

What evolvability really is

Rachael L. Brown

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 paper 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 too 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 upon the outcomes of evolution (as opposed to the causal influence of selection, which is often characterised 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.

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, tidying-up evolvability requires us to carve it up into a number of distinct concepts with distinct terms.

This “cluster concept” approach lies 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 the possibility of a “common currency” for dealing with evolvability questions open (though the exact nature of that currency is not clarified).

In this paper, I build upon Sterelny’s ([2007]) account to present a unified concept of evolvability, driven by the theoretical role played by the term. While explaining or accounting for evolvability is the defining research program in Evo-devo (Hendrikse [2007]; Brigandt [forthcoming]), within broader evolutionary biology evolvability is used to explain the evolutionary trajectory of populations by capturing the influence that the internal features of populations can have upon 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), evolvability is an abstract and robust dispositional property of populations whose physical base is the many non-selection based features of populations (such as mutation rate, developmental constraint and population structure) which can influence the parts of phenotypic space populations are able to access over evolutionary time.

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

I begin the paper with an overview of the problem of evolvability using a case study from the recent literature in Evo-devo (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—lineage explanations (Calcott [2009])—play an important role in the explanatory agenda of Evo-devo. They also present an important alternative to the traditional selection-based explanatory approach in evolutionary biology (Calcott [2009]). I then point out a further third type of explanation—“evolvability-based explanation”—which, I claim, is also important in evolutionary biology more broadly, as an alternative to the predominant selection-based explanatory

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.

approach. I identify a number of properties that evolvability must have in order to play this theoretical role. Having made clear these properties as a criterion of adequacy, I am in a position to propose an account of evolvability that satisfies this role in Section 4 of the paper. In Section 5, I demonstrate how the theoretical machinery provided by this analysis gives us a clear and natural formal representation of evolvability, hypotheses about evolvability and the features of the world that contribute to it. It allows us to readily make sense of existing definitions and proposed cluster concepts of evolvability within a common currency—a common currency that adequately captures the role played by evolvability in evolutionary biology.

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]). The uniformity in limb length ratio is unsurprising, given that the forelimbs and hindlimbs of tetrapod are serially homologous structures. They evolved when the underlying genetic architecture (and thus the developmental program) for one modular morphological structure (a set of limbs) was duplicated and expressed in a new location resulting in replication of that morphological structure (Hall [1995]; Capdevila and Izpisúa [2000]; 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. Thus 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 (Schwenk and Wagner [2003, p.52]; Maynard Smith et al. [1985]).² While 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 here. While we are tetrapods, we have notably shorter arms than legs (Hallgrímsson et al. [2002]). Explaining human limb morphology requires us to understand how our non 1:1 hindlimb to forelimb length ratio arose despite the primitive pattern amongst vertebrate tetrapods being

² Amundson ([1994]) notes two importantly distinct concepts constraint 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.

for non-independent hindlimb and forelimb evolution. It requires us to explain why the constraint that usually exists within tetrapods due to serial homology fails.

In a recent paper, Young et al. ([2010]) describe this divergence in the limb morphology of humans from the tetrapod standard as being an example of a difference in *evolvability*. In order to explain this difference in evolvability, Young et al. ([2010]) 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 there is significantly greater variation in arm and leg length within individuals.

This disparity in limb length variation is difficult to explain by selection alone. While 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 paper, Young et al. ([2010]) attribute the increased 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.

While the case study above seems straightforward enough, what Young et al. ([2010]) mean by “evolvability” in their paper is far from clear. 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 in their work, 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.

<i>The term “evolvability is used to refer to:</i>	<i>Reference(s)</i>
(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 Szathmary ([1995]); Pigliucci ([2008])
(5) The current genetic variation in a population (rather than the prospective variation).	Houle ([1992])

Table 1. Common usages of the term “evolvability” in evolutionary biology^{3,4}

Young et al.’s ([2010]) use of “evolvability” could refer to any of usages (1), (3) or (4). The relaxation of developmental constraints acting upon 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 usage of these three Young et

³ Note 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 (e.g. form, movement, behaviour) (West-Eberhard [2003], p. 34)—(3) 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.

