and Millstein (2003b).

[11] The famous 1965 'tomahawk toss' on *The Tonight Show Starring Johnny Carson* is a classic example of an unplanned event that looks like it could have been planned. Another example is the rock formation in New Hampshire that was known as 'The Old Man of the Mountain'.

[12] Beatty (1984) has emphasized the fact that Darwin used a multiplicity of chance concepts in characterizing the origin of new variations.

improbability is evidence of design. Darwinian natural selection shows how wrong this is with respect to biological improbability (Dawkins 2006, p. 139; emphasis in original).

In order for an undesigned process to be operating, there must be a complete absence of any 'intentionally guided' causes; thus, these causes are *prohibited* from this concept of chance. Any other cause may be considered; none need be ignored (though there may be other reasons, such as pragmatic reasons, for ignoring certain causes). Undesigned processes may give rise to outcomes that appear designed (what Dawkins calls 'designoids'), but they may not.

If no causes are ignored, under determinism a *token* non-intentional cause will of course uniquely determine one future outcome. In such cases, chance as undesigned can be construed as being true of a *type* of non-intentional cause whose tokens can give rise to different possible outcomes, some of which appear designed and some of which do not.

20.3.4 Chance as sampling (both discriminate and indiscriminate)

Discriminate sampling processes are processes in which physical differences among entities are causally *relevant* to differences in which entities are 'picked'. It can be thought of as 'sloppy' picking; the physical characteristics of some of the entities are the reason that they get picked, but they will not necessarily get picked; other entities that lack the characteristic in question might get picked instead. *Natural selection* is a chance evolutionary process in this sense. That is to say, natural selection is a process in which heritable physical differences among entities (e.g. organisms) are causally relevant to differences in reproductive success.

Indiscriminate sampling processes, on the other hand, are processes in which physical differences among entities are causally *irrelevant* to differences in which entities are 'picked'. This is the sort of picking that would occur if one were picking while blindfolded and if the physical differences in question were color differences only. *Random drift* is a chance evolutionary process in this sense. That is to say, as I have argued elsewhere (Millstein 2002, 2005), random drift is a process in which heritable differences among (for example) gametes[13] are causally irrelevant to which gametes are successfully joined (i.e. which gametes participate in successful fertilizations that yield zygotes). Biologists have also developed macroevolutionary models in which physical differences between taxa are causally irrelevant to difference in rates of branching and extinction within the taxa (see Millstein 2000a for a discussion).

[13] Note that both discriminate and indiscriminate sampling processes can occur at any level of the biological hierarchy, e.g. DNA bases, gametes, organisms, groups, etc. Also, they can occur simultaneously, as in the nearly neutral theory of molecular evolution (see Dietrich and Millstein 2008 for a discussion).

A sampling process takes into account the proportion of types within the population that is being sampled, the size of the sample, and the picking mechanism(s); these are the considered causes. Given those causes (and possibly indeterminism), there are different samples that can be produced; the samples differ in the proportion of types. A discriminate sampling process will also consider the physical characteristics that give rise to relative capacities to be 'picked'; this will further constrain the possible outcomes, or at least their expected frequency of appearance. 'Petty influences', such as the locations of entities within the population, are ignored; no causes are prohibited from operating. Sampling processes give rise to different possible proportions of types subsequent to picking (in evolutionary cases, this is the next generation).

20.3.5 Chance as coincidence, i.e. 'accident'

This concept of chance is associated with Aristotle; it implies the confluence of independent causal chains. For example, there may be a causal chain that leads to a white Toyota Prius being in the intersection of 3rd St. and B St. at 1:02 PM – and an entirely different and independent causal chain that led a green Ford Expedition to be in the same intersection at the same point in time. The collision of the cars was due to chance; it was a coincidence that they were in the intersection at the same time.

Note that under determinism, no two causal chains are truly independent, i.e. it is likely that there is a common cause if one looks back far enough in time (to the Big Bang, if necessary). Cournot (1843) provides a useful way of handling chance as coincidence under determinism. He describes two pairs of brothers – one pair serves in the same army, one pair serves in different armies, and yet in both cases the brothers perish on the same day. The brothers' deaths are both independent to a degree, yet the latter is more independent than the former, and thus chance to a greater degree.

