Evolvability

A Unifying Concept in Evolutionary Biology?

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1 Introduction: Evolvability

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The concept of evolvability emerged in the 1990s in association with new research fields with ambitions to extend or challenge mainstream evolutionary theory. This chapter briefly outlines debates and controversies surrounding the evolvability concept, and explains the motivation for this edited volume on the subject.

1.1 Motivation for This Book

In the early 1990s a novel concept emerged in evolutionary biology that soon became fashionable as a banner for a range of new research fields that challenged or expanded on neo-Darwinian orthodoxy. This concept was *evolvability,* the ability to evolve. Despite a variety of definitions and uses, the common denominator was a focus on the dispositions or preconditions for evolution by natural selection to occur. Many uses of the concept were associated with a structural, as opposed to a functional, perspective on evolution (e.g., Gould 2002; Amundson 2005; Wagner 2014), and it found popularity among those who sought to expand evolutionary theory in new directions and among critics of mainstream neo-Darwinism. The term also found use among more conventional evolutionary biologists as a label for new ways of measuring genetic and mutational variation (e.g., Houle 1992) and among those that wanted a less controversial term for constraints on evolution (see Brigandt 2015). Consequently, evolvability is, or is becoming, part of the theoretical foundation of fields as diverse as evolutionary developmental biology (evo-devo), evolutionary quantitative genetics (EQG), paleobiology, and artificial life. It also plays an increasing role in studies of macroevolution, in systems biology, and in digital and experimental evolution.

After 30 years of expanding research under the evolvability banner, it is time to take stock of what we have learned and to assess the influence and novelty of the concept itself. There is no shortage of reviews, perspectives, and assessments of evolvability (e.g., Alberch 1991; Wagner and Altenberg 1996; Love 2003; Nehaniv 2003; Hansen and Houle 2004; Schlichting and Murren 2004; Hansen 2006, 2016; Sniegowski and Murphy 2006; Hendrikse et al. 2007; Sterelny 2007, 2011; Pigliucci 2008; Brookfield 2009; Wagner 2010; Pavličev and Wagner 2012; Brown 2014; Kopp and Matuszewki 2014; Brigandt 2015; Vasas et al. 2015; Minelli 2017; Payne and Wagner 2019; Hansen and Pélabon 2021; Porto 2021; Watson 2021; Love et al. 2022; Nuño de la Rosa and Villegas 2022; Riederer et al. 2022), and the concept, if not always the term, has been instrumental in some influential books with structural perspectives on evolution (Kauffman 1993; Dennett 1995; Maynard Smith and Szathmáry 1995; Dawkins 1996; Raff 1996; Gerhart and Kirschner 1997; Gould 2002; A. Wagner 2005; G. P. Wagner 2014). Nevertheless, there is not yet any broad overview of the different lines of research that fall under the banner, and no comprehensive attempt has been made at synthesizing the knowledge gained in the different fields.

During the academic year 2019/2020, two of us (TFH and CP) organized a work group on "Evolvability: A new and unifying concept in evolutionary biology?" at the Centre of Advanced Study (CAS) in Oslo, to which we invited researchers with backgrounds in evo-devo, EQG, systems biology, paleobiology, and macroevolution, as well as philosophers and historians of biology. This book is an outgrowth of this project, and most of the contributors visited and participated in the discussions of the work group. Unfortunately, the project was cut short by the COVID pandemic in 2020, diminishing discussions on the macroevolutionary parts in particular. The resulting book is thus somewhat weighted toward development, population genetics, and microevolutionary perspectives, but we still see it as substantially synthetic across disciplines, and we hope it can stimulate further investigations and discussions of evolvability.

