

Evolvability as a Disposition: Philosophical Distinctions, Scientific Implications

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Abstract

A disposition or dispositional property is a capacity, ability, or potential to display or exhibit some outcome. Evolvability refers to a disposition to evolve. This chapter discusses why the dispositional nature of evolvability matters—why philosophical distinctions about dispositions can have scientific implications. To that end, we build a conceptual toolkit with vocabulary from prior philosophical analyses using a different disposition: protein foldability. We then apply this toolkit to address several methodological questions related to evolvability. What entities are the bearers of evolvability? What features causally contribute to the disposition of evolvability? How does evolvability manifest? The various possible answers to these questions available from philosophical distinctions suggest key implications for why the concept of evolvability as a disposition is useful in evolutionary research. These include (1) securing scientific virtues (e.g., explanatory depth and generalization, prediction or retrodiction, and control or manipulation) and (2) fostering interdisciplinary collaboration through the coordination of definitional diversity and different types of inquiry. Together these facilitate concentration on a variety of research questions at different levels of organization and on distinct time scales, all of which should be expected for a complex dispositional property such as evolvability.

Keywords: evolvability, dispositions, philosophical toolkit, intrinsicality, contributors to evolvability

1 Introduction

A disposition or dispositional property is a capacity, ability, or potential to exhibit some outcome. Since one can possess an ability without currently displaying it, dispositions are attributed whenever it makes sense to distinguish between an object having a property and manifesting that property. For example, the fragility of a window is its disposition to break under certain conditions (e.g., upon impact from a rock). The window is fragile even if it never breaks, and we can make claims about its degree and kind of fragility despite its manifestation not being directly observed. This contrasts with non-dispositional or so-called “categorical” properties of the window, such as its size or shape, for which a distinction between the property and its manifestation is irrelevant. Dispositional properties are common in biology (Hüttemann and Kaiser 2018), including the foldability of proteins or the differentiability or pluripotency of cells. The most recognizable example in evolutionary biology is fitness, where the capacity to survive and reproduce is distinct from actual reproductive success (Mills and Beatty 1979). There also is an abundance of dispositional notions in the field of evolutionary developmental biology (evo-devo), such as forms of developmental plasticity like the capacity to exhibit different morphological traits in seasonal polyphenisms (Austin 2017; Austin and Nuño de la Rosa 2021).

Evolvability—the core notion of this volume—is a disposition. Scientific definitions make this dispositional character plain by construing evolvability as “the *ability* of a population to respond to selection” (Flatt 2005, 306), “an organism’s *capacity* to generate heritable phenotypic variation” (Kirschner and Gerhart 1998, 8420), or “the *ability* of a biological system to produce phenotypic variation that is both heritable and adaptive” (Payne and Wagner 2019, 24). Evolvability can but need not manifest in a higher rate of evolution because two populations with an identical ability to evolve may come to exhibit different evolutionary outcomes due to chance—just like in the case of fitness as a capacity to reproduce—or due to the two populations being exposed to different environmental conditions. Twenty-five years ago, Wagner and

Altenberg (1996) noted that *evolvability* and *variability* are dispositions and should be distinguished from actual evolutionary outcomes and observable variation (see also Hansen 2006). This encourages making the dispositional property of evolvability a target for scientific investigation, especially how this capacity has changed through the history of life (i.e., the evolution of evolvability). Indeed, the increasing prominence of the notion of evolvability marks an important change in recent scientific theorizing (Brigandt 2015; Nuño de la Rosa 2017) and its dispositional character may be part of the reason why the concept of evolvability nowadays enjoys widespread use in a variety of biological fields investigating evolution.

One task of this chapter is to argue that the dispositional nature of evolvability matters, and show what is distinctive about evolvability compared to other dispositions in evolutionary biology. However, as the limited array of evolvability definitions described above makes plain, there are different conceptions of evolvability being used by different disciplines, from quantitative genetics and evo-devo, to evolutionary systems biology and paleontology. As a result, we also address what kind of disposition evolvability is in these different contexts, and how these conceptions and disciplinary approaches to such a complex disposition are related. To this end, we first build a philosophical toolkit related to dispositions before deploying it to both make sense of the plurality of evolvability definitions and draw implications for its scientific significance and explanatory value as a dispositional concept. Importantly, our analysis does not provide definitive claims about particular cases of evolvability but rather generates resources for more nuanced interpretations relevant to further empirical and theoretical evaluation.

2 Vocabulary: Building a toolkit for evolvability

In order to analyze evolvability as a disposition, it is useful to build a conceptual toolkit partially based on vocabulary from prior philosophical discussions. While there are different, often non-overlapping bodies of literature within philosophy that reflect on dispositions (such as

metaphysics, philosophy of science, or philosophy of probability), it is possible to identify some core ideas that will be helpful in our analysis (see Choi and Fara 2021 for an overview). To do so we first focus on a different disposition—protein foldability—so that the basic distinctions are laid out in advance of their application to evolvability. Although protein foldability provides sufficient biological details to illustrate the value of most disposition vocabulary (see Box 1), there are limitations to the example as a template that we note in Section 3 before turning to evolvability explicitly.

[Insert Box 1 here]

Foldability is the disposition of a protein to have the relationships between its linearly arranged structural components—amino acids—rearranged (‘folded’) into higher-order, three-dimensional configurations to accomplish cellular functions. Biologists attribute this disposition to proteins because proteins adopt one or more three-dimensional (tertiary) structures or conformations that are typically necessary for the protein to be functional. (These conformations exhibit variation that can be represented with probability distributions.) The process of achieving a three-dimensional structure is sometimes described as spontaneous: “A polypeptide chain of a given amino acid sequence can spontaneously arrange itself into a three-dimensional shape” (Campbell and Reece 2002, 78). This appeal to spontaneity denotes something happening when certain conditions arise. Just as glass shatters upon projectile impact (fragility) or salt dissolves when stirred into water (solubility), a protein has a disposition to fold (foldability) into one or more conformations with functional properties under appropriate *stimulus conditions* in its chemical milieu (e.g., upon entering the endoplasmic reticulum [ER]). The display of a tertiary structure and corresponding function is a *manifestation* of the disposition. Because foldability as the capacity to fold explains the resulting patterns of folded-and-functional proteins (the manifestation), dispositions have an important *explanatory* role in molecular biology. A dispositional property can be ascribed to an individual macromolecule (a *token*) or a class of the

same polypeptides (a *type*). However, predicting how this folding occurs and understanding mechanistically why a specific functional outcome is achieved have been refractory questions. Some of the empirical details making these questions difficult to solve serve to further build a toolkit for talking about dispositions.