In evolutionary biology, the question has arisen as to whether extinction is a chance process in this sense; for example, David Raup writes:

> The main question, to be visited again and again, is whether the billions of species that died in the geologic past died because they were less fit (bad genes) or merely because they were *in the wrong place at the wrong time* (bad luck) (Raup 1992, p. xi; emphasis added).

So, for example, consider a causal chain that ends with an asteroid impact on the Earth and the causal chain of the persistence of a particular species. If these two causal chains intersect without having had a common cause, then their confluence was a coincidence. Genetic draft (Gillespie 2000ab; Skipper 2006) also exhibits this sense of chance. Genetic draft[14] is a process of linked selection where it is a matter of chance which of two neutral alleles

[14] The phenomenon is called 'genetic draft' because some of its predicted outcomes are similar to those of genetic drift and because it involves 'hitchhiking', i.e. linked selection.

(in a two-locus model) happens to be linked to a site that undergoes an advantageous mutation, and where the timing of these mutations, followed by a rapid selective 'sweep' to fixation, is random. In models of genetic draft, the linking of a particular neutral allele to a locus where an advantageous mutation occurs represent two independent causal chains that intersect in a point in space-time.

Thus, chance as coincidence takes into account the two (or more) causal chains, while prohibiting those causal chains that have a (recent, under determinism) common cause. By ignoring the timing and/or location of the causal chains, as possible outcomes the chains may or may not intersect. Returning to the example I gave at the outset of this section, this captures the sense that had things been just a little bit different (had I left a little earlier, or gone a different route), the accident would not have occurred.

20.3.6 Evolutionary chance

Evolutionary chance (the term is due to Eble 1999) is exhibited when phenomena are independent of the generally adaptive direction of natural selection. This sense of chance has its origins in Darwin's thinking; it is one of the several senses in which he held new variations to be chance (we have seen two others so far, chance as ignorance and chance as not designed) but it is perhaps the sense that has been most influential and persistent in evolutionary biology. That is to say, Darwin (in his non-Lamarckian moments) believed that new variations were not directed, but rather that they were due to chance in the sense that they did not arise because they would be beneficial for the organism. Today, biologists generally believe that mutations, as a source of new variations in a population, are chance in this sense – mutations may be adaptive, maladaptive, or neutral – although there is some debate over whether all mutations are chance mutations.[15] Recombination (the chromosomal crossover between chromosome pairs that occurs during meiosis, giving rise to new gene combinations) is another source of new variation in populations and is similarly conceived of in terms of evolutionary chance.

Random drift, which as we saw earlier is a form of chance as indiscriminate sampling, also exhibits evolutionary chance. Although drift may sometimes proceed in an adaptive direction, it is no more likely to do so than it is to

[15] See Millstein (1997) and Merlin (2009) for a discussion. In order to account for the nuances of this complicated debate, the concept of chance mutation needs further refinement. Millstein (1997) argues that a mutation is directed if and only if it is specifically caused by environmental stress in an exclusively adaptive manner. Otherwise (if the mutation is non-specific, or specific but not exclusively adaptive, or not caused by environmental stress) it is a chance mutation. Merlin (2009) modifies this account of chance mutation. However, these refinements, while crucial for a full understanding of the debates over directed mutation, are not essential for the discussion here.

proceed in a maladaptive or neutral direction, in contrast to natural selection, which is weighted in an adaptive direction (and thus natural selection does *not* exhibit evolutionary chance, though it *is* chance in the sense of discriminate sampling, as we saw above). Similarly, the stochastic models of macroevolution that were mentioned earlier manifest evolutionary chance.

An anonymous referee has raised the concern that if drift exhibits more than one type of chance, the concepts of chance as indiscriminate sampling and evolutionary chance are not actually different from one another. However, such a concern is misplaced. Clearly, indiscriminate sampling is manifested in many non-evolutionary contexts, such as the sampling of coloured balls from an urn (a model that is used to aid in understanding drift, but which is not itself random drift; to name one obvious difference, there is no reproduction involved in sampling balls from an urn as there is with random drift). Evolutionary chance, on the other hand, can be manifested in phenomena where indiscriminate sampling is not manifested, such as chance mutation, where it is not the case that there is some standing variation from which some variants are 'picked' and some are not. Rather, mutations are 'mistakes' made during the DNA replication process with the consequence that the new nucleotide sequences differ from the previous nucleotide sequences. The fact that there are phenomena that exhibit indiscriminate sampling, but not evolutionary chance, and phenomena that exhibit evolutionary chance, but not indiscriminate sampling, shows that the two concepts are different – as does the fact that they differ in their considered causes, ignored causes, and prohibited causes, as previously described. (See Millstein 2000 for arguments concerning the distinctiveness of some of the other concepts of chance.)