1.2 Debates and Controversies

Despite occasional earlier usage and related concepts (Sansom 2009; Brigandt 2015; Nuño de la Rosa 2017; Crother and Murray 2019), the concept of evolvability, or more precisely, *the evolution of evolvability,* arguably appeared in an essay by Dawkins (1988). This essay was part of an edited volume on artificial life and an outcome of a Santa Fe workshop on this topic. In his essay, Dawkins built on his "biomorph" artificial-life simulations and sought to characterize the fundamental preconditions for evolution to occur ("replication" and "embryology") and to ask how these preconditions themselves could evolve. He immediately sensed the radical nature of this question and started his essay with an apologetic assurance that he remained "a dyed-in-the-wool, radical neo-Darwinian." Why would such a question about the evolution of evolvability be thought a challenge to neo-Darwinism? The answer may no longer be obvious, but likely reflects a scarcity of such questions in the evolutionary biology of the time. Although similar questions had been asked on the edges of the main paradigm (e.g., Riedl 1978; Conrad 1983; Wagner 1986), the existence, or at least production, of genetic variation for natural selection to operate had the status of an axiomatic premise in textbooks and authoritative accounts of evolutionary theory. Asking new questions can happen within a paradigm, however, and need not be controversial. Okasha (2021) sees the ability to *endogenize* and explain previously external assumptions as a striking feature of evolutionary biology and a contributer to its success and generality. The endogenization of evolvability, in the form of studying the origin and structuring of genetic variability, is a paradigmatic example. The nonradical way of doing this can be seen in the books by Dennett (1995) and Maynard Smith and Szathmáry (1995), which both asked new and far-reaching questions about the origin and evolution of structures and systems that facilitate evolution, but situated these questions within and in support of the neo-Darwinian framework. In contrast, Kauffman (1993) placed his work on evolvable systems in opposition to mainstream evolutionary theory.

We can recognize four positions about the novelty of evolvability: (1) Evolvability is a radically new concept that transcends orthodox evolutionary theory. (2) Evolvability is a novel concept associated with new questions and research strategies, but these have been accommodated (endogenized) by standard evolutionary theory. (3) Evolvability is a new term with new sociological roles, but conceptually a continuation of older concepts, such as developmental constraint (e.g., Brigandt 2015). (4) There is nothing new but a pretentious name.

Reflecting perceptions of the status of the fields themselves, researchers in evo-devo may tend toward positions 1, 2, or 3, while evolutionary quantitative geneticists may tend toward positions 2, 3, or 4. The most extreme positions 1 and 4 are on display in the debates about the extended synthesis, in which evolvability is sometimes packaged with such concepts as niche construction, epigenetic inheritance, and mutation- or plasticity-driven evolution, and then either reified as overturning the old order (e.g., Laland et al. 2014) or dismissed as nothing new (e.g., Wray et al. 2014; Charlesworth et al. 2017).

Philosophers and historians of biology debate the historical and conceptual relationships among notions of evolvability in the different research fields. While some want a single unified concept (e.g., Sterelny 2007; Brown 2014), others see clusters of unrelated use (Love 2003; Pigliucci 2008; Nuño de la Rosa 2017). At first glance, the evolvability concepts in evo-devo and EQG appear different, with the former focused on the ability of the individual organism, or the genotype-phenotype map, to produce new potentially adaptive variants, and the latter focused on standing genetic variation and the ability of the population to respond to selection. There is crosstalk, however, and in EQG there has been increasing focus on how the genotype-phenotype map, in terms of pleiotropy, epistasis, and norms of reaction, acts to structure both mutational and standing variation (Hansen and Pélabon 2021). There is also a small, but persistent, stream of research aiming to connect evo-devo to population genetics and thus to population variation (e.g., Wagner and Altenberg 1996; Hansen 2006). In this endeavor, evolvability is a common focus, and if not unified, it may be unifying.

Unification is harder to perceive across scales of evolution. Perhaps reflecting the lack of a well-developed theory of macroevolution, there is no obvious connection between notions of microevolutionary evolvability describing genetic or mutational variability in quantitative terms and qualitative notions of macroevolutionary evolvability in terms of innovation and transitions among body plans. In his book on innovation, Andreas Wagner (2011) explicitly separated qualitative macroevolutionary “innovability” from evolvability, or from what he perceived as more quantitative, overly varied and “muddled” uses of evolvability. Innovation has both qualitative and quantitative aspects, however, and Günter Wagner (2014) distinguished between two types of innovation, with one being the qualitative origin of new character identities and the other being the more quantitative origin of new variational modalities.

Another point of contention regards the evolution of evolvability. Although initial concerns to demonstrate that evolvability could evolve at all now seem naive, there are more subtle matters to settle in terms of whether and when adaptations for evolvability can evolve, and the levels of selection that may cause such evolution. From the macroevolutionary point of view, one may ask whether changes in evolvability emerge gradually or if they require special events, such as transitions to states that permit qualitatively new evolutionary possibilities. The latter may involve the evolution of new character identities, body plans, or inheritance systems. Interest in the evolution of evolvability also leads to empirical questions about differences in evolvability among clades and traits, and to whether this may generate differences in diversity or disparity.