Initially, protein folding was understood to result from physical properties of the component amino acid residues in a polypeptide (e.g., hydrophobic residues avoid interaction with surrounding water by segregating to internal regions). These components and their interaction were thought to constitute the *causal basis* of foldability: “the native conformation is determined by the totality of interatomic interactions, and hence by the amino acid sequence, in a given environment” (Anfinsen 1973, 223). Some of the strongest evidence for this came from experiments on the denaturation and refolding of ribonuclease proteins *in vitro*. These experiments suggested that the causal basis was *intrinsic* to the linear polypeptide; that is, the folding of a protein that yields functionality results from the properties of the amino acid residues in the polypeptide and their chemical interactions alone—the polypeptide primary structure contains all of the information required for achieving a three-dimensional conformation. This causal basis provides increased *explanatory depth* (Weslake 2010) in our understanding of protein folding, accounting for both how the process of folding occurs and why one or more functional conformations are regularly achieved and relatively stable.

However, the proteins investigated in these experiments did not fold as rapidly as in their cellular context (a discrepancy in the *rate* of expected manifestation). This suggested that there were relevant *background conditions* (Hüttemann and Kaiser 2018) to consider for protein folding, whether in terms of how foldability was stimulated by particular environmental circumstances or what kinds of causal interactions the amino acid components engaged in. For example, Anfinsen’s group found that folding was faster when the *in vitro* solution contained an enzyme from the ER. Additionally, under *in vitro* conditions, some proteins do not fold

functionally (i.e., the disposition fails to manifest) or do not fold functionally as commonly (i.e., the disposition is only sometimes manifested). This latter question of the frequency of successful manifestation has been described in terms of whether a disposition is *deterministic* (always manifesting under a stimulus condition) or *probabilistic* (manifesting under a stimulus condition with some quantitative frequency). The existence of the “unfolded protein response” (Hetz 2012) in cells points toward foldability as a probabilistic disposition or a *propensity*.

A further complication relates to the assumption that proteins have a single native conformation. Intrinsically disordered proteins (IDPs) highlight that the sequence-structure-function relationship for foldability is not universal; many proteins do not form stable and static three-dimensional configurations, but instead assume a large number of structural conformations over time under different stimulus conditions (Tompa 2010). The same disposition can yield multiple outcomes (i.e., a *multi-track* disposition) and these can be quantified with a probability distribution over the possible manifestations. Most dispositions are probabilistic in nature, manifesting only with a certain probability, but the multi-track foldability of IDPs reminds us that there can be different probabilities of manifesting in particular ways.

These additional issues with the manifestation of foldability prompted detailed studies of the background conditions, which revealed the importance of distinct chaperone proteins that monitor protein folding during *de novo* synthesis, quality control, and the response to stress in the crowded environments of cells. Sometimes chaperones provide a sequestered domain and at other times actively facilitate folding. Even when mutations are introduced that lead to altered amino acid components in a polypeptide, which should prevent achieving a functional conformation, folding can be induced by the overproduction of chaperones (Maisnier-Patin et al. 2005). Depending on how foldability is modeled, this role of chaperones can be understood differently, either as an appropriate background or stimulus conditions or as *extrinsic* components of or contributors to the causal basis of the disposition (Hüttemann and Love 2011).

At a minimum, the causal basis of foldability is more complex and relationally intertwined than previously thought (see below, Section 3.2).

3 Methodological questions: Putting the toolkit to use

This philosophical toolkit for studying dispositional properties orients us to several methodological questions that frame research into evolvability. For example, at what rates and on what time scales does evolvability manifest? Are the contributors to the causal basis of evolvability only intrinsic to the bearer of evolvability? What is being measured when studying evolvability empirically (causal basis, disposition, manifestation, or something else)?

Additionally, further questions not directly addressed in the example of protein foldability must be explored, such as the difference between an individual entity versus an aggregate of entities having a disposition, the quantitative measure and comparison of dispositions, the distinctive behavior of dispositions at different time scales, or the evolutionary transformation of dispositions. We now turn to these and allied questions with special attention to the variety of definitions of evolvability, including understanding why different definitions need not be in conflict and how different construals of evolvability are related.

3.1 Who are the bearers of the dispositional property of evolvability?

In the case of complex dispositions, it is useful to clarify what is the *bearer* of a disposition. For evolvability, the bearer is whatever entity is evolvable and thus possesses the capacity to evolve. Once there is specificity about a particular bearer of evolvability, then we are better positioned to examine the constituents of its causal basis (Section 3.2). In addition to common cases where an *individual* object possesses a disposition, we also need to consider that an *aggregate* of individual objects also can have a dispositional property (which also matters for protein

foldability; Invernizzi et al. 2012). Both options appear in scientific definitions of evolvability. When evolvability is interpreted as a population-level capacity, it is an aggregate of individual organisms that bear the disposition: “the ability of a *population* to respond to selection” (Flatt 2005, 306; see also Wagner 2014). In contrast, the bearer of evolvability appears to be an individual object if the disposition is construed as a property of an organism: “evolvability is an *organism’s* capacity to generate heritable phenotypic variation” (Kirschner and Gerhart 1998, 8420; see also Yang 2001). For accounts that focus on the evolvability of a species or a higher taxon (Hopkins 2011; McGuire and Davis 2014), both options are utilized: sometimes a lineage is conceptualized as an individual (an entity persisting as the same thing across time even while its constituent parts change; Rieppel 2007), and sometimes as an aggregate of organisms that compose an evolvable taxon.