Thus, evolutionary chance is primarily characterized by the causes that it prohibits entirely, namely, causes that proceed primarily in an adaptive direction. All other causes are taken into account, except for those that might be ignored for other (e.g. pragmatic) reasons. As a consequence, outcomes may be in an adaptive direction, but they may also be in maladaptive or neutral directions.

If no causes are ignored, under determinism a *token* not-adaptively-biased cause will of course uniquely determine one future outcome. In such cases, evolutionary chance can be construed as being true of a *type* of not-adaptively-biased cause whose tokens can give rise to adaptive, maladaptive, or neutral outcomes.

20.3.7 Chance as contingency

Stephen Jay Gould's *Wonderful Life: The Burgess Shale and the Nature of History* makes the case for the role of contingency in the evolution of life on his planet, using the movie *It's a Wonderful Life* as a metaphor.[16] Gould explains that when Clarence (a guardian angel) shows George what life in the town of Bedford Falls would have been like without him, the movie gave 'the finest illustration that I [Gould] have ever encountered for the basic principle of contingency – a replay of the tape yielding an entirely different but equally sensible outcome; *small and apparently insignificant changes*, George's absence among others, lead to cascades of accumulating difference' (Gould 1989, p. 287; emphasis added). Similarly, Gould says, '[a]lter any event, *ever so slightly and without apparent importance at the time*, and evolution cascades into a radically different channel' (Gould 1989, p. 51; emphasis added). In other words, if we replay the tape of life with small (and seemingly 'insignificant') changes at the outset, a radically different outcome will result: this is an example of what Gould calls (and what I will call) contingency.[17] Contingency thus involves sensitivity to initial conditions.

Other examples of chance as contingency occur in evolutionary biology. For example, Beatty describes how differences in the order of mutations in similar ancestral orchid populations can account for the vast diversity of orchids species (Beatty 2006b). Genetic draft, mentioned above, may be analogous here, if different timing of mutations to advantageous alleles that are linked to neutral alleles would lead to very different outcomes (Gillespie 2000ab; Skipper 2006). These examples show that the initial conditions to which the relevant processes are sensitive can be small changes in *timing* as well as small qualitative changes, e.g., 'If *Pikaia* does not survive in the replay, we are wiped out of future history – all of us, from shark to robin to orangutan' (Gould 1989, 323).

If a causal process is sensitive to initial conditions (the considered causes), then small differences in initial conditions (the ignored causes) will yield very different possible outcomes.[18] These processes are contingent. Causal

[16] Beatty (1995, 2006a) analyses Gould's concept of 'contingency' in detail; my presentation of it differs slightly from his. In particular, Beatty describes two meanings of contingency: unpredictability and causal dependence. Beatty describes unpredictability as 'different, unpredictable outcomes from the same or indistinguishable prior states' (Beatty 2006a, p. 339). If the prior states are truly identical, then contingency is the same concept as what I have called 'indeterministic chance' above. It seems to me that Gould denies this meaning when he differentiates contingency from the 'truly random' (Gould 1989, p. 284). Causal dependence, on the other hand, is described as 'the particular outcome depends strongly on which particular states preceded it' (Beatty 2006a, p. 339). That is closer to the view that I will describe.

[17] Sixty-eight years earlier, Poincaré describes chance in the same way, where 'slight differences in the initial conditions produce great differences in the final phenomena' (1921, p. 397). One of his examples is a perfectly symmetrical cone on a perfectly vertical axis, with no forces acting on it. I do not know whether Gould read Poincaré; no doubt this idea has been articulated many times.

[18] Chaotic processes are examples of contingent processes; however, being sensitive to initial conditions is only one characteristic of chaotic processes. That is, all chaotic processes are contingent, but not all contingent processes are chaotic.

processes that are not sensitive to initial conditions (i.e. that will tend to yield the same outcome even if the initial conditions differ slightly), are not contingent (so, these processes are 'prohibited').