⁴ Note, 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.

al. ([2010]) actually intend is not clear, and thus, determining the nature of their claims and assessing them is difficult.⁵

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 respect to future mutational events, and thus, have very low prospective genetic variation. In what follows, I offer a solution to the problem of many usages of 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 research being relatively small-scale (for example explaining the evolution of a particular trait), and for 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, organisation and biological order. Fundamentally, however, evolutionary biologists are interested in explaining why the tree of life is as it is.

⁵ 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 interested in the influence of evolvability here with respect to any other traits. This is commonly the case. Biologists most often are 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.

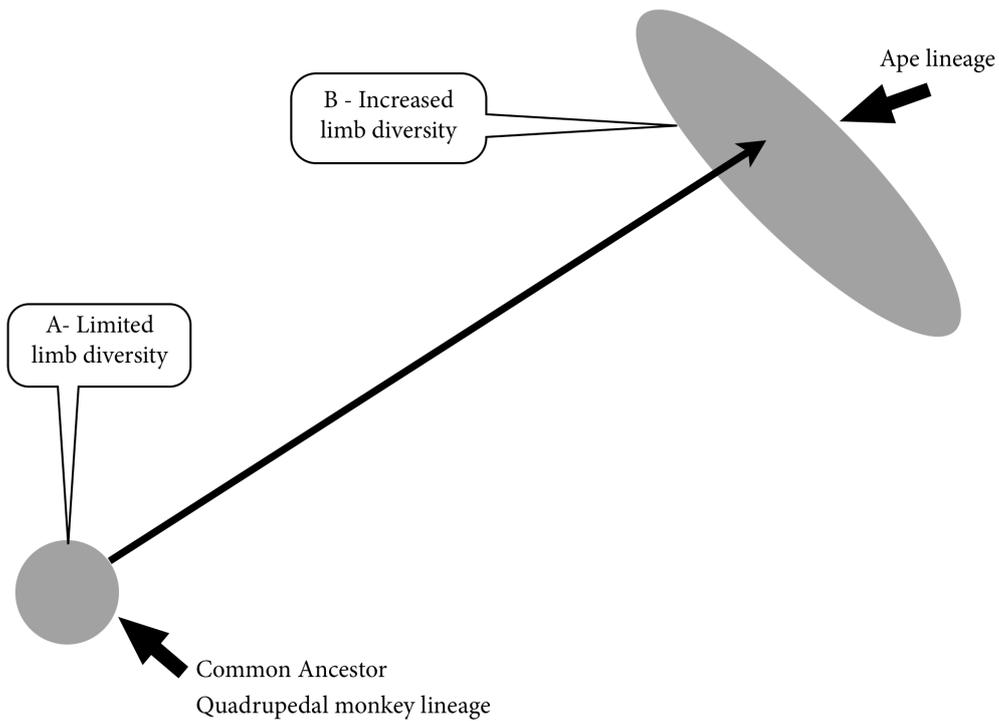


Figure 1: The explanatory interest in the Young et al. ([2010]) paper. Why is it that the quadrupedal monkey lineage has maintained a similar level of limb diversity (A) to the common ancestor and the ape lineage has increased in their limb diversity (B)?

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”⁶ with low limb length ratio diversity, to one of higher diversity, while the monkey lineage (and indeed most tetrapods) have made no such move, maintaining similar limb length ratio diversity to the common ancestor (Fig. 1). Young et al.’s ([2010]) concern is to explain a feature of the tree of life.

3.2 Selection-based explanations

While 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 are explanations that explain features of the tree of life by referring to evolution by natural selection. They refer to

⁶ A natural way to think of morphological space in this context is as analogous to Dennett’s “design space” concept (Dennett [1996], [1997]).

differences in the selection pressures acting upon populations at a given time that increase the probability of a particular evolutionary outcome at some subsequent time.⁷ For example, were the selection pressures acting upon the ancestral quadrupedal monkey populations different to those acting upon 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 upon 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 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 general trends and underlying processes that generate 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 what they are. To do this, selection-based explanations compare (rather than contrast) our world with other possible microphysical worlds, identifying those in which the evolutionary outcome or outcomes of interest would have occurred and the features common to those worlds. In the case of selection-based explanation, the thought being that even if many details of the system differed, as long as the selection pressure were to remain the same, then the evolutionary outcome of interest would still be likely to occur.