How should we interpret these divergent viewpoints about what possesses evolvability? One possibility is to adopt a more abstract definition, such as by understanding evolvability as “the ability of a *biological system* to produce phenotypic variation” (Payne and Wagner 2019, 24). A ‘biological system’ could be an individual (an *organism* is a biological system) or an aggregate of individuals, including a whole population of conspecific organisms or an interacting microbial system consisting of individuals from various species. However, it is practically necessary for many scientific investigations to have an account that more concretely specifies the bearer of evolvability. In population and quantitative genetics, it is typically populations of individuals (or their traits) that are assumed to be the units of evolutionary change: populations (as aggregates) possess evolvability in the sense of having the ability to respond to selection. In evo-devo, the focus is on how the configuration of development for organisms from a certain taxon biases phenotypic evolution. In such a context, evolvability is conceptualized as a property of organisms in the sense of the ability to generate functional phenotypic variants. These different definitions of evolvability need not be in conflict, but can refer to different aspects of the

evolutionary process or be useful tools that have appropriate uses in the context of different approaches.

At the same time, the notion that an organism would be evolvable appears misguided; only a population or lineage of individuals evolves, not an organism. This issue can be resolved by making use of the toolkit distinction between types and tokens. While one token organism cannot evolve, a type or kind of organism exemplified in a population of individuals can undergo evolutionary change. This type or kind is representative, sometimes only implicitly, of a population or aggregated unit. Thus, the above definitions that talk about an organism's evolvability can be read as referring to a *type* of organism, such as organisms from a particular species or exhibiting shared constellations of traits. Likewise, when a developmental system is seen as the bearer of evolvability—"evolvability, the capacity of a *developmental system* to evolve" (Hendrikse et al. 2007, 394)—it is not a token developmental system of one individual organism, but the type of developmental system that is evolvable (Nuño de la Rosa and Villegas 2019).¹ An analogous bearer of evolvability is the genotype-phenotype map: "evolvability as a property of the *genotype-phenotype map* (the genetic system) and not as a population property" (Hansen 2006, 129). As noted above, another prominent bearer of evolvability is a *trait*, given that phenotypic traits (Opedal et al. 2017; Roseman et al. 2010) or characters (Wagner and Altenberg 1996) are evolvable. Traits on quite different levels of organization can exhibit evolvability, from molecular traits (e.g., protein domains and transcription factor binding sites) to physiological traits (e.g., metabolic rates and immune responses), from complex morphological traits (e.g., insect wings and vertebrate limbs) to life-history traits (e.g., size at maturity and clutch size).

Although there are a variety of relevant bearers of evolvability that different interpretations concentrate on, it is also the case that there are connections between these interpretations. The same researcher may offer both a generic or abstract and a specific or concrete characterization

of evolvability, and then use them for distinct purposes. For instance, from the perspective of quantitative genetics, Houle (1992) construes evolvability generally as “the ability of a *population* to respond to natural or artificial selection” (195), while also laying out a quantitative measure for the evolvability of a specific *phenotypic trait* (in terms of the trait’s additive genetic variance). This permits a comparison of the abilities of different traits within the same population to respond to selection. A specific definition focusing on traits also facilitates comparisons of the same trait in different populations, especially if construed as a trait-type; a generic definition only stating that evolvability is a capacity of a population would not accomplish this. Interrelations of these kinds between conceptions of evolvability applied to diverse bearers appear commonly for different research questions.

3.2 What is the causal basis of evolvability?

Once the particular bearer of evolvability is in view (whether it be traits, organisms, populations, or taxa), a natural subsequent concern is to understand the disposition’s causal basis—what makes a particular bearer (token or type) evolvable. For example, Wagner and Altenberg (1996) focus on the evolvability of characters and argue that what accounts for this evolvability (i.e., the disposition’s causal basis) is the structure of the genotype-phenotype map: “The genotype-phenotype map *determines the variability of characters*” (967). This structure governs the way in which random genetic mutation translates into non-random, structured, and possibly adaptive phenotypic variation for characters exhibited by particular types of organismal systems (Nuño de la Rosa and Villegas 2019). Many accounts point to the genotype-phenotype map and similar features of development underlying the variational properties of phenotypes as the *causal basis* of evolvability: “evolvability ... is largely *a function of the developmental system’s ability to generate variation*” (Hendrikse et al. 2007, 394).

As noted (Section 3.1), the genotype-phenotype map can itself be the *bearer of*

evolvability. This holds for accounts that focus on how the genotype-phenotype map as an entity evolves or can evolve, including discussions of whether a particular genotype-phenotype map is an adaptation (Pavlicev and Hansen 2011). This is a reminder of the value of the philosophical toolkit. What is a *bearer* in one analysis of evolvability can be a *causal basis* in another analysis. It is crucial to be explicit about whether a feature, such as the genotype-phenotype map, is considered to be the disposition's bearer (the entity possessing the capacity to evolve) or the causal basis (of some other bearer of evolvability). Keeping this in view can both facilitate the identification of possible ambiguities in how researchers are using evolvability and patterns of connection across different interpretations. For example, Hansen (2006) claims that he "follow[s] Wagner & Altenberg (1996) in defining evolvability as *a property of the genotype-phenotype map (the genetic system) and not as a population property*" (129). Although this appears to assert that the genotype-phenotype map (and not a population) is the disposition's bearer, Hansen also states that the genotype-phenotype map "*determines the variational properties of the phenotype*" (123). The latter suggests that the genotype-phenotype map is the causal basis, while the phenotype is the bearer (which aligns with our earlier reconstruction of Wagner and Altenberg 1996). More generally, equivocal statements like 'evolvability is a property of X' could be intended either as 'evolvability is a capacity of X' (which refers to the *bearer* X) or as 'evolvability is a function of X' (which refers to the *causal basis* X; see the above quote from Hendrikse Hendrikse et al. 2007). In addition to clarifying this potential ambiguity, researchers also may notice that these ambiguities serve as reminders of key nodes of research: the genotype-phenotype map needs to be investigated both as a bearer of and the causal basis for evolvability.

