What Evolvability Really Is

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ABSTRACT

In recent years, the concept of evolvability has been gaining in prominence both within evolutionary developmental biology (evo-devo) and the broader field of evolutionary biology. Despite this, there remains considerable disagreement about what evolvability is. This article offers a solution to this problem. I argue that, in focusing too closely on the role played by evolvability as an explanandum in evo-devo, existing philosophical attempts to clarify the evolvability concept have been overly narrow. Within evolutionary biology more broadly, evolvability offers a robust explanation for the evolutionary trajectories of populations. Evolvability is an abstract, robust, dispositional property of populations, which captures the joint causal influence of their internal features on the outcomes of evolution (as opposed to the causal influence of selection, which is often characterized as external). When considering the nature of the physical basis of this disposition, it becomes clear that the many existing definitions of evolvability at play within evo-devo should be understood as capturing only aspects of a much broader phenomenon.

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1 Introduction

Over the past twenty years, there has been increasing interest in ‘evolvability’ from within evolutionary biology and evo-devo more specifically (Kirschner and Gerhart [1998], [2006]; Pigliucci [2008]; Brookfield [2009]). Despite its growing role in science, there remains significant confusion surrounding what is meant by evolvability.

The prevailing philosophical response to this lack of conceptual clarity can be seen in the work of Massimo Pigliucci ([2008]), John Brookfield ([2001], [2009]), and Alan Love ([2003]). Their proposed accounts of evolvability are best thought of as ‘cluster concept’ approaches. According to Pigliucci ([2008]), Brookfield ([2001], [2009]), and Love ([2003]), the conceptual difficulties surrounding evolvability are the consequence of the term being used to refer to multiple distinct, but overlapping, phenomena related to the supply of variation, rather than any unified kind. Given this, they argue, to tidy-up evolvability we must carve it up into a number of distinct named concepts.

This cluster concept approach stands in contrast to work by Kim Sterelny ([2007]) who argues for a unified evolvability concept. According to Sterelny ([2007]), evolvability refers to the differing ‘evolutionary potential’ of lineages. Rather than being solely related to the supply of variation to selection, evolvability is the much broader dispositional property of lineages to evolve complex adaptation. In contrast to the cluster concept view, Sterelny’s ([2007]) account provides us with the advantage of leaving open the possibility of a ‘common currency’ for dealing with evolvability questions (though the exact nature of that currency is not clarified).

In this article I offer a new approach to evolvability, which is inspired by Sterelny ([2007]). The unified concept of evolvability I present herein is driven by the theoretical role played by the term. Explaining or accounting for evolvability is the defining research program in evo-devo (Hendrikse *et al.* [2007]; Brigandt [forthcoming]). Within broader evolutionary biology, it is also used to explain the evolutionary trajectory of populations by capturing the influence that the internal features of populations can have on the outcomes of evolution. Thus, rather than being any particular lower-level feature of populations (such as the standing genetic variation or its potential for novel mutation), I argue that evolvability is an abstract and robust dispositional property of populations whose physical basis is the many non-selection-based features of populations (such as mutation rate, developmental constraint, and population structure) that can influence the parts of phenotypic space populations are able to access over evolutionary time.

The account of evolvability I offer here solves the challenge that the conceptual confusion surrounding evolvability presents to evo-devo as a science. Unlike other accounts of evolvability in the literature, the account I offer

makes clear the important roles played by evolvability within evolutionary biology and evo-devo, and the relationship between these roles. At a broad level, a unified concept of evolvability allows evolutionary biologists to refer to the causal influence of the internal features of populations on their evolutionary trajectories without needing to understand those mechanisms in detail. Within evo-devo, evolvability presents as an explanandum rather than an explanans. Research here is concerned with making clear what this physical basis of evolvability is and how it comes about.

I begin the article with an overview of the problem of evolvability using a case study from the recent literature in evo-devo on the evolution of the primate limbs (Section 2). In Section 3, I explore the theoretical role of evolvability in evolutionary biology. First, I point out two types of explanation already identified within evolutionary biology: selection-based explanations and lineage explanations.¹ The latter of these play an important role in the explanatory agenda of evo-devo (Calcott [2009]). They also present an important alternative to the traditional selection-based explanatory approach in evolutionary biology. I then point out a further third type of explanation—‘evolvability-based explanation’—that, I claim, is also important in evolutionary biology more broadly as an alternative to the predominant selection-based explanatory approach. I identify a number of properties that evolvability must have to play this theoretical role. Having clarified these criteria of adequacy, I propose an account of evolvability that satisfies them in Section 4 of the article. In Section 5, I demonstrate how the theoretical machinery provided by this analysis gives us a clear and natural formal representation of evolvability, a conceptual framework for making hypotheses about evolvability and a foundation for investigating the features of the world that contribute to it. The analysis also allows us to readily make sense of existing definitions and proposed concepts of evolvability within a common currency.

2 The Problem of Evolvability

It is a notable feature of the tetrapod superclass that the lengths of the forelimbs and hindlimbs of its members tend to be in a ratio of 1:1 (Young and Hallgrímsson [2005]). This uniformity in limb length ratio is unsurprising, given that the forelimbs and hindlimbs of tetrapods are serially homologous structures. They evolved when the underlying genetic architecture (and thus the developmental program) for one modular morphological structure (i.e. a set of limbs) was duplicated and expressed in a new location resulting in replication of that structure (Hall [1995]; Capdevila and Izpisua [2000];

¹ This list is not intended to be exhaustive of the types of explanation seen in evolutionary biology. Drift, for example, is clearly an important explanans in evolutionary biology but will not be discussed here.