Finally, there are debates about the proper definition, characterization, and measurement of evolvability. In evo-devo, there are debates about the relationship of evolvability to modularity and integration, and in EQG there are debates about the scaling and parameterization of univariate and multivariate genetic variation that best predict evolvability.

1.3 The Chapters

Figure 1.1 provides a roadmap to the chapters in terms of where they connect to the disciplinary and conceptual landscape of evolvability research. The chapters may be read in any order depending on the interests of the reader.

1.3.1 Historical Aspects

This volume opens with a contribution from Nuño de la Rosa (chapter 2), in which she first reviews the bibliometric study of evolvability research presented in Nuño de la Rosa (2017). Indeed, the six evolvability "research fronts" identified as co-citation clusters in Nuño de la Rosa (2017) were a motivation and guide for our CAS working group. Although the six clusters, *Complex networks*, *Molecular evolution, Quantitative genetics, Population genetics, Marcroevolution,* and *Evo-devo,* may not correspond entirely to our figure 1.1, they illustrate how the evolvability concept is being used in different disciplines and trace some of the connections between them. Villegas et al. (chapter 3) update this analysis by adding citations between 2014 and 2021. They identify *Network analysis, Evo-devo, Quantitative genetics,* and *Molecular evolution* as the four main clusters of contemporary evolvability citation. Going back to chapter 2, Nuño de la Rosa then moves from a quantitative to a qualitative approach. She presents preliminary results from a set of interviews with researchers on their attitudes toward evolvability, conducted as a part of the CAS project. These interviews put on display a range of different opinions about the novelty and utility of the concept, as well as on its historical origin(s). Nuño de la Rosa then finishes her chapter with a philosophical discussion about the progress of science, even suggesting a new role for the term "evolvability" in explaining internal theoretical mechanisms that facilitate particular directions of research.

1.3.2 Conceptual Framework

Moving from history to philosophy, Villegas et al. (chapter 3) ask what conceptual roles are played by evolvability in the different research fronts. These include setting a research agenda and characterizing the phenomena to be studied. Evolvability also plays a role in explaining, predicting, or controlling other phenomena (evolvability as explanans), and as a target for explanation, prediction, or control (evolvability as explanandum). Villegas et al. then discuss the connections between these roles and the unity of the evolvability concept itself.

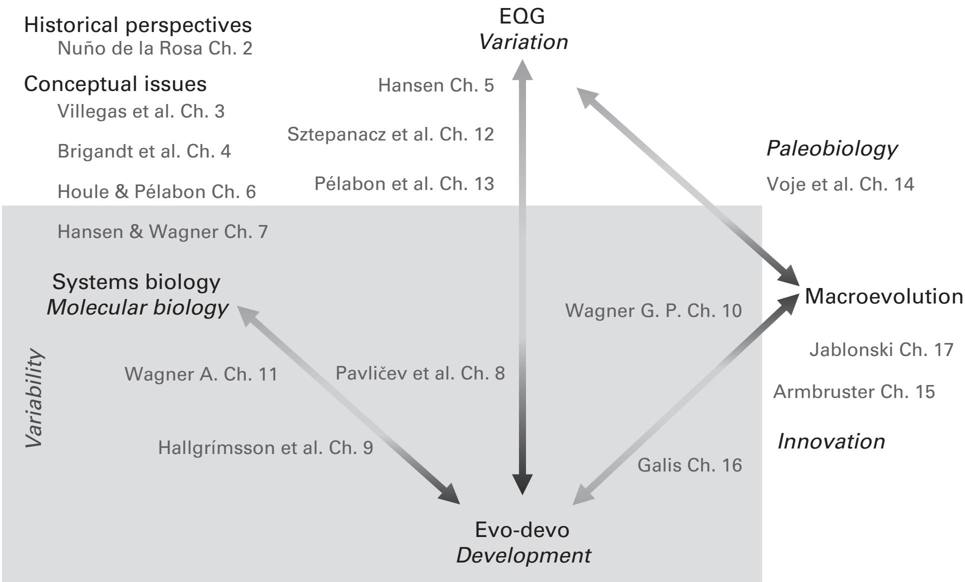

Figure 1.1
Roadmap for evolvability research: The chapters of this book are mapped out in relation to the research areas that we, the editors, see them as most connected to. We have indicated connections between research areas with arrows and placed some of the chapters in relation to these. The shaded area labeled "Variability" indicates focus on the disposition for variation (e.g., mutability), as opposed to variation as a disposition for evolution.