Focusing on the genotype-phenotype map as the causal basis of evolvability tends to accent features *internal* to organisms: "The evolvability of an organism is its *intrinsic* capacity for evolutionary change. ... It is a function of the range of phenotypic variation the genetic and developmental architecture of the organism can generate" (Yang 2001, 59). These internal

properties of the genotype-phenotype map or particular developmental mechanisms that contribute to its structure can then be examined in more detail, such as how modularity is conducive to evolvability (Kirschner and Gerhart 1998; Pavlicev and Hansen 2011; Wagner and Altenberg 1996). Additionally, we can ask whether evolvability is always an intrinsic capacity. Our formulation of the toolkit using protein foldability raised the possibility that biological dispositions can have an *extrinsic* causal basis in the sense that some features external to the bearer are relevant to the disposition being present (Hüttemann and Kaiser 2018; Love 2003). A protein's foldability is not always due to its internal amino acid sequence, but can depend on the presence of chaperones.² If so, such external factors are not just stimulus conditions that can trigger the disposition (e.g., directional selection in the case of evolvability) or mere background conditions (e.g., conditions on Earth making life itself possible), but would need to be included in models of the disposition's nature (see Box 1).

In the case of evolvability, the distinction between internal and external is ultimately a matter of theoretical perspective; there is a methodological choice about whether to investigate some factors external to an evolvable entity because they impact evolvability or relegate them to the background conditions under which evolvability takes place. Consider several scenarios where evolvability may not be an intrinsic disposition, but also can be seen as contingent on external factors. If the focus is on a phenotypic trait's evolvability, then it may be the case that extrinsic features compose at least part of the causal basis of this trait's evolvability, such as pleiotropic relations to other traits or the frequency of the trait within the whole population. For example, in species of tiger salamanders, some changes in morphological traits are caused in part by increased body size variation within a larval population (Whiteman et al. 2003). In these kinds of cases, evolvability could hinge—at least to some degree—on features beyond the genetic and developmental basis underlying the phenotypic character in an individual since the source of variation in body size for the population that impacts a morphological trait's capacity

to evolve could derive from environmental factors, such as spatial heterogeneity in nutritional availability.

Regarding other bearers of evolvability, there are a variety of considerations that point to an extrinsic basis, including interactions with entities in the environment that have an impact on a population's or taxon's evolvability (Love 2003; Sterelny 2011). From a paleontological perspective, species and higher taxa can exhibit evolvability by having lower extinction rates and by possessing the ability to undergo adaptive radiation and diversify. A taxon's extinction rate also can depend on its geographic range (Jablonski 1987), but this is not primarily an intrinsic, internal property of the organisms making up a population or taxon because it can include landscape topography or the ecological diversity across the range (Love 2003). In cases of ecosystem engineering, a taxon's ability to undergo radiation and diversification is dependent on transformed ecological conditions, where the resulting ecological feedback can yield self-propagating radiations (Erwin 2012). A classical example is the radiation of mammals due to empty niches left by the extinction of non-avian dinosaurs (Alroy 1999). Such ecological conditions, consisting in abiotic conditions as well as interactions with other taxa, would causally contribute to the basis of a taxon's evolvability relationally or extrinsically.

Methodologies within evo-devo make it natural to view evolvability as a disposition with an intrinsic basis, where evolvability resides within an organism, whose developmental architecture yields its ability to generate phenotypic variation. At the same time, phenotypic plasticity—which arises from an *interaction* between the organism and its environment—is nowadays understood to be relevant for biasing phenotypic variation and the generation of novelty (Kavanagh 2020; Levis and Pfennig 2020; Parsons et al. 2020; West-Eberhard 2003). However, phenotypic plasticity can still be seen as an endogenous capacity of the organism if one takes the criterion of only considering evolutionary products as the causal basis for variability and evolvability. The environmental factors relevant to an organism's plastic response might then be

interpreted as the stimulus conditions of evolvability as an intrinsic disposition.

But niche construction and symbiosis, as further eco-devo notions relevant to the generation of novelty, are more difficult to fit into an ‘intrinsicity’ framework than phenotypic plasticity. Symbiosis has contributed to the origin of multicellularity as a major transition, as well as to the origin—in fact multiple origins—of herbivory (Gilbert 2020). In niche construction, organisms not only encounter a given environment to which they adapt, but their physiological and behavioral activities modify the environment in an adaptive fashion, resulting in feedback loops and organism-environment coevolution (Clark et al. 2020; Scott-Phillips et al. 2014). Examples include the evolution of lactose intolerance in humans influencing the rate and direction of evolution (Scott-Phillips et al. 2014) and horned dung beetle larvae manipulating the surrounding dung, which influences morphological development, sexual dimorphism, and life history (Schwab et al. 2016). In both symbiosis and niche construction, ecological interactions between the organism and some of the biotic or abiotic entities in its environment have undergone adaptive evolution and increased the evolvability of organisms in the lineage. Such ongoing evolutionary interactions transform features internal as well as external to organisms, exhibiting an iterative dynamics between ‘internalization’ of environmental factors and ‘externalization’ of an organism’s internal structures (Laubichler and Renn 2015).

In quantitative genetics, where the focus is often on the capacity of a population to respond to selection, a core aspect of evolvability is the additive genetic variance within the population (see also Chapters 10 and 13). One common quantitative measure of a phenotype’s evolvability is $I_A = V_A / \bar{X}^2$, where V_A is the phenotype’s additive genetic variance (the amount of the phenotype’s variance that is due to additive genetic variation) and \bar{X} is the phenotype’s mean value within the population (Houle 1992). The V_A for a phenotypic trait in a single population (with a fixed genetic composition) can change when the environment changes, just as the property of heritability is environment-dependent (Rice 2012). Such an environmental

dependency can arise in cases of phenotypic plasticity where a phenotype's value changes together with the environment, which then can change the population's phenotypic variation. For the same reason, the phenotype's mean value \bar{X} across the population can be subject to change when the environment changes—without the population and its genetic composition changing. Therefore, the evolvability $I_A = V_A / \bar{X}^2$ for a trait in a given population can be different if this population is in two different environments (see also Section 7 in Chapter 13). This suggests that evolvability (as construed in quantitative genetics) is not solely an intrinsic property of a population, but is also dependent on the population's environment; the disposition of evolvability's causal basis is partly extrinsic.