An anonymous referee has raised the concern 'that the notion of chance as sensitivity to initial conditions does not directly refer to the unpredictability of the final result due to our ignorance of little differences at the level of initial conditions. Rather, it refers to the disproportion between little changes at the level of causes (initial conditions) and big changes at the level of effects (result). Chance is this disproportion, which makes the prediction very difficult and even impossible in the long term. If it is so, there are no ignored causes in this case (but there can be always ignored causes for other reasons, like in the case of other concepts of chance).' Here I would reply that what makes a phenomenon contingent is not our *ignorance* about the effects of small changes in initial conditions; the phenomenon would still be sensitive to initial conditions even if we knew those differences in initial conditions and their effects. Rather, I draw attention to the wide range of possible outcomes from similar initial conditions, a characteristic that chance as contingency shares with the other concepts of chance.

See Table 20.1 for a summary of the seven concepts of chance.

20.4 Connecting the UCC to probability

I have shown how each of the seven concepts of chance can be characterized in terms of the UCC. Note, however, that the seven concepts of chance are not to be 'eliminated' or made unnecessary simply because a common conception has been found. Each of them is more precise than the general definition; each 'gets at' a different aspect of chance. To put the point another way – each of the concepts of chance entails the general concept, but not vice versa. That is not to say that a particular phenomenon can't manifest more than one concept of chance. For example, as we have seen, random drift exhibits more than one concept of chance (chance as sampling and evolutionary chance), as do new variations (chance as ignorance, at least for Darwin; chance as not designed; and evolutionary chance). Which concepts of chance a given phenomenon manifests (if any) is an empirical question (though there may of course be a conceptual/theoretical component); again, note in particular that indeterministic chance may or may not be appropriate for a given phenomenon, and that it may be manifested in conjunction with one or more of the other concepts.

One benefit of characterizing the seven concepts of chance in terms of the UCC is that it provides a straightforward way for us to translate these more colloquial uses of chance into probabilistic terms. The translation between

Table 20.1 Summary of the seven concepts of chance, using the parameters of the UCC as illustrated in Figure 20.1

Concept of chance	Considered causes	Ignored causes	Prohibited causes	Different possible outcomes
Indeterministic chance	All (more precisely, the complete state of the world at t_n).	None.	None.	Any type of outcome in principle, though possibilities will be restricted by the included causes.
Chance as ignorance	All the causes that we know (or whose effects can calculate easily).	All other causes.	None.	Any type of outcome, though possibilities will be restricted by the included causes.
Chance as not designed	Any type of causes other than 'intentionally guided' causes.	None by definition, though some may be ignored for other reasons.	Intentionally guided causes.	Events that appear designed or events that do not appear designed.
Chance as sampling	Proportion of types within the population, size of sample, 'picking' mechanism. If discriminate, also includes relative capacities to be picked.	'Petty influences', such as the locations of entities.	None.	Different proportions of types in the population subsequent to the 'picking'.
Chance as coincidence	Two or more causal chains.	The timing and/or location of the causal chains.	A common cause for the causal chains.	The causal chains intersect or the causal chains do not intersect.
Evolutionary chance	Any cause that does not proceed primarily in an adaptive direction.	None by definition though some may be ignored for other reasons.	Any cause that proceeds primarily in an adaptive direction.	Outcomes may be adaptive, maladaptive, or neutral.
Chance as contingency	Causal processes that are sensitive to initial conditions.	Small, seemingly 'insignificant' causes.	Causal processes that are not sensitive to initial conditions.	Very different outcomes, depending on which small causes are ignored.

UCC and a (conditional) probability[19] is as follows. The UCC corresponds to the *probability of a particular outcome given the specified subset of causes.* Or, more formally, a given instantiation of the UCC can be translated to *Pr(outcome/subset of causes)*, where 'subset of causes' are the considered causes and 'outcome' is one of the possible outcomes, for that instantiation of the UCC.[20]

Here is an example of how this works. As described above, for chance as indiscriminate sampling, the considered causes are the proportion of types within the population, the size of sample, and the 'picking' mechanism. For chance as sampling petty influences are ignored, and so are not included in the subset of causes; no causes are prohibited, however. For random drift in particular, the UCC might be instantiated with the current proportions of phenotypes with respect to a given heritable trait, a given size of the population, and the particular environmental factor(s) that interact with that trait. This subset of causes yields different possible outcomes, where the different outcomes are different proportions of phenotypes in the subsequent generation.