One of the novel aspects of evolvability is its dispositional nature (Wagner and Altenberg 1996; Love 2003; Nuño de la Rosa and Villegas 2022). Evolvability heralded a focus on dispositions or potentials in evolutionary research. In a key contribution, Günter Wagner and Lee Altenberg (1996) emphasized the distinction between variation and variability, with the latter as the potential for the former, and pointed out that these need to be treated and studied as different phenomena. Naturally, they linked evolvability with variability as joint dispositional concepts, and in most fields evolvability is operationalized as a disposition for variation or innovation. In chapter 4, Brigandt et al. discuss the nature of dispositional concepts in general and then investigate manifestations in the different areas of evolvability research. They discuss the utility of evolvability as disposition and the implications this has for unification across fields.

In many ways, quantitative genetics is the odd field out in evolvability research. In EQG, the concept of evolvability has a distinct origin as a name for a particular way of scaling genetic variation and as a replacement for the (dubious) use of heritability as a measure of evolutionary potential (Houle 1992; Hansen et al. 2011). Hence, in EQG, evolvability is mainly linked with realized nondispositional variation and less with variability. Properly constructed, however, it is still a dispositional concept, but now as a disposition for a population to respond to selection, which, at least in the short term, depends on (genetic) variation. Whether in name or not, evolvability is a major research topic in EQG. Hansen and Pélabon (2021) have argued that the key event establishing EQG as a research field was Lande and Arnold's (1983) conceptual separation of selection and evolvability in the form of the selection gradient and the additive genetic variance matrix known as the G-matrix. In chapter 5, Hansen provides a primer on EQG and discusses the various evolvability measures that have appeared around the focal concept of the G-matrix. This chapter is intended as background reading for those interested in the quantitative-genetics perspective, and it explains the meanings of key concepts in evolvability research, such as additivity and epistasis.

In chapter 6, Houle and Pélabon present a conceptual framework for operationalizing evolvability in terms of answers to "*Of-Under-Over*" questions. That is: Evolvability *of* what? *Under* which conditions? And *Over* which period of time? They use this framework to discuss the differences and unity of the concept across research fields.

In chapter 7, Hansen and Wagner outline the conceptual basis and theoretical tools for understanding the evolution of evolvability. This entails distinguishing levels and types of selection and modes of evolution and identifying the organismal properties that mediate evolvability. They additionally review the evolution of three such properties: sexual recombination, coordinated variation, and mutability.

1.3.3 The Genotype-Phenotype Map

The structuralist connotations of evolvability are most obvious in its connection with the genotype-phenotype map. Many early discussions of evolvability emphasized the role of the genotype-phenotype map in structuring variation (e.g., Dawkins 1988; Alberch 1991; Wagner and Altenberg 1996), and major determinants of evolvability, such as continuity, modularity, robustness, and epistasis, can be seen as properties of the genotype-phenotype map. In chapter 8, Pavličev et al. discuss the relationship between evolvability and the genotype-phenotype map from a theoretical perspective, with particular emphasis on pleiotropy (modularity) and epistasis (context dependency). They delineate different conceptualizations of the genotype-phenotype map and argue for a research program based on mechanistic modeling and integration of the genotype-phenotype map into evolutionary models.

In chapter 9, Hallgrímsson et al. discuss the genotype-phenotype map and its implications for evolvability from an empirical perspective grounded in developmental biology. They assess the empirical basis for dimensionality and integration of the map, and they analyze how discontinuous variation can arise from metastability in seemingly robust developmental systems.

In chapter 10, Günter P. Wagner presents a new model for a genotype-phenotype map based on basic principles of trait growth and uses it to show how developmental interdependencies may affect quantitative measures of evolvability. He further explores the consequences of changes in evolvability on the evolution of body shape and illustrates how evolvability may evolve as a by-product of selection on developmental processes.

Robustness toward genetic and environmental perturbations is a central aspect of the genotype-phenotype map with a complicated relationship to evolvability. At first sight, it seems that robustness would reduce evolvability by repressing the potential for variation. Robustness also provides opportunities for systems drift and accumulation of hidden variation, however, and may thus enhance the potential for evolutionary exploration and innovation (e.g., A. Wagner 2005, 2008). In chapter 11, Andreas Wagner explores these issues and reviews some of his extensive work on the relationship between robustness and evolvability.

1.3.4 Microevolutionary Perspectives

Microevolutionary perspectives on evolvability are mostly associated with quantitative genetics approaches or with experimental evolution. As mentioned in section 1.3.2, EQG is characterized by quantitative measures of evolvability designed to predict quantitative responses to defined selection pressures (Hansen, chapter 5; Houle and Pélabon, chapter 6). The question of what determines short-term evolvability in this sense is taken up in several chapters. In chapter 12, Sztepanacz et al. discuss the influence of mating systems and population structures on evolvability. They particularly address the effects of inbreeding on evolvability, and they discuss how evolvability relates to sexual selection. In chapter 13, Pélabon et al. provide further discussion of how ecological factors influence evolvability and its evolution. They discuss the influence of selection, gene flow and population size on the evolution of evolvability and take up the important question of how organismal plasticity and stress may interact with evolvability.

How far microevolutionary processes can be extrapolated to explain macroevolution has been a recurrent question in evolutionary biology for at least 80 years (Futuyma 2015). Accordingly, it has been suggested that patterns of short-term evolvability could limit or bias evolution at longer timescales (e.g., Schluter 1996; Hansen and Houle 2004). On one hand, estimates of standing genetic variation discussed in chapters 5, 6, 12, and 13 indicate that evolvability is usually sufficient to allow large changes on timescales above a few tens or hundreds of generations at least, and would not seriously constrain evolution on macroevolutionary timescales. On the other hand, there is accumulating evidence that quantitative measures of evolvability correlate with divergence among populations and species on fairly long timescales. This conundrum is reviewed in chapter 14 by Voje et al., who go on to discuss ideas for how these observations can be reconciled. They argue that progress would require developing models that link microevolutionary theory with the temporal dynamics of the fitness landscape.

1.3.5 Macroevolutionary Perspectives

While Voje et al. (chapter 14) consider macroevolution on moderately long timescales, they do so in terms of quantitative changes that can be directly related to microevolutionary measures of selection and evolvability. In contrast, many macroevolutionary phenomena involve qualitative changes that are not easily captured by or related to quantitative measures. The approaches of evo-devo, for example, often invoke developmental, physiological, or gene-regulatory mechanisms to understand the basis or potential for larger morphological changes.

In chapter 15, Armbruster discusses the developmental and physiological basis for repeated evolutionary patterns in the evolution of flowering plants. In doing so, he employs classical concepts in developmental evolution, such as allometry, heterochrony and exaptation, as well as newer evo-devo concepts such as co-option and modularity. He illustrates how these concepts can be used to understand the potential for evolution and discusses how to separate the roles of selectability and evolvability in macroevolution.

In chapter 16, Galis discusses constraints on early development and their consequences for the evolvability of animal body plans. She considers two hypotheses to explain the strongly conserved phase in early development known as the phylotypic stage. One hypothesis explains the phylotypic stage as consequence of pleiotropic constraints due to strong inductive interactions during this developmental stage, and the other explains it as a consequence of the genetic robustness of the gene networks that underlie organogenesis. Galis favors the former hypothesis.

A common characterization of macroevolution is evolution above the species level. In chapter 17, Jablonski takes up the effects of evolvability on speciation and extinction, and evaluates its role as an explanatory factor in diversification at the clade level. The general methodological challenge is to distinguish the effects on macroevolution of intrinsic factors, such as evolvability, from extrinsic factors, such as changes in the biotic or abiotic environment. This requires both comparative and paleobiological approaches, and new methods for their integration.

1.3.6 A New and Unifying Concept?

In the concluding chapter 18, Houle et al. summarize what we have learned about the question initially asked: Is evolvability a new and unifying concept in evolutionary biology? In this chapter, we consider both the points of views expressed in the other chapters of this book, as well as our own judgment and reflections after nearly 3 years of discussion and interaction with the participants of the CAS evolvability project.

1.4 Missing Pieces

Although these chapters cover a wide range of topics and offer different opinions and perspectives, there are some noticeable biases and omissions. A full treatment of evolvability research could have included discussions of major transitions, innovation, experimental evolution, regulatory evolution, niche construction, nongenetic evolution, and the origin of life. Separate chapters on mutation, molecular and biochemical evolution, modularity, and character identity would also have been natural, even if these topics are discussed in some of the chapters we do have. From the philosophical and historical points of view, we could have included treatments of pre-1990 research on evolutionary potential, arguments for a unified evolvability concept, and discussions of the extended evolutionary synthesis. Finally, we note the absence of perspectives from computer science, artificial life, and digital evolution.

Nevertheless, we hope that this book can be a useful source for contemporary debates and research on the potential for evolution.

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