An overarching lesson that emerges from these considerations of why or when evolvability might have an extrinsic, relational causal basis is that these judgments depend on the specific definition of evolvability being used. If a definition does not just concern the production of phenotypic variation, but also includes that the phenotypic variation has to be *adaptive* (Payne and Wagner 2019), then the external context of individual organisms or populations of organisms is implicated because a trait's adaptiveness depends on the environment. In a similar vein, the relevant causal basis also varies depending on the bearer of evolvability. For example, population size is an intrinsic factor for the ability of a *population* to respond to selection, but population size is obviously external to an *organism's morphological structure* which forms the core of evo-devo models of evolvability. If the bearer possessing evolvability is not an organism with its developmental structure, but rather is understood as a larger biological system (which contains organism-environment interactions), then this system exhibiting evolvability would also be the complete causal basis, rendering the disposition intrinsic (Nuño de la Rosa and Villegas 2019).

Because of these different possible methodological choices and explanatory strategies, it may be preferable to talk in terms of *causal contributors to evolvability*, rather than one unique

causal basis. This explicitly acknowledges the diversity of individual causal factors involved: from the internal properties of individuals (e.g., the genotype-phenotype map and developmental architecture) to population-level features (e.g., genetic variance), from aspects of the abiotic or biotic environment of the individuals composing a population to organism-environment interactions. Which of these causal contributors are actively investigated with respect to evolvability is a *methodological* choice. Some biologists may consider environmental features as a causal background condition and focus on the genotype-phenotype maps of different taxa as the primary driver of evolvability; others will incorporate environmental or extrinsic features into an explanatory framework for particular instances of evolvability; and yet others will take some environmental factors as stimulus conditions that manifest evolvability, such as a particular selective regime. Cases where capacities for niche construction or ecosystem engineering might enhance evolvability suggest that organism-environment reciprocal interactions need to be modeled. In some situations, examining specific causal contributors (while relegating others as background conditions) may be a standard methodological preference adopted by some research groups; in other cases, an adjudication of what contributors must be included to yield an adequate explanation of a specific instance of evolvability may be required (Baedke et al. 2020).

3.3 How does evolvability manifest?

Given this plurality of bearers and causal contributors, what characterizes evolvability as a distinct property? Dispositions are defined by their manifestation—and sometimes their stimulus conditions too—regardless of the variety of possible causal mechanisms that bring about this manifestation. For example, fragility is individualized as a disposition by a breaking behavior under certain conditions (such as being hit), despite the many, distinct molecular compositions that can be the causal basis of fragility. Therefore, even if evolvability can be instantiated by many diverse causal contributors in different contexts, it is a single dispositional property

because it is defined by a manifestation: evolving in a particular way. Importantly, many if not all living systems are trivially evolvable or have been in their evolutionary history; every broken object was trivially breakable in the first place. However, when fragility is invoked, the aim is to specify a tendency of certain objects to break *compared to others* (i.e., non-fragile items). The same is true for evolvability: evolvability is invoked to specify that some living systems (or configurations thereof) tend to evolve more readily than others (e.g., to diverge more or to evolve at a higher rate). These comparisons might include “vertical” contrasts with the ancestors of those systems or “horizontal” contrasts with other lineages. This is a restricted, comparative sense of evolvability that is distinct from the less informative and quasi-universal capacity to evolve (Love 2003).

Thus, in order to make sense of a comparative notion of evolvability in a specific context, it is crucial to specify the *kind* of evolutionary manifestation in view. Different definitions of evolvability focus on different possible manifestations. For example, if evolvability is defined as “the ability of a population to respond to selection” (Houle 1992), then this property will be manifested in a particular directional pattern of variation in the population across a certain number of generations under a selective regime, where that selection regime can be considered as the stimulus condition. If evolvability is understood as the ability to generate *new* phenotypic variants (Wagner 2005), then it will be expressed in the form of novelties or morphological disparity. In these cases, mutations are typically considered to be the stimulus conditions. If evolvability is conceived as the capacity to provide *adaptive* phenotypic variation (Payne and Wagner 2019), it will manifest in the alignment of new variants with the direction of selection, which contrasts with definitions focused on the production of heritable phenotypic variation without reference to its adaptive value. The meaning of ‘new’, ‘adaptive’ or ‘diverse’ needs to be specified in each context in order for these manifestations of evolvability to be defined

precisely.³ For example, a character can be considered new if it is not homologous to the ancestral character or provides novel potential for future variation (Brigandt and Love 2012).

It is not only the *type* of evolutionary change (adaptive, new, diverse, etc.) that must be specified; in addition, an appropriate *timescale* needs to be chosen. The complexities mentioned so far should make it obvious there is not one unique, privileged timescale for evolvability. Instead, different approaches will choose a timescale that is relevant to their methodological perspective and research question, while ensuring that the timescale used to measure the stimulus condition (e.g., the period during which an average selection differential obtains) matches the timescale for the ensuing manifestation of a population's or taxon's evolvability. Theoretical models and field studies in quantitative genetics will typically choose shorter timescales than paleontological investigations. An important question in this vicinity is the extent to which results from microevolutionary timescales can be projected to mesoevolutionary or macroevolutionary scales; much of the information available for current populations, such as the genetic basis of variation or selective pressures, is inaccessible for evolution on longer timescales (see also Chapter 17). Limitations to or caution about such projectability justify the need to use more than one timescale in evolvability studies, especially given that different approaches also might focus on a different kind of evolvability, such as a population's evolvability in terms of changes in a phenotypic trait as opposed to a taxon's evolvability in terms of differential phylogenetic branching and extinction rates.

