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REVIEW

Navigating the Evolvability Landscape — Essay Review of Hansen T.F., Houle, D., Pavlicev, M., & Pelabon, C. (Eds.). (2023). Evolvability: A Unifying Concept in Evolutionary Biology? MIT Press

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Abstract

This article reviews the edited volume "Evolvability: A Unifying Concept in Evolutionary Biology?" through biological and philosophical lenses. The book provides diverse angles on evolvability, which is affected by various hierarchical levels, timescales, and types of variation, thus moving beyond a purely genomics perspective. Evolvability is important to biosemiotics because understanding the dynamics of topological genotype spaces could help one better comprehend the phenotypic spaces of meaning, as developmental codes and interrelations can influence the emergence of biological novelty over time. This book is successful in provoking thought on evolvability's role as both a product and a driver of evolutionary innovations and explores the philosophical implications of how evolution has the capacity to generate novel forms of meaning.

Keywords Evolvability · Evolutionary Biology · Philosophy of Biology · Genotype–Phenotype Mapping

"*Nothing in biology makes sense except in the light of evolution*" (Dobzhansky, 1973; Racine, 2022). Yet evolution itself remains profoundly puzzling. The edited book volume "Evolvability: A Unifying Concept in Evolutionary Biology" (Hansen et al., 2023) introduces evolvability as a unifying concept intertwining genetics, development, and environment. Just as a landscape shapes the wanderer's path, evolvability guides the meandering course of life. Through this evolving landscape, new and previously forms emerge.

Spanning 18 chapters, the book covers viewpoints on evolvability from renowned experts in the field. While evolutionary potential has become an increasingly

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acknowledged concept in evolutionary research, this book represents the latest attempt to synthesize the diverse threads of inquiry under a unifying framework. Fundamentally, evolvability refers to the capacity of a living system to generate adaptive genetic diversity and undergo evolution (Hansen & Pélabon, 2021). However, evolvability is a multidimensional concept (Janković & Ćirković, 2016) that encompasses various hierarchical levels, timescales, and types of variation of observable characteristics. One recurring theme is the need to delineate the multiple dimensions encapsulated within evolvability clearly. For example, Hansen describes the concept as a propensity to evolve based on availability, generation, and potential effects of genomic variability. Others frame the meaning of the word as the ability to vary in characteristics or traits, to respond to selection, and to explore adaptive possibilities or creative potential. Several authors argue for greater precision in defining the specific aspect of evolvability under investigation, whether it be short-term quantitative trait evolution or the generation of significant breakthroughs over macroevolutionary timeframes. A key distinction manifests between short-term quantitative evolvability, often measured as additive genetic variance, versus long-term capacity to generate significant advancements. Developing a typology of evolvability could aid theoretical synthesis and avoid confusion stemming from conflated notions (Brown, 2014; Crother & Murray, 2019).

This edited volume is distinguished by its interdisciplinary approach, blending insights from quantitative genetics, developmental biology, paleontology, and evolutionary ecology. Some segments, such as Chapter 5, delve extensively into mathematical models and equations that underpin key aspects of evolvability. For instance, offers a thorough overview of evolutionary genetics, examining key equations like the Lande equation, given as $\Delta\bar{z} = G\beta$, and the Breeder's equation $\Delta\bar{z} = V_A\beta = h^2S$, where V_A is the additive genetic variance, h^2 is the heritability, and S is the selection differential. The Lande equation is important as it relates the response to selection of a multivariate trait z to the G-matrix that quantifies the genetic variance for each trait and the genetic covariance between pairs of traits, and the selection gradient β that signifies directional selection on traits. The Lande equation provides a clear demarcation between evolvability and selection, allowing each to be studied in isolation as well as in conjunction with a unified theoretical framework, and is vital for understanding how gene pool diversity and selective pressure influence evolutionary trajectory.

The book doesn't shy away from critiquing common methodologies for measuring evolutionary potential and modeling genotype–phenotype ("GP") maps (Brun-Usan et al., 2022). Specifically, Chapters 6 and 7 point out the limitations of metrics like additive genetic variance and bring to light the context-dependencies of proposed evolvability attributes, emphasizing the necessity for a theory that connects these attributes to evolvability. Chapters 8 and 10 explain the structural properties of GP maps and their implications for evolvability, including an analysis of how the mapping between an organism's genetic information and its physical characteristics can affect evolutionary changes. The authors contend that the GP map itself can be regarded as a carrier of evolvability, as its properties directly determine the creation of inheritable trait diversity. Comprehending the topology of this mapping is vital for predicting evolutionary potential. Chapter 10 presents empirical evidence

and modeling that demonstrate