Ruvinsky and Gibson-Brown [2000]; Wellik and Capecchi [2003]; Young and Hallgrímsson [2005]). Their common origin means that the genetic and developmental architectures for the two sets of limbs in tetrapods are often very similar. Hence, mutations in the genes ostensibly governing the development of one of the limbs can also influence the developmental systems governing the phenotype of the other limb set. This is a classic case of developmental constraint: a developmental mechanism or process that limits or biases variation in phenotypes (Maynard Smith *et al.* [1985]; Schwenk and Wagner [2003]).² Although mutations within the tetrapod genome may be random and unbiased, the complex and interrelated nature of the developmental systems within organisms governing limb development have resulted in a bias within the supply of phenotypic variation towards limb co-variation.

Humans are one exception to the rule. Although we are tetrapods, we have significantly shorter arms than legs (Hallgrímsson *et al.* [2002]). Explaining human limb morphology requires us to understand how our hindlimb to forelimb length ratio arose despite the primitive pattern of correlated hindlimb and forelimb evolution amongst vertebrate tetrapods. It requires us to explain why the constraint that usually exists within tetrapods due to serial homology fails to hold here.

In a recent article, Young *et al.* ([2010]) describe this divergence in the limb morphology of humans from the tetrapod standard as an example of a difference in evolvability. To explain this difference in evolvability, they compared the limb length integration of the apes (chimpanzees, gorillas, and gibbons) and the quadrupedal Old and New World Monkeys (macaques, leaf monkeys, squirrel, and owl monkeys). What they found was a disparity in relative limb lengths between the quadrupedal monkeys (to whom hominids are relatively distantly related) and the apes (which include the hominid last common ancestor). The arms and legs of quadrupedal monkeys are basically the same length in each individual, but amongst the apes we see significant divergence in the length of arms and length of legs within individuals.

This disparity in limb length variation is difficult to explain by selection alone. Although selection can potentially explain why a particular limb morphology was maintained in a population, it cannot explain how that morphology arose in the first place. In this case in particular, the origination of a non-1:1 hindlimb to forelimb length ratio is puzzling because of the known constraints on limb evolution in the tetrapod superclass due to serial homology. In their article, Young *et al.* ([2010]) attribute the increased

² Amundson ([1994]) identifies two importantly distinct concepts of constraint that are of interest to evolutionary biology—one concerns constraints on form (constraints_F), the other concerns constraints on adaptation (constraints_A), the latter being a restricted set of the former. The notion of developmental constraint being discussed here concerns the broader notion of constraint—constraints_F.

diversity in the ape lineage to a reduction in the developmental constraint governing limb integration in a common ancestor of the apes but not the quadrupedal monkeys. In ancestral ape populations, the relaxation of the developmental constraint on limb evolution increased their evolvability with respect to independent limb evolution and thereby ‘facilitated’ the evolution by natural selection of the type of limb length ratio seen in humans.

Although the case study above seems straightforward enough, it is far from clear what Young *et al.* ([2010]) mean by ‘evolvability’ in their work. Although it is obvious that they associate the reduction in developmental constraint in the apes with an increase in evolvability, and that they associate the type of constraint generated by serial homology with a lack of evolvability, there are multiple (equally good) ways we could interpret their claims. This lack of clarity arises not because of confusion on their part, but because of the many existing usages of the term ‘evolvability’ in evolutionary biology. Table 1 gives a summary of the common usages of the term in the literature.

Young *et al.*’s ([2010]) use of ‘evolvability’ could refer to any of usages (1), (3), or (4). The relaxation of developmental constraints acting on the phenotypes of individuals within any given population, such as the relaxation of the hindlimb to forelimb co-variation in the ape lineages, increases the capacity of that population to generate heritable phenotypic variation in the future. The relaxation of constraint also increases the intrinsic capacity of organisms within the population to vary phenotypically and increases the potential of that population to generate novel mutations useful for future adaptation. Which of these three usages Young *et al.* ([2010]) actually intend is not clear, and, for this reason, determining the nature of, and assessing, their claims is difficult.³

Our difficulty in interpreting and assessing the evolvability-related claims of Young *et al.* ([2010]) is not unusual. As Table 1 attests, despite there being similarities between the different usages of the term ‘evolvability’ (for example (1) and (3) both refer to heritable variation), it is used in many ways within the evo-devo literature. These usages differ significantly enough to cause conceptual confusion. For example, a population could be classed as highly evolvable with respect to usage (1), but (simultaneously be) classed as not highly evolvable with respect to usage (5). This is because any particular population could display a high amount of current genetic variation, but be constrained with

³ Note also that Young *et al.* (2010) are only interested in evolvability to the extent that it is important to the evolution of a particular character: the ratio of hindlimb length to forelimb length. They are not, in this instance, interested in the influence of evolvability with respect to any other traits. This is commonly the case. Biologists are most often interested in explaining particular characters when discussing evolvability rather than general classes of characters or types of characters, even when talking about evolvability at a taxon level.