Once a suitable kind and timescale for the manifestation of the disposition to evolve is specified, it becomes more meaningful to talk about biological systems being more or less evolvable and, importantly, some systems being more evolvable than others. In this sense, evolvability is a graded disposition, manifesting with different strengths in different systems, which in turn can show a capacity to evolve *more often* or at a *higher rate* than others. In order to make such claims in a precise manner, however, there must be a way to measure evolvability

(Chapter 10). The dispositions of particular *tokens* are not directly measurable simply because, by definition, capacities as such are not observable properties. However, one can measure a disposition's strength by other means. One straightforward way to do this is by measuring rates of manifestation in aggregates or *types*. Mutation rates, rates of short-term response to selection, or long-term morphological disparity may serve as a proxy for the evolvability of some biological systems. For example, Landry et al. (2007) measured mutation rates in gene networks and suggested this can be a good estimate of the evolvability of gene expression under no selection. However, since evolvability is not always manifested, this approach has limitations. A population can be very evolvable and yet fail to evolve because it has not experienced the appropriate stimulus conditions or encountered interfering factors, just like a potentially fit phenotype can fail to spread and reach fixation in a population due to genetic drift. A different way to measure evolvability indirectly is by measuring one or more of its corresponding causal contributors. This offers a basis for comparative claims in terms of the same properties constituting a causal basis for evolvability in different biological systems. For example, one trait of a population might have a higher evolvability *than* another trait in the same population (because it has more underlying additive genetic variation), or one taxon can be more evolvable with respect to a trait *than* another taxon because its developmental architecture permits the generation of more morphological variation in a specific direction.

This line of reasoning brings us to another distinction from the philosophical toolkit: deterministic versus probabilistic dispositions (or propensities). Although some dispositions always exhibit their characteristic manifestation whenever the stimulus conditions obtain, there are cases where the manifestation occurs with a certain probability. An atom's radioactive decay is probabilistic just like biological fitness, understood as the capacity of an organism to survive and reproduce. Evolvability is a probabilistic disposition (Brown 2013; Nuño de la Rosa and Villegas 2019) because there is rarely a single, determined effect that will necessarily follow

when it manifests. Instead, changes in selective pressures or genotypic alterations, as triggers of evolvability, can bring about a range of different results. Evolvability then manifests probabilistically, meaning that it tends towards a particular manifestation only with a certain probability (or probability distribution).

Probabilities are generally preferred to measure propensities in science (Cartwright 1989). The propensity of a coin to land heads is manifested in a balanced pattern: a probability of 0.5 for heads and 0.5 for tails. This manifestation is an abstract behavior (represented by a mathematical property), which contrasts with the particular effects of a specific coin when it is actually tossed. Similarly, in the case of evolvability we may define its manifestation as a probabilistic pattern of possible evolutionary trajectories, measured in probabilities. This brings us to a related idea from our toolbox: evolvability as a *multi-track* disposition. Consider evolvability in an RNA model with a genotype-phenotype map that relates primary RNA sequences to their folded secondary structure. In this type of model, evolvability can be measured as the probability of a point mutation yielding one among several possible novel secondary structures (Nuño de la Rosa and Villegas 2019). Each of those possible secondary structures is a different possibility—the secondary structures are different *tracks* that can be followed in the manifestation of evolvability. The same is seen in the evolvability of a phenotypic trait. When starting out with one phenotypic trait (or one of its underlying genotypes), a sequence of genetic changes can lead to several possible new phenotypes, each with an associated probability. Due to the architecture of the genotype-phenotype map, different phenotypes will have different likelihoods of arising from a particular phenotypic starting point, which can be captured by a *probability distribution* across outcome phenotypes, i.e., multiple tracks (Stadler et al. 2001).

One primary reason why evolvability is probabilistic and multi-track derives from evolutionary events being subject to stochasticity. Whether a new phenotype will occur or how

common it will be in a population is, at least in part, a matter of chance with respect to a variety of processes: sexual reproduction, population composition, mutational events, developmental noise, and environmental fluctuation. However, stochasticity is not the only reason for the probabilistic nature of evolvability. Evolvability studies reflect the interest of researchers in possible evolutionary trajectories, not merely those actually manifested. In conceiving of possible evolutionary changes that the evolvability of a system can bring about under different scenarios, researchers sometimes use coarse-grained descriptions that allow for different realizations. For example, if we are interested in the mean change of a quantitative trait in a population, we are not only concerned with the probability of a change from value z_1 to value z_2 . Rather, we are typically interested in a probability distribution for an array of possible changes in value for that trait. This is especially pertinent for the manifestation of evolvability on longer timescales that refer to very general patterns, which highlights the role of *contingency* and chance in evolution (Blount et al. 2018).

Philosophers have typically assumed that the stimulus conditions and manifestation of a disposition are one-time *events*. In the case of glass having the disposition to break, the stimulus condition of being hit by an object and the manifestation of breaking are events with a short and well-demarked duration. Only recently have some philosophers come to appreciate that, at least in the case of biological dispositions, the stimulus conditions or manifestation may be an *ongoing process* (Hüttemann and Kaiser 2018). This conceptual point is relevant for evolvability. The stimulus conditions for evolvability may be the occurrence of natural selection or some other ecological conditions, such as extinction events or factors producing random drift. Even if discrete changes in selective pressures trigger changes in the manifestation of evolvability for traits, neither selection nor the response of biological systems to it are time-point events; instead, they are best understood as ecological conditions or processes extended over longer durations of time. As a result, evolvability becomes a moving target. Not only are the stimulus conditions and

manifestation of the disposition processes without a fixed termination point. In addition, the biological system itself undergoes modifications as evolvability manifests, which may also entail a change in the system's evolvability (e.g., through modifications of one or more causal contributors). In this kind of circumstance, the original disposition has undergone modification before its manifestation could terminate. The evolutionary alteration of gene regulatory networks might reduce pleiotropy and thereby increase evolvability—the activation of a system's evolvability can result in increases to its longer-term evolvability.