In 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 Fig. 2 (below). While a robust processes explanation only cites 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, not only is information about all the ways in which the outcome of interest could have occurred important, but also the number of ways in which the outcome of interest could have failed to have occurred. Without both these types of information the robustness of the outcome is unclear. For a selection-based explanation to be robust, it must be the case that the explanatory selection pressure is 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 case, we can say that the outcome of interest robustly occurs given the presence of the explanatory selection pressure.

⁷ 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]).

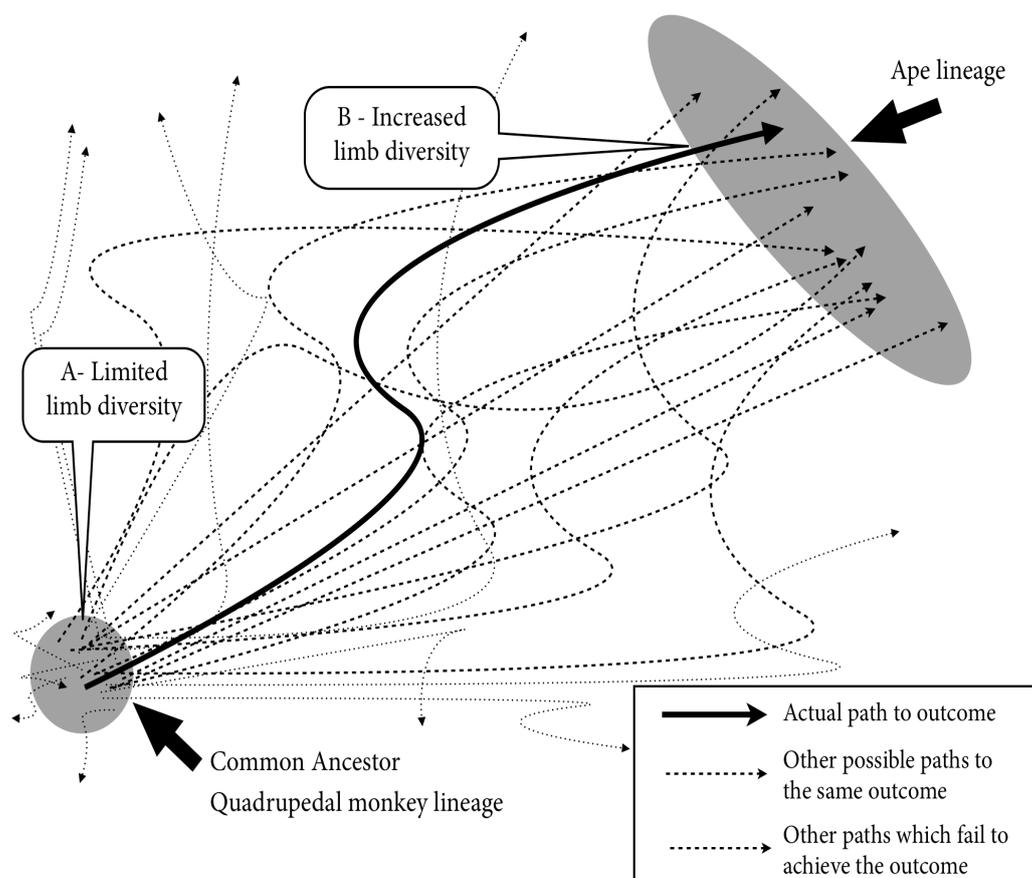


Figure 2: A selection-based explanation of the case study given in Young et al. ([2010]) would include information about the actual path taken for the ape lineage to increase their diversity as well as information about other possible ways in which the same outcome could have been achieved. Information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

3.3 Lineage explanations

While evolution by natural selection offers one prominent means of explaining the patterns we see in the tree of life, it is not the only explanation available to us. Evo-devo provides an alternative 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 upon the *internal* resources available to organisms through processes such as development. One prominent type of explanation this focus 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 on that before it, and thus the sequence provides a trajectory via which one mechanism evolves incrementally into another and thus serves to explain 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. Thus together, these two lineage explanations would provide an account of why there is a difference in limb divergence between the two lineages. Fig. 3 illustrates the type of information required.