Table 1. Common usages of the term ‘evolvability’ in evolutionary biology^{a,b}

The term ‘evolvability’ is used to refer to:	Reference(s)
(1) The capacity of populations to generate heritable phenotypic variation.	(Wagner and Altenberg [1996]); (Wagner [2008])
(2) The capacity of the individuals within a population for adaptive phenotypic plasticity.	(West-Eberhard [2003])
(3) The intrinsic capacity of the individuals within a population to generate phenotypic variation in response to genotypic variation.	(Kirschner and Gerhart [2006])
(4) The potential of a population to produce novel mutations for use in the evolution of adaptations in the medium- to long-term.	(Maynard Smith and Szathmáry [1995]); (Pigliucci [2008])
(5) The current genetic variation in a population (rather than the prospective variation).	(Houle [1992])

^aNote that (2) and (3) are not identical. While both refer to phenotypic plasticity (the ability of an organism to respond to an environmental input with a change in phenotype, (West-Eberhard [2003], p. 34)), (2) refers more specifically to adaptive phenotypic plasticity. This being the ability of an organism to respond to an environmental input in an appropriate (i.e. beneficial) manner.
^bNote unlike (1) and (4), which concern the capacity to generate variation in the future, (5) concerns current variation; the interest being in how the nature of this current variation contributes to the ability of the population in question to respond to current selective pressures.

respect to future mutational events, and hence have very low prospective genetic variation.

In what follows, I offer a solution to the problem of the many usages of the term *evolvability* in evolutionary biology. I begin by outlining the theoretical role played by *evolvability*.

3 The Theoretical Role of *Evolvability* in Evolutionary Biology

3.1 The explanatory targets of evolutionary biology

The core explanatory interest of evolutionary biology is to explain the features of the tree of life (Sterelny and Griffiths [1999], pp. 22–30). The scope of this interest varies from research group to research group, the central focus of some being relatively small-scale (for example, explaining the evolution of a particular trait), and others large-scale (for example, explaining differing patterns of diversity in lineages). The targets of research in evolutionary biology include many different features of the tree of life including *adaptedness*, *diversity*, *disparity*, *complexity*, *organization*, and *biological order*.

Fundamentally, however, all such research is interested in explaining why the tree of life is as it is.

We can see this interest reflected in our case study. Young *et al.* ([2010]) are concerned with explaining why the ape lineage has moved from a part of ‘morphological space’ with low limb length ratio diversity to one of higher diversity,⁴ while the monkey lineage (and indeed most tetrapods) have made no such move, maintaining similar limb length ratio diversity to the common ancestor (Figure 1). Thus, Young *et al.*’s ([2010]) concern is to explain a feature of the tree of life.

3.2 Selection-based explanations

Although the scope of research in evolutionary biology is varied, the central theme of evolutionary biology over the past century has been the role of natural selection in generating adaptedness and diversity in the tree of life. A central type of explanation generated by this program is what I call a selection-based explanation. Selection-based explanations explain features of the tree of life by reference to evolution by natural selection. They refer to differences in the selection pressures acting on populations at a given time that increase the probability of a particular evolutionary outcome at some subsequent time.⁵ For example, if the selection pressures acting on the ancestral quadrupedal monkey populations were different to those acting on the ancestral ape populations, evolution by natural selection would offer an explanation for the disparity in limb length variation between the lineages. This is because differences in the selection pressures acting on the ancestral populations in each lineage could serve to raise the probability of subsequent limb divergence in the ape lineage, relative to the probability of subsequent limb divergence arising in the monkey lineage (indeed, Young *et al.* ([2010]) agree that this is likely to be, at least, part of the explanation for the difference in forelimb to hindlimb length ratio diversity).

Selection-based explanations are a type of robust-process explanation (Jackson and Pettit [1992]; Sterelny [1996]). Such explanations account for events of interest by providing us with information about the general trends and underlying processes that give rise to those events, rather than detailed information about the actual events that occurred. They tell us whether there are any robust difference-makers generating the outcome of interest and, if so, what they are. To do this, selection-based explanations compare (rather than

⁴ A natural way to think of morphological space in this context is as being analogous to Dennett’s ([1996], [1997]) concept of ‘design space’.

⁵ I am assuming a fairly well accepted ‘probability raising’ account of causation here. The basic principle of such an account is that some potential cause, *C*, is the cause of some outcome, *E*, just in case the probability of the outcome *E* given the presence of the potential cause *C* is lower than the probability of the outcome *E* given the absence of the potential cause *C* (Hitchcock [2011]).

Figure 1. A graphical representation of the explanatory interest in Young *et al.*'s ([2010]) article. They ask: Why is it that the quadrupedal monkey lineage has maintained a similar level of limb diversity, *A*, to the common ancestor and the ape lineage has increased in their limb diversity, *B*?

contrast) our world with other possible microphysical worlds, identifying those where the evolutionary outcome or outcomes of interest would have occurred and the features common to those worlds. The thought being that, even if many details of the system differed, as long as the selection pressure were to remain the same (within fairly broad limits), the evolutionary outcome of interest would still be likely to occur.

By virtue of being robust-process explanations, selection-based explanations carry information about not just how things happened but how they might have happened were things different. This informational profile for our case study is represented in Figure 2. While a robust-processes explanation cites only those factors that are actually causally relevant to the actual path from *A* (limited limb diversity) to *B* (increased limb diversity), which particular causal factors are cited depends on their robustness. As such, when considering the accuracy of a robust-process explanation, of importance is information about all of the ways that the outcome of interest could have occurred but also the number of ways that the outcome of interest could have failed to occur. Without both of these types of information, the robustness of the outcome is unclear. For a selection-based explanation to be robust, the explanatory selection pressure must be common to a large number of the paths from *A* to *B*, and not to the paths that fail to move from *A* to *B*. If this is the

Figure 2. Robust-process explanation. A selection-based explanation of the case study given in Young *et al.* ([2010]) should include information about the actual path taken for the ape lineage to increase their diversity as well as information about other possible ways that the same outcome could have been achieved. Information about ways that the outcome could have failed to occur is also important, as it provides information about how robust the outcome of interest is.

case, then we can say that the outcome of interest robustly occurs given the presence of the explanatory selection pressure.