4 Implications: Why is the disposition of evolvability useful?

Having surveyed how the philosophical toolkit related to dispositions applies to different aspects of evolvability, a natural question is how the dispositional character of evolvability matters for ongoing biological inquiry. For example, various efforts are dedicated to quantitatively measuring and representing evolvability (e.g., using G-matrices and M-matrices, or genotype networks) in order to make accurate evolutionary *predictions*. Since evolvability is not merely a property of one particular population, it is desirable to establish *generalizations* across populations and taxa. In addition to the scientific aims of predicting some outcome under natural circumstances or generalizing conclusions from isolated investigations, evolvability is also useful for the purpose of *control* or intervention on natural systems, including breeding and conservation efforts or for protein engineering (see Chapter 4).

Knowing about evolvability permits one to manipulate natural systems because evolvability is a *causal* capacity. In general, dispositions are scientifically important because they embody causal potency—they bring about their manifestations (Austin 2017). This points to their *explanatory* role because a disposition explains the occurrence of its characteristic manifestation. In addition to documenting phenotypic variation, a primary aim of evolutionary biology is to understand the very *ability* to produce variation, exhibit evolutionary transformation, and yield

phylogenetic diversification, precisely because evolvability explains these evolutionary outcomes of interest. The same is true for other dispositions in evolutionary biology (Austin and Nuño de la Rosa 2021). *Phenotypic plasticity* (as the capacity to generate several phenotypes) explains the possibility of various phenotypes resulting from one genotype, as well as why a particular phenotype resulted from particular environmental circumstances. *Developmental robustness* explains why a functional phenotype was maintained despite environmental or genetic perturbations during ontogeny. Likewise, *phenotypic variability* accounts for the generation of a distribution of variant phenotypes and *modularity* is the basis for the capacity of different organismal characters to vary quasi-independently of each other, which is instrumental to explain the possibility of ongoing adaptation. However, *evolvability* may be distinctive as a disposition. For example, plasticity, organismal robustness to environmental perturbation, and phenotypic variability primarily pertain to short-term effects, whereas evolvability also captures long-term evolutionary potential, thereby accounting for change and innovation across longer timescales.

One of the most important features of evolvability as a disposition is that it does not just explain one characteristic manifestation or the *actual* evolutionary outcome observed. Instead, the disposition of evolvability has *explanatory depth* because a biological system's evolvability explains a whole *range of possible manifestations* under different potential stimulus conditions. This can be seen in quantitative genetics where evolvability is understood as the ability of a population to respond to selection by means of phenotypic change. The stimulus condition of primary interest is the strength of selection acting on traits, and the manifestation is a change in the population's (mean) phenotypes. In the case of several phenotypic traits, evolvability can be captured by the additive genetic variances of traits and the additive genetic covariances between different traits (Hansen 2016). This permits a prediction of how these phenotypic traits would change in each *possible* scenario if a particular degree of selection were to act on these traits.

This approach not only observes one particular pattern of within-population phenotypic change in order to infer the selection pressure that obtained (based on the population's additive genetic variance), but it also aims to predict the phenotypic change that would result from any of *many different* possible selection pressures. This type of prediction is useful for anticipating the effectiveness of a potential breeding strategy or ecological intervention (among other things). As a consequence of a population's evolvability (including trait covariances and different amounts of additive genetic variances for different traits), the phenotypic response may well deviate from the direction of selection (Hansen 2016). Unlike simply documenting actual phenotypic variation, this type of study of a disposition facilitates an understanding of how a population would respond to various possible situations.

In a similar vein, paleontologists may try to understand a range of possible evolutionary trajectories in addition to explaining a particular trajectory of morphological change seen in the fossil record. Would a larger or different range of outcomes have been possible from an ancestral starting point? Would a particular evolutionary outcome known from the fossil record be likely to reoccur if evolution restarted from this ancestral point? Evolvability—as the capacity of taxa to generate specific patterns of morphological transformation and diversification—can account for the possibility or difficulty of obtaining alternative outcomes. Paleontological research also can employ computer simulations to investigate these types of scenarios. For example, although extinction events have a destructive effect in the short run, one may explore whether it is possible (and under which conditions it is possible) for extinctions to accelerate evolution *in the long run*. Prior extinction events might have selected for taxa that can rapidly occupy vacated niches; these taxa have a high evolvability with respect to future extinction events as a possible stimulus condition of macro-evolvability (Lehman and Miikkulainen 2015). Studies of evolutionary novelty (including in evo-devo) may have one particular morphological transition in view, such as the origin of the nervous system. Considered from the vantage point of

evolvability, this morphological transition can be investigated more broadly with respect to the range of possible evolutionary outcomes under different stimulus conditions in light of assumed developmental contributors to the causal basis.

A recurring research task for evolutionary biologists is to understand how *evolvability itself evolves* (Draghi and Wagner 2008; Wagner and Altenberg 1996). Yet the question of the evolution of capacities has been absent from the classical philosophical literature on dispositions. Here we encounter a seeming puzzle given the dispositional nature of evolvability. Selection can act on actual variation, but not the potential for variation: “the basic problem with the evolution of evolvability is that selection cannot act on potentials or *abilities* – only on results.” (Watson 2021, 143). Once again, the philosophical toolkit suggests a way to get traction on this puzzle (see Box 1). Selection acts on the *manifestations* of the evolvability disposition (resulting in evolutionary change), but this does not amount to selection operating on the disposition itself. Importantly, selection can also act on the *causal basis* of the disposition to evolve. One relevant causal contributor to evolvability is the genetic architecture of organisms (Hansen 2006) and the structure of organismal development (Kirschner and Gerhart 2005). Genetic architecture and developmental mechanisms are not just potentialities, but concrete traits on which natural selection can act. As a result, even though selection does not act directly on a disposition, the evolution of the disposition to evolve can be understood in terms of selection on one or more contributors to evolvability’s causal basis; modifications of the phenotype-genotype map, or the mechanisms it represents, can result in substantial evolutionary changes in evolvability. This is another important aspect where the dispositional nature of evolvability matters: it serves to clarify distinct ways in which it could evolve by pointing to its relevant causal basis, its manifestation, etc. Nonetheless, evolvability is a *multiply realizable* disposition insofar as it can be enabled by different mechanisms. The explanatory relevance of evolvability is not effaced

once we uncover its causal basis.