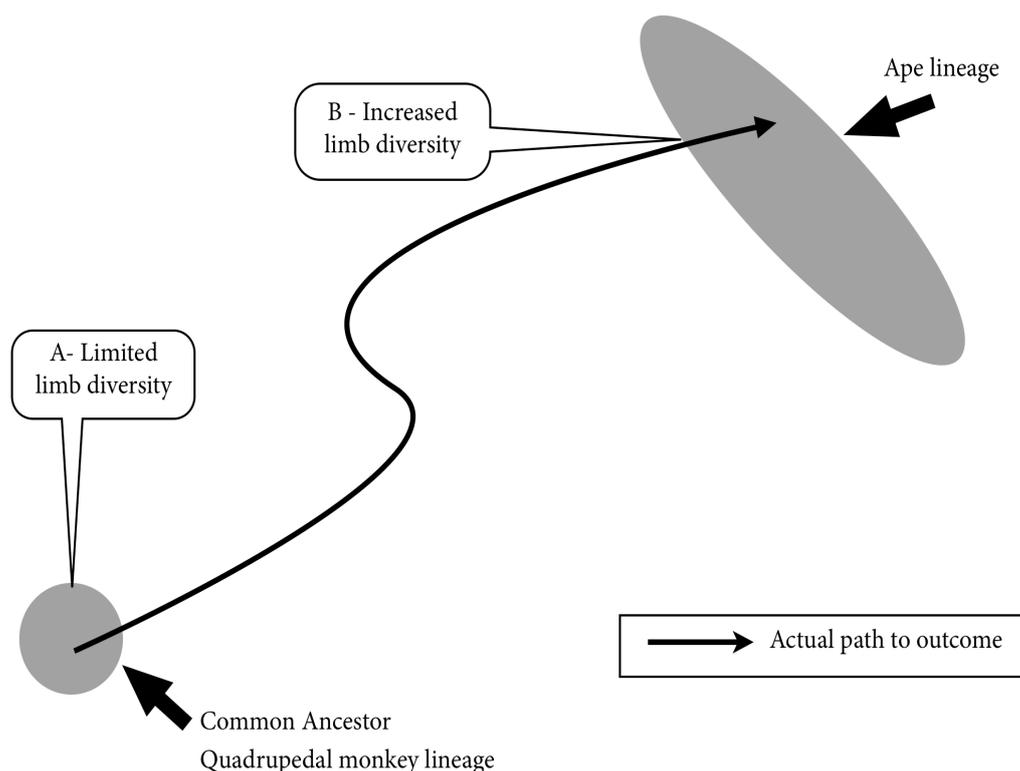


Figure 3: A lineage explanation of the case study given in Young et al. ([2010]) would include information about the actual path taken for the ape lineage to increase their diversity as well as information about the actual maintenance of similar limited limb diversity to the common ancestor in the quadrupedal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

Unlike selection-based explanations, lineage explanations do not offer information about causal robustness. Rather, they provide us with 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. While 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 explanation in evolutionary biology. In particular, they help us to explain novelty by providing information about how developmental changes generate novel phenotypic variants (Calcott [2009]). Lineage explanations do not exhaust the explanatory agenda of Evo-devo nor evolutionary biology however.

Selection can only act upon 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 selection-based explanation. The other relates to the influence of biases in the supply of variation upon which make trajectories readily available or rarely available (Gould [1989]; West-Eberhard [2003]; Arthur [2004]; Kirschner and Gerhart [2006]). Lineage explanations, while focusing upon the internal resources of organisms, cannot tell us about the extent to which the supply of variation and/or selection is responsible for any of the evolutionary trajectories they map. This is because they do not include information about how robust a trajectory is. In lacking robustness information, lineage explanations do not provide the type of information that would be required to contrast the influence of selection versus the internal resources of populations upon 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 where others do not. In claiming apes are more evolvable than quadrupedal monkeys Young et al. ([2010]) point to the disparity in limb independence between apes and quadrupedal monkeys. 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—in the past, the probability of the ancestral ape populations evolving greater limb diversity was higher than that for the ancestral quadrupedal monkey populations because of the relaxation in developmental constraint in the ape populations. Implicit in this project is what I call an evolvability-based explanation.