So, for this sort of random drift, chance as indiscriminate sampling can be characterized as:

> Pr (a particular proportion of phenotypes in the subsequent generation / current proportions of phenotypes with respect to a given heritable trait & size of population & environmental factor(s) interacting with those traits)

or, in a particular case, where the population consists of yellow, brown, and pink snails:

> Pr (0.6 yellows, 0.3 pinks, and 0.1 browns in the subsequent generation /
> 0.5 yellows, 0.4 pinks, and 0.1 browns (heritable colors) &
> 200 snails & drought to which all snails are equally susceptible).

Once the translation is effected, it may now be possible to characterize our fairly colloquial uses of chance in quantitative terms for a particular case. For example, for random drift and chance as indiscriminate sampling, we could calculate the probability of a particular change in the population through

[19] Hájek (2007) argues that all genuinely informative theories of probability suffer from the reference class problem, a problem that can (in its metaphysical form) be dissolved by recognizing that conditional probabilities are the proper primitive of probability theory. I have much sympathy with his arguments, although nothing turns on them here.

[20] Here I make no claim as to whether the product of such a translation would satisfy all of Kolmogorov's axioms; such a demonstration would take us astray from the main points of this paper. Here I will simply note that some of the main candidates for interpretations of probability, such as the propensity interpretation, do not satisfy all of the Kolmogorov axioms, either (see, e.g. Hájek 2009 for a discussion).

the usual means of calculating such probabilities (laboratory experiments, observations of similar populations, etc.).

The other concepts of chance can be translated into probabilities in the same way: we can describe the probability of a particular outcome given the subset of causes for the concept of chance at hand (including the considered causes and excluding the ignored and prohibited causes), and then determine the values of those probabilities in the usual way that such probabilities are estimated. Although it might seem strange to quantify what seem like colloquial concepts of chance, this is not completely new for evolutionary biology. For example, Lenormand, Roze, and Rousset (2009) describe mathematical models of evolutionary chance. In principle, we could use the quantitative probability measures to compare different colloquial senses of chance. For example, we could compare an instance of chance as sampling (say, an outcome with a probability of 0.3) to an instance of chance as contingency (say, an outcome with a probability of 0.6). It remains to be seen, however, whether such comparisons would prove useful.

Also, if we had reason to think that a particular interpretation of probability was the appropriate interpretation for a particular case, we could link it to our chance concepts via the UCC. For example, we have good reason to think that our random drift probabilities are propensities, either deterministic or indeterminisitic (Millstein 2003b). Propensities are grounded in, and arise from, the physical characteristics of a system. The physical characteristics of the system, however, are just what I have been calling the considered causes, and it is their dispositions that are the source of the probability measures. In such cases, we would have good reason to think that this form of chance as indiscriminate sampling was a (deterministic or indeterministic) propensity.

However, the concepts of chance themselves can in principle be understood through any defensible interpretation of probability (with the exception of indeterministic chance, which is most naturally understood in terms of indeterministic propensities). Consider, for example, chance as ignorance. This might seem like an epistemic probability (that is, a probability that is concerned with the knowledge or beliefs of human beings), and it could indeed be interpreted that way; however, it need not be. Consider again the case of the coin flip; we need not be truly ignorant of the causes apart from the flipping mechanism and the coin itself (such as wind resistance). More to the point, we can understand the 50% probability we ascribe as arising from the physical characteristics of that type of setup (the considered causes) or the possible outcomes of that type of setup, making one of the objective probability interpretations (propensity or frequentist, respectively) a possible interpretation. On the other hand, by construing the relevant considered causes and observed outcomes as Bayesian evidence, one can likewise translate any of the concepts of chance into subjective probabilities.

20.5 Conclusion

There are at least seven particular, colloquial uses of chance in evolutionary biology. With the exception of indeterministic chance, each is meaningful regardless of whether the evolutionary process is deterministic or indeterministic. Each of the seven can be translated into the Unified Chance Concept (UCC) by specifying the types of causes that are taken into account (i.e. considered), the types of causes that are ignored or prohibited, and the possible types of outcomes. Again, however, let me emphasize that the existence of a more general concept does not entail that the more specific meanings are eliminated; the plurality of concepts is useful in illuminating different aspects of chance phenomena.

The UCC has the following benefits: The UCC reveals what is in common to the different chance concepts (what makes 'chance' chance). The UCC may aid in finding other concepts of chance, perhaps even outside of evolutionary biology. And most importantly, the UCC connects colloquial concepts of chance to probability, permitting them to be quantified, compared, and understood in terms of more formal interpretations of probability.

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