3.3 Lineage explanations

Evolution by natural selection is one prominent explanation of the patterns we see in the tree of life, but it is not the only explanation available to us. Evo-devo is an alternative (though complementary) approach. Rather than looking to selection to explain the tree of life—the externalist project in evolutionary biology (Godfrey-Smith [1998]; Godfrey-Smith and Wilkins [2008])—the focus of explanation in evo-devo is the internal resources available to organisms through processes such as development. One prominent type of explanation this emphasis provides is known as a lineage explanation (Calcott [2009]). Lineage explanations account for features of the tree of life by explicitly identifying feasible trajectories through phenotypic space. For example, a lineage explanation might plot a feasible trajectory from an ancestral trait to an observed trait. To do this, lineage explanations provide a

detailed sequence of functional mechanisms, these being changes to developmental mechanisms (broadly construed). Each mechanism is a minor modification to that before it; consequently, the sequence provides a trajectory through which one mechanism evolves incrementally into another, and in this way explains that trajectory in the world.

One way to explain the difference in evolutionary trajectory of the apes and quadrupedal monkeys with respect to limb morphology would be to provide a lineage explanation for each morphology and then compare them. Given the claims of Young *et al.* ([2010]), we should see reduction in developmental constraint in the lineage explanation for the ape lineage and no such reduction in the lineage explanation for the quadrupedal monkey lineage. Hence, together these two lineage explanations would provide an account of why there is a difference in limb evolution between the two lineages. Figure 3 illustrates the information required.

Unlike selection-based explanations, lineage explanations do not offer information about causal robustness. Rather, they provide detailed information about the actual sequence of events generating the outcome in question. In this way, lineage explanations are a type of actual-sequence explanation (Jackson and Pettit [1992]; Sterelny [1996]). Such explanations provide a detailed account of the chain of causal events that caused the circumstance of interest. They include information that allows us to identify the actual microphysical world we are in, and highlight the differences between that world and close possible worlds. Although such explanations include the actual difference-makers with respect to the outcome in our world, they are insufficient to make any predictions or explanations about other cases (both in our world and others).

Lineage explanations provide a useful and complementary alternative to selection-based explanations in evolutionary biology. In particular, they help to explain novelty by providing information about how developmental changes generate novel phenotypic variants (Calcott [2009]). Lineage explanations do not, however, exhaust the explanatory agenda of evo-devo nor evolutionary biology. Selection can only act on what is available to it and, as such, features of populations that alter the supply of phenotypic variation to selection can alter the outcomes of the evolutionary process. As a consequence of this, any trajectory through phenotypic space can be robust for two sets of reasons. One of these relates to the selective features identified in a selection-based explanation. The other relates to the influence of biases in the supply of variation that make trajectories readily available or rarely available (Gould [1989]; West-Eberhard [2003]; Arthur [2004]; Kirschner and Gerhart [2006]). Lineage explanations, while focusing on the internal resources of organisms, cannot tell us about the extent that the supply of variation and/or selection is responsible for any of the evolutionary trajectories they map. This is because

Figure 3. Actual-sequence explanation. A lineage explanation of the case study given in Young *et al.* ([2010]) would include information about the actual path taken by the ape lineage to increase their diversity, as well as information about the actual maintenance of similar limited limb diversity to the common ancestor in the quadrupedal monkey lineage, by providing a sequence of mechanisms.

they do not include information about how robust a trajectory is. Lacking this information, lineage explanations do not provide the type of information required to contrast the influence of selection with the internal resources of populations on the outcomes of selection. Another type of explanation is required.

3.4 Evolvability-based explanations

The study of development is not just important to explaining the outcomes of evolution in a direct, causal, mechanistic sense, but also in providing information about why some phenotypes evolve while others do not. In claiming apes are more evolvable than quadrupedal monkeys, Young *et al.* ([2010]) point to the disparity in limb independence between those lineages. They say that this disparity is (at least in part) because of the relaxation of developmental constraints in the apes. In the monkey lineage, evolving longer hindlimbs always entails evolving longer forelimbs and vice versa, whereas in the ape lineage, this interdependence has been reduced. A natural way to express this hypothesis is as follows: the probability of the ancestral ape populations evolving greater limb diversity was higher than that of the ancestral quadrupedal

monkey populations because of the relaxation in developmental constraint in the ape populations. Implicit in this claim is what I call an evolvability-based explanation.

Like lineage explanations, evolvability-based explanations account for the outcomes of evolution by concentrating on the internal features of populations. They differ from lineage explanations in that they explain evolution by reference to the broad internal disposition of a population to evolve rather than for any actual evolutionary trajectory. Dispositions are easy to understand in terms of probabilities, so I will use probability here. Evolvability-based explanations refer to differences in the internal (rather than external) features of populations that increase the probability of a particular evolutionary outcome in the future (for example, adaptedness, diversity). Their general form is as follows: it was, 'selection aside,' more probable that population *x* would evolve the characteristic or characteristics of interest than population *y*. Evolvability-based explanations account for features of the tree of life by considering the role that the internal features of populations can have on the outcomes of evolution. They are also robust-process explanations.