Like lineage explanations, evolvability-based explanations account for the outcomes of evolution by focusing upon 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 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 (e.g. 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 explain features of the tree of life because they consider the role that the internal features of populations can have upon 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 doing this, 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 upon the outcomes of evolution.

For many in Evo-devo, the evolvability research agenda is complementary to that offered by selection-based explanation. Evo-devo, in focusing upon evolvability (rather than selection), is simply focusing upon 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]).

While evolvability-based explanations are useful for contrasting the influence of selection with the influence of the internal features of populations upon the outcomes of selection, by themselves they only offer 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, upon 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 in their paper rather than provide evolvability as a stand-alone explanation. While this is the case, evolvability is nonetheless explanatorily salient and useful in this situation. By referring to evolvability early in the paper, Young et. al. to 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 paper, in pointing to the relaxation of developmental constraint, Young et al. ([2010]) 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 us alone. They offer an account of the physical realisers of the disposition (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 (Sterelny [2007]; Love [2003]). 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 effect 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 organisms within populations and their interactions. When we contrast the causal influence of the internal features of a population (evolvability) upon its evolutionary trajectory with the influence of its environment, 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 upon a population are one lower-level feature that forms part of the supervenience base for evolvability. There are however many other candidate features which 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 the usages of the term in Table 1 refer to properties of populations 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 a population. Evolvability, the broad disposition of populations to evolve supervenes on these many lower level properties. In this light, the standard definitions of evolvability given in Table 1 must be understood as focusing upon an aspect of the categorical base of a much broader disposition.⁸

While often the features listed in Table 1 are 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 (Sterelny [2007]; Pearce [2011]). In particular, they may be responsible for the maintenance of the supply of variation. 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: While 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]).

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. Thus, the evolvability of a population is more than simply any one of these features but the joint causal effect of many lower level features.

⁸ 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, it is important to be clear that this is what is intended by the usages in Table 1.

4 What Evolvability Really Is

As argued in Section 3, when evolutionary biologists make 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 assessments 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 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).

$$(E) \quad \Pr_{x, b}(f_t)$$

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 upon patterns in the tree of life and makes clear other factors which may impact upon this influence (such as time scale).

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

4.1 Making sense of f_t

In this paper, 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, the proposition 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 another. For example, while ancestral ape populations were more evolvable than ancestral monkey populations with respect to having longer legs than arms, they were not with respect to having arms and legs of the same length. This is because, while the developmental constraint upon 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. In doing this they make other outcomes less probable. Were we not to include the variable f_t we would fail to capture this important fact about evolvability.

As said, f_t is a proposition describing some future possible state of the population of interest to evolutionary biology.⁹ That state may relate to any one of the patterns in the tree of life that interest evolutionary biologists discussed in Section 3.1. For example, adaptedness, diversity, organisation or complexity.¹⁰ 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 whose focus is quite narrow. For example, part of the discussion within Young et al. ([2010]) concerns 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 whose focus is not so narrow. Evolutionary biologists also make broad claims about large-scale patterns in evolution. 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 in which the populations in question (whether it be cichlids or other fish species in the lakes) went on to have an increase in diversity and

⁹ 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.

¹⁰ Interestingly, it is conceivable that one likely pattern of interest to evolutionary biology I have not discussed here is differences in extinction rates between lineages. Extinction risk is very much 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 of prima facie interest to evolutionary biologists and is capable of being captured by this analysis.

adaptedness. In this sense, (E) is a measure of the robustness of the truth of x and b and f_t .¹¹

You may have noticed that I have time-indexed f_t . 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], p. 396). For instance, consider the primate limb case again. We want to know why the ape lineage has more limb diversification than their fellow primates, the quadrupedal monkeys. Imagine 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? While 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 our evolvability measure did not include timescale, we would have to say that both the ancestral ape and quadrupedal monkey populations were equally evolvable with respect to a non 1:1 forelimb to hindlimb length ratio, but 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 timescale.