Another apparent challenge that we encountered above is the presence of various definitions of evolvability. In fact, there need not be a single evolvability disposition; instead, different scientific fields can focus legitimately on different concrete dispositions. For example, the evolvability of a population in terms of changes in phenotypic traits can be a different disposition from the evolvability of a taxon in terms of taxonomic diversification. Our toolkit helps clarify that there are different kinds of evolvability and the corresponding dispositions can be subject to distinct investigative projects. Most importantly, in the face of definitional diversity, the philosophical toolkit illustrates that different definitions can be legitimate and need not be in competition. For instance, the bearer of a disposition can be an individual or an aggregate. Correspondingly, the capacity to generate novel morphological variation may be a property of an organism or a developmental system, but evolvability as the ability to respond to selection is a property of a population or aggregate of individuals. We also distinguished between the disposition, its manifestation, and the disposition's causal basis. One reason why these distinctions matter is that how evolvability is defined—e.g., simply in terms of generating variation or more specifically in terms of adaptive variation—has implications for what is the corresponding manifestation and causal basis. Adopting a particular definition of evolvability or deciding on a specific bearer of evolvability is a methodological choice; once this choice is explicitly recognized, then it increases clarity about the relevant manifestation and causal basis.

An additional reason why these distinctions are useful is that different scientific activities can target different aspects of a disposition (see also Chapter 4). *Predicting* the outcome of evolvability concerns its manifestation (as does *intervening* into populations and ecosystems to effect some desired outcome), whereas *explaining* evolvability is about understanding the disposition's causal basis, an investigative context where developmental mechanisms are

relevant, even if this does not suffice for the endeavor of making predictions for specific populations.

Although different definitions of evolvability may not be reducible to one another and different fields may focus on different kinds of evolvability, there still can be systematic relations between them that are the subject of investigation. For example, individual organisms (as the bearer on some definitions) have the disposition to generate adaptive variation, which in turn forms the causal basis for the evolvability of populations (the focus of other definitions). One can likewise reveal connections between different approaches to investigating evolvability. To the extent that the same kind of evolvability requires investigation from different perspectives because it is a complex phenomenon, studies of evolvability in evolutionary biology demand *interdisciplinary collaboration*. One biological field may address specific aspects of a disposition, such as paleontology elucidating phylogenetic patterns of diversification (the manifestation of taxon evolvability) or attempt to understand the ecological and biogeographical conditions that (as part of the causal basis) enabled high rates of diversification and reduced rates of extinction. One field might concentrate on the manifestation (or the disposition), while another is needed to uncover aspects of the causal basis. A case in point is when quantitative genetics measures realized phenotypic variation and additive genetic variation, whereas *evo-devo* seeks to characterize the developmental architecture of organisms that constitutes key aspects of the causal basis of evolvability. Insofar as different approaches investigate different aspects of evolvability, there are connections among such approaches that structure interdisciplinary collaboration (see also Chapter 4). Because evolvability occurs on multiple timescales and is exhibited by entities on different levels of organization, contributions from different biological fields are needed to dissect its multifaceted complexity. And, given the diversity of causal contributors to evolvability—from the internal constitution of organisms to

organism-environment interactions and various ecological conditions—an interdisciplinary strategy seems most appropriate for understanding it. Keeping in view that evolvability is a disposition and utilizing the resources of the philosophical toolkit described herein are critical to accomplishing this task.

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Notes

1. The type-token distinction also matters for population and taxon-level perspectives because, in addition to attributing evolvability to a specific token population, it also makes sense to talk

about the evolvability of types of population (e.g., sexual as opposed to asexual populations or taxa).

2. The features and behavior of biological entities are often context-dependent. For instance, the existence of a functional gene can depend on external factors such as its genomic or regulatory context (Brigandt 2017). Likewise, the ‘stemness’ (a dispositional property) of a cell can depend on the cell being situated in an appropriate stem cell “niche” (Laplane and Solary 2019).

3. This reveals an analogy to protein foldability as a disposition. Rather than understanding ‘foldability’ as the generation of any tertiary structure, one might require that foldability involves the production of a *functional* protein.

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Box 1**Philosophical vocabulary for dispositions**

Background conditions: the wider set of circumstances instantiated when a disposition is manifested that may or may not be relevant (e.g., temperature or humidity of the room where salt is being stirred into water).

Bearer: the entity that has a disposition or exhibits a dispositional property. This can be an individual or an aggregate and considered as either a token or a type (i.e., a single token individual or a class of similar individuals; a single population of entities or a class of similar populations of entities).

Causal Basis: the underlying properties that contribute to the capacity (e.g., the molecular structure of salt crystals).

Disposition or Dispositional Property: the capacity itself (e.g., solubility, fragility, foldability, or evolvability).

Explanatory depth: the aim of an account of a disposition that demonstrates how the causal basis contributes to the process of disposition manifestation, why a particular manifestation is regularly achieved and relatively stable, or what the effects of various possible stimulus conditions would be.

Intrinsic/Extrinsic: whether or not a dispositional property is constituted or has its causal basis “internally” (e.g., parts and their interactions) or whether “external” features (e.g., environmental elements) also contribute to the capacity.

Manifestation: the actual display of the disposition (e.g., the glass breaking or the protein folding correctly), which might vary in rate (slower or faster), intensity (“strength”), or number (multi-track dispositions, such as different “correct” conformations of an IDP).

Probabilistic/Deterministic: whether or not a disposition manifests always (deterministically) or only some of the time (probabilistically) under the appropriate stimulus conditions.

Single-track/Multi-track: whether for given stimulus conditions a disposition has a single outcome (manifestation) or more than one (where a probability distribution can be assigned to sets of outcomes).

Stimulus Conditions: the environmental circumstances under which the disposition is manifested (e.g., stirring salt into water).

Token/type: dispositions can be ascribed to single entities (tokens) or classes of similar entities (types).