Evolvability-based explanations abstract away from the intricate causal details of a given situation. Abstractness and robustness are related properties. In simply abstracting away from the microphysical details of a state of affairs in a relatively principled manner (i.e. not excluding any robust difference-makers), one gains robustness in an explanation because the more abstract an explanation is, the more microphysical worlds it should apply to and, thus, the more robust it is (Jackson and Pettit [1992]; Sterelny [1996]). In this way, evolvability-based explanations provide the type of information about counterfactual situations that lineage explanations do not offer. They also provide us with a means to contrast the influence of selection with the influence of the internal features of populations on the outcomes of evolution.

For many in evo-devo, the evolvability research agenda is complementary to that offered by selection-based explanation. In focusing on evolvability (rather than selection), evo-devo is simply concentrating on a different set of lower-level factors within the same system (Brigandt [forthcoming]). In this sense, evolvability (via evolvability-based explanation) provides a means of delineating evo-devo as an autonomous field of research. In doing this, however, it does not prevent the integration of evo-devo into evolutionary biology more broadly but, rather, makes clear its contribution to the broader explanatory project (Hendrikse *et al.* [2007]).

Although evolvability-based explanations are useful for contrasting the influence of selection with the influence of the internal features of populations on the outcomes of selection, by themselves they offer only a relatively shallow explanation. In explaining evolvability, work in evo-devo adds depth to our understanding of the influence of development, and other internal resources of

populations, on evolution beyond the simple comparison of the influence of the external and internal features of populations. The case study makes particular sense in this light. Young *et al.* ([2010]) are seeking to account for evolvability, rather than provide evolvability as a stand-alone explanation. Even though this is the case, evolvability is nonetheless explanatorily salient and useful in this situation. By referring to evolvability early in the article, Young *et al.* ([2010]) draw the focus of the discussion away from selection and towards differences in the internal features of the ancestral ape and monkey populations without needing to specify any of those features in particular. Later in the article, in pointing to the relaxation of developmental constraint, they provide causal detail and depth to the otherwise shallow explanation that the differential evolvability of the ancestral ape and quadrupedal monkey population with respect to limb length morphology offers alone. They provide an account of the physical realisers of the disposition (i.e. evolvability) that they seek to explain. Having made clear the role played by evolvability in evolutionary biology and evo-devo, let us now turn to what this means for evolvability.

3.5 What properties must evolvability have?

It is clear that evolvability-based explanations refer to a dispositional property of populations (Love [2003]; Sterelny [2007]). This is because they concern the tendencies of the system in question to evolve. Being highly evolvable with respect to some trait does not guarantee the evolution of that trait in a population: first, because the evolution of any population is constrained by selection, and second, because the outcomes of evolution are susceptible to the effects of chance events. For these two reasons, evolvability-based explanations must refer a dispositional property rather than a property that is always manifest.

The disposition to evolve has a broad physical base. It supervenes on many of the more concrete features of the individuals within populations and their interactions. When we contrast the causal influence of the internal features of a population on its evolutionary trajectory (i.e. evolvability) with the influence of its environment on that trajectory, any internal feature of populations that can (all other things being equal) raise the probability of one evolutionary outcome over another is important. The developmental constraints on a population are one lower-level feature that forms part of the supervenience base for evolvability. There are also other candidate features that are likely to contribute to this base (Hendrikse *et al.* [2007]).

The usages of the term evolvability given in Table 1 are a good starting point here. All these refer to properties that could increase the probability of one evolutionary outcome over another in the populations that have them.

For example, (5) the current genetic variation in a population, clearly influences the likelihood of some evolutionary outcomes over others (especially on finite timescales). Similarly, (3) the intrinsic capacity of the individuals within a population to generate phenotypic variation in response to genotypic variation, will alter the structure and nature of the phenotypic variation available to selection, and thus the potential evolutionary outcomes available to that population. Evolvability (i.e. the broad disposition of populations to evolve) supervenes on these many lower-level properties. In this light, the usages in Table 1 must each be understood as focusing on an aspect of the categorical base of a much broader disposition.⁶

Although the features listed in Table 1 are often equated with evolvability or thought of as evolvability itself, they only represent part of the causal picture relevant to evolvability. Many other features of populations and environments beyond those given by Table 1 alter the likelihood of particular evolutionary outcomes by indirectly affecting the supply of variation; in particular, they may be responsible for the maintenance of the supply of variation (Sterelny [2007]; Pearce [2011]). For example, if we were concerned with the probability of a population evolving adaptations, the following internal features of populations are also relevant:

- Low mutation rate: Although variation is necessary for evolution by natural selection, too much variation will result in the dilution of the results of selection. In other words, the changes in trait distribution between generations of a population will be attributable to phenotypic variation rather than selection (Sterelny and Griffiths [1999], p. 36).
- The preservation of favourable variation within individuals: If a favourable phenotypic variation arises within an individual, it needs to be maintained so that it can be inherited within the population (Sterelny [2007]).
- The preservation of favourable variants within the population: Once favourable phenotypic variants have arisen in a population, they need to be protected within the population such that further variation can accumulate. One obvious mechanism for this is inheritance (both vertical and horizontal) in replicating a trait and amplifying its distribution in the population. This both protects the presence of the variant from chance events and from other less random events like the potentially swamping effect of immigration (Sterelny [2007]).

⁶ I suspect the standard notions of evolvability are often pragmatically motivated and intended to point to proxies for evolvability rather than pick out evolvability itself (which, on the account offered here, is a particularly difficult property of populations to assess directly in its entirety). If this is the case, however, then it is important to be clear that this is what is intended by the usages in Table 1.

The causal influence of many of these features is not independent. The supply of variation, for example, is related to the preservation of favourable variants within individuals. For this reason, the evolvability of a population is more than any one of these features but is, rather, the joint causal effect of multiple lower-level features.

4 What Evolvability Really Is

As argued in Section 3, when evolutionary biologists give evolvability-based explanations, they are fundamentally concerned with an abstract robust disposition of populations to evolve in certain ways. This is made clear when we represent the disposition using probability. In what follows, I present an account of evolvability as a probability that reflects the earlier discussion about its explanatory role. In doing so, I point out a number of often overlooked factors that are relevant to our assessment of the evolvability of populations, and to our use of evolvability in explanation.

Given the explanatory role outlined in Section 3, evolvability is the objective probability of a particular feature or set of features, F , arising at some future time, T , given the state of a population, X , and relevant features of its environment, B , at some particular starting point. For example, we can think of the evolvability of the ancestral ape populations with respect to limb length diversity as being the probability of the ancestral ape populations increasing in limb length diversity, given the joint effect of the features of those ancestral populations and the relevant features of their environment. E is a formal representation of this probability as a claim about the relationship between propositions in a formal language (denoted by lower case italics).

$$E : Prx, b(f_t)$$

In the formal language, x is a proposition that describes a population or lineage of interest; b is a proposition describing the relevant features of the environment in which that population exists; f_t is a proposition that describes a future possible state of that population indexed to a particular time, t ; E is the probability of the proposition f_t being true given the truth of the propositions x and b . In other words, E is the probability of a certain future state (described by f_t) being the case given that the relevant features of the environment (described by b) and the internal features of the population (described by x) are thus and so. In laying out the factors relevant to evolvability, E captures the potential influence of the many internal features of populations on patterns in the tree of life and makes clear other factors that may affect this influence (such as time scale and context).

I now give a more specific rendering of each of the variables, f_t , x , and b . In doing this, I make explicit a number of factors that otherwise might be overlooked in our understanding of evolvability.

4.1 Making sense of f_t

In this article, I claim that the evolvability of a particular population at a given time is a measure of their capacity to change over time with respect to some future state, given some starting state of affairs. The proposition f_t describes that future state of affairs. In short, f_t captures the intuitive notion that evolvability is in part a measure of how easy it is for a population to move over time in particular directions through design space.

The content of f_t is important to any evolvability measure because a population can be more evolvable than another with respect to one future state, but not to another future state. For example, although ancestral ape populations were more evolvable than ancestral monkey populations with respect to having longer legs than arms, they were not more evolvable with respect to having a 1:1 arm to leg length ratio. This is because, while the developmental constraint on independent limb evolution in the quadrupedal monkey lineage reduces the probability of populations in that lineage evolving longer legs than arms, it increases the probability of populations in that lineage evolving arms and legs of the same length—constraints make some evolutionary outcomes more probable, and, in doing this, they make other outcomes less probable. To not include the variable f_t would be to fail to capture this important fact about evolvability.

As has been stated, f_t is a proposition describing some future possible state of the population of interest to evolutionary biology.⁷ That state may relate to any one of the patterns in the tree of life that interest evolutionary biologists that are discussed in Section 3.1; for example, adaptedness, diversity, organization, or complexity.⁸

As well as varying with respect to the nature of the pattern of interest, the proposition given by f_t will vary in scope depending on the circumstances. Sometimes evolutionary biologists are interested in hypotheses of quite narrow focus. For example, as discussed in Section 3.4, Young *et al.*

⁷ Each of the variables in E is a proposition. It should be noted, however, that we would expect, given the complexity of the states of affairs being described, that these propositions will be long conjunctions of smaller propositions describing elements of the state of affairs of interest.

⁸ Interestingly, it is conceivable that one likely pattern of interest to evolutionary biology which I have not discussed here is differences in extinction rates between lineages. Extinction risk is, in part, a result of the internal features of populations, rather than merely their environments. For example, the features of some populations, such as extremely high mutation rate can make them more likely to go extinct than others, regardless of selection pressures. While I have not seen anyone talk about evolvability in this way, the tendency to go extinct appears to be of prima facie interest to evolutionary biologists and is capable of being captured by this analysis.

([2010]) are concerned with the relative evolvability of the ancestral quadrupedal monkey populations versus the ancestral ape populations with respect to having a forelimb to hindlimb length ratio that is not 1:1. Other times, evolutionary biologists are interested in hypotheses of a less narrow focus. For example, discussions about the adaptive radiation of the cichlid lineage in the African Lakes concern a much broader interest—the evolvability of the ancestral cichlid populations (as opposed to those of other similar fish species found in the lakes) with respect to increased diversity and adaptedness. f_t , in this case, would pick out all the possible worlds where the populations in question (whether it be cichlids or other fish species in the lakes) went on to have an increase in diversity and adaptedness. In this sense, E is a measure of the robustness of the truth of x and b and f_t .⁹

Note that I have time-indexed f . The subscript t denotes time. This is because evolutionary biologists are concerned with more than just mere change in a particular feature of a population or lineage. The rate of that change is important (Hendrikse *et al.* [2007]). For example, consider the primate limb case again; of interest is why the ape lineage has more limb diversification than their fellow primates, the quadrupedal monkeys. What if both the ancestral ape and quadrupedal monkey populations were under the same selection pressure for a flexible forelimb to hindlimb length ratio, and we had no timescale over which to assess their evolvability? Although the ancestral ape population has a ‘head start’ on the ancestral quadrupedal monkey population—in that, for it, the relevant developmental constraints limiting the independent evolution of the limbs are already reduced—these constraints are, in principle, able to be reduced in the monkey lineage, given enough time. In other words, both ancestral populations were just as likely to reach a certain part of design space over infinite time. If the evolvability measure did not include some reference to a timescale, we would have to say that both the ancestral ape and quadrupedal monkey populations were equally evolvable with respect to a non-equal forelimb to hindlimb length ratio. That does not seem right. Evolvability assessments are about not just change but also rate of change. Those populations with features that allow them to evolve complex adaptations faster are more evolvable than those populations that evolve them but only slowly (even if, in principle, both are capable of evolving those complex adaptations), thus E must include a timescale.

⁹ E is only really a good description of evolvability with respect to dichotomous features. For example, being bipedal or not, rather than being more diverse or not. In many cases we will be concerned with traits or features in which there is a continuous distribution (for example, ‘being more diverse’ or ‘wing size’). In such cases I think we are interested in evolvability as is represented by slightly modified version of E that uses expected value (i.e. EVx , $b(f_t)$). I have not included an in depth discussion of this here in the interests of time, as here I merely wish to defend the notion of evolvability as a probability.

What measure of time would be appropriate in this circumstance is unclear, although it is reasonable to expect that it will vary depending on the explanatory context. Evolutionary biologists, more broadly, often use generation time when referring to rate of change, but this is problematic here because generation time itself is likely to be a feature of populations that could contribute to evolvability. This is because the supply of genetic and phenotypic variation to a population is in part a product of how many reproductive events are occurring in that population due to the relationship between reproduction and recombination. A simple thought experiment illustrates this as follows. Two populations have the same propensity for variation due to reproduction but one has a shorter generation time than another. Over a specific time period, all other things being equal, the population that turns over generations faster is likely to have a greater supply of variation, and hence, intuitively, should have greater evolvability. Were one to use generation time to measure time in E , however, this difference would not be apparent. Although what measure of time is appropriate to E is not yet apparent, it is clear that generation time is not the answer.

4.2 Making sense of x and b

As stated above, evolvability abstractly captures the causal effect of the many features of individuals in a population, their relationships, and the relevant features of the environment on an evolutionary outcome of interest. It provides a way of representing the causal effect of a number of features that may be quite unrelated to each other; x and b describe these features. Very crudely, x describes the features of the population of interest and b describes the relevant environmental context. Both propositions will be very complicated. That said, neither x nor b need be exhaustive descriptions. Moreover, they should not be; evolvability is an abstract property that captures the role of internal, rather than external, adaptive causal factors in generating the outcomes of evolution. Hence, only the internal features of any given state of affairs should contribute to it directly. In particular, the physical basis of evolvability for a population cannot include any selection-relevant features. For this reason, x and b need only describe those features of the population and environment that are causally relevant to this internally derived propensity.¹⁰ I will now clarify what this means by considering each variable in turn.

¹⁰ The partitioning of the (x, b) pair into x and b is not strictly necessary for the analysis of evolvability in E . One could feasibly represent the state of affairs by a single proposition that describes both the environment and the population in question, and it would not alter the value of the probability. I have included the partition, however, because it makes clear that the environment is important (something I will come to shortly). It is sufficient to note for the time being that there are good reasons to partition the state of affairs and, further, that the partition does not effect our evolvability assessments. This is because, whether one thinks of

With respect to x , we should be concerned here with any internal feature of populations that can, all other things being equal, raise the probability of one future evolutionary outcome for that population over another. The primate limb case study is illustrative here. Young *et al.* ([2010]) argue that the differences in limb diversity between the ape and quadrupedal monkey are the product of the relaxation of developmental constraints. The developmental constraints on a population are one lower-level feature that affects the evolvability of that population. As discussed in Section 3.5, there are, however, many other candidates for this causal role (for example, population structure).

A more formal way to think of the appropriate features for inclusion in the description given by x borrows from the manipulationist literature on causation. Accounts of causation of this type all rely on the same basic premise: if you can systematically intervene on variable A to bring about a change in variable B , then A is a cause for B (Woodward [2003]; Reisman and Forber [2005]). One can establish the causal influence of a particular feature of a state of affairs on evolvability by considering the effect that an intervention on that feature would have on the probability of certain evolutionary outcomes. M , a modification of the basic manipulationist premise, is a formal characterization of this. I take M to be a sufficient condition for a feature of the world to be relevant to the evolvability of a population. Hence, it is also a sufficient condition for the description of that feature to be included in the propositions given by x and b .

M: z has a causal effect on the evolvability of a population if there are circumstances (v) where some intervention would change the value of z (and no other variable) and the evolvability of that population would also change.

As stated previously, b is a proposition describing the relevant features of the environment. It is extremely important because of the dispositional nature of evolvability. As pointed out by Sterelny ([2007]) and Love ([2003]), many of the properties of populations relevant to evolvability are not intrinsic, and thus the evolvability of a population itself is context dependent. The types of environmental properties that are important will depend on the features of the populations in question. Some obvious candidates are temperature (which influences mutation rate) and the level of isolation of the population (which

some proposition represented by the pair (x, b) as being about the population or the environment, it is unimportant to the probability given by E . It will, however, make a difference when interpreting the probability. In other words, a single evolvability assessment can be interpreted as being for slightly differently divided sets of population-environment propositions. This gives the account the virtue of being useful for people with varying levels of sympathy towards externalist accounts such as the extended phenotype and niche construction. The set of propositions represented by x and b can be partitioned in many different ways without changing the evolvability assessments given by E as long as the propositions in the set (x, b) remain the same.

influences the genetic composition of the population). In this sense, any attribution of evolvability must include reference to the aspects of the environment relevant to the instantiation of the relevant properties of the populations. *b* is intended to capture this.

One difficulty this presents is that many features of the environment will act both in the instantiation of some extrinsic property of a population and as a selection pressure. Temperature is a good example of this; the environmental temperature can alter the mutation rate of some species (Lindgren [1972]) but can also readily serve as a selection pressure. One means to avoid this may be to have very fine-grained propositions with respect to the environment that make it possible to partition it into the selection-relevant and non-selection-relevant aspects. I am skeptical as to the extent that this is possible; for this reason evolvability and selection ultimately may be more idealized notions than first thought. Brigandt ([forthcoming]) also notes this issue without offering a resolution.

Having presented a detailed account of the factors that contribute to the dispositional property that is evolvability, I now return to our case study for illustration.

5 What of the Limbs? The Power of *E*

A key feature of the approach to evolvability I defend here, in particular the formalism presented in *E*, is that it provides us with a ready conceptual framework for clearly representing hypotheses concerning evolvability. For example, take the common-language claim ‘ancestral ape populations were more evolvable with respect to limb diversity than the ancestral quadrupedal monkey populations’. Using my account of evolvability, that statement should be understood as the claim that ‘the probability that ancestral ape populations, *A*, would evolve limb diversity, *L*, over time *T*, in environment *B* is greater than the probability that ancestral quadrupedal monkey populations, *M*, would evolve limb diversity, *L*, over time *T* in environment *B*’. This is represented propositionally using the schema given in *E* in (Equation 1).

$$\Pr a, b(l_i) > \Pr m, b(l_i) \quad (1)$$

In re-wording and representing the common-language claim being made in this way, we make very clear what hypothesis is being made and what is relevant to assessing the truth of that hypothesis.

Other hypotheses can also be represented. For example, Young *et al.* ([2010]) argue that developmental constraint is the source of the difference in evolvability with respect to limb diversity between the ape lineage and the quadrupedal monkey lineage. Their hypothesis, thus, can be rendered as ‘the probability that the ancestral ape populations, *A*, would evolve limb diversity,

L , over time T in environment B would be approximately equal to the probability that the ancestral quadrupedal monkey populations would evolve limb diversity, L , over time T in environment B if we were to intervene on the monkey populations and remove the constraint on independent limb evolution, $\neg C$. Once again, this can be represented clearly using the formal schema as in (Equation 2). What is being hypothesized by Young *et al.* ([2010]) and what would need to be true to prove that hypothesis is made very clear.

$$\Pr a, b(l_i) \approx \Pr \neg c, b(l_i) \quad (2)$$

There are many other hypotheses we might wish to test with respect to evolvability. These hypotheses vary with respect to their scope; they can be concerned with the evolution of particular traits or general trends. They can vary with respect to their temporal depth; do we want to assess evolvability over thousands of years or millions of years? They can vary with respect to the specificity of the internal causal influences they concern. The emphasis of much work within evo-devo and the standard definitions become clearer in this light. If, for example, we are simply focusing on the influence of the standing genotypic variance in a population (or any of the features in Table 1, for that matter) on the outcomes of evolution, rather than the many features that make up the physical basis of evolvability, we can capture this by restricting x to merely those propositions relating to the standing variation. The common currency in E allows us to clarify this narrower focus while retaining clarity about exactly what is being claimed more broadly.

6 Conclusion

In this article, I have made a number of key claims. First, that the evolvability concept plays an important explanatory role in evolutionary biology. It not only delineates the scope of enquiry for evo-devo, but also gives us a means for talking at an abstract level about the role that the internal features of populations can play in evolution. Second, evolvability is both an explanans and an explanandum. Evolvability-based explanations refer to differences in the features of populations that robustly increase the probability of a particular evolutionary outcome in the future. These explanations lie in contrast to those that are selection-based (i.e. refer to differences in fitness that robustly increase the probability of a particular evolutionary outcome in the future) and differ significantly from lineage explanations (an already identified explanatory type peculiar to evo-devo). Third, the best way to understand evolvability, given its explanatory role, is as the robust and abstract dispositional property of populations to evolve. The categorical basis of this disposition is the many non-selection-based features of populations (such as population structure, mutation rate, genetic constraint, and developmental

compartmentalization) that can act as difference-makers on the evolutionary trajectory of populations. Although the many existing definitions of evolvability concentrate on aspects of this categorical base, their scope is narrower than the much broader phenomenon that is evolvability. Fourth, and finally, the analysis I offer here provides us with a clear and unambiguous framework through which we can come to understand the probabilistic causal relationship between such lower-order causal features of populations or lineages and higher-order patterns in the tree of life.

Acknowledgements

I am very grateful to Brett Calcott, Peter Godfrey-Smith, Arnon Levy, Aidan Lyon, Daniel Nolan, Anya Plutynski, Wolfgang Schwartz, Kim Sterelny, and three anonymous reviewers for their constructive comments on earlier drafts of the manuscript. I also thank audiences at the Australian National University; National University of Singapore; Konrad Lorenz Institute for Evolution and Cognition Research; 2011 Inter-University Centre Philosophy of Science Conference in Dubrovnik; and the 2011 ISHPSSB meeting in Salt Lake City for their encouragement and helpful suggestions. Financial support for this work was provided by the Australian National University and the Konrad Lorenz Institute for Evolution and Cognition Research, Altenberg, Austria.

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