What measure of time would be appropriate in this circumstance is unclear to me though it seems likely that it will vary depending upon 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. Imagine two populations that have the same propensity for variation due to reproduction but one has a shorter generation time than another. Over a specific time period, the population that turns over generations faster is likely to have a greater supply of variation and hence intuitively should have greater evolvability. If however, I were to use generation

¹¹ (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. $EV_{x, b}(f_t)$). 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.

time as my measure of time in (E) this difference would not be apparent. While what measure of time is appropriate to (E), it is clear that generation time is not it.

4.2 Making sense of x and b

As said previously, evolvability abstractly captures the effect of the many features individuals in a population, their causal relationships and the relevant features of environment upon 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 of those things. Indeed, they shouldn't be. Evolvability is an abstract property that captures the role of internal, rather than external adaptive causal players in generating the outcomes of evolution. Thus, 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. Thus x , b need only describe those features of the population and environment that are causally relevant to this internally derived propensity.¹² I will now make clearer what this means by considering each variable in turn.

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. In their paper, 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 upon a population are one lower-level feature that affects the evolvability of that population. As discussed in Section 3.4, there are however many other candidates for this causal role, for example population structure.

¹² The partitioning of the (x, b) pair into x and b isn't 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 up and, further to that, the partition does not effect our evolvability assessments. This is because, whether one thinks of 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 provides the account with 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 up different ways without generating differing evolvability assessments as long as the propositions in the set remain the same.

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 upon 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 role of a particular aspect of certain state of affairs upon evolvability by considering what the effect of an intervention upon those aspects of the situation would have upon the probability of a particular population evolving. (M), a modification of the basic manipulationist premise, is a formal characterisation of this. I take it to be a sufficient condition for a feature of the world to be relevant to the evolvability of a population, and thus, 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 upon the evolvability of a population if there are circumstances (v) in which some intervention changes the value of z (and no other variable) and the evolvability of that population changes.

As said, 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 in nature and thus the evolvability of a population itself is context dependent. The types of environmental properties that are important here will depend upon the features of the populations in question. Some obvious candidates are temperature (which influences mutation rate), the level of isolation of the population (which will influence the genes in 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 both act to result in the instantiation of some extrinsic property of a population and act 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 also can 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 partition up the selection-relevant and non-selection relevant aspects. I am skeptical as to the extent to which this is possible. Ultimately evolvability and selection may be more idealised notions than first thought given this. Brigandt ([forthcoming]) also notes this issue without 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 have defended 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 (i).

$$(i) \Pr_{a,b}(l_t) > \Pr_{m,b}(l_t)$$

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 in their paper 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. Young et al.’s ([2010]) hypothesis here is thus that “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 (M) 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 in (E) as in (ii). What is being hypothesised by Young et al. ([2010]) and what would need to be true to prove that hypothesis is made very clear.

$$(ii) \Pr_{a,b}(l_t) \approx \Pr_{\neg c,b}(l_t)$$

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 focus of much work within Evo-devo and the standard definitions become clearer in this light. If for example, we are simply focusing upon the influence of the standing genotypic variance in a population (or any of the features in Table 1 for that matter) upon the outcomes of evolution,

rather than the many features 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 make clear this narrower focus while retaining clarity about exactly what is being claimed more broadly.

6 Conclusion

In this paper, I make 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 which 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 compartmentalisation), which can act as difference makers upon the evolutionary trajectory of populations. While, the many existing definitions of evolvability focus upon 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 such lower-order causal features of populations and lineages and higher-order patterns in the tree of life.

*Rachael L. Brown
School of Philosophy,
Research School of Social Sciences and
Tempo and Mode: Centre for Macroevolution and Macroecology,
Australian National University,
Canberra, ACT 0200,
Australia
rachael.brown@anu.edu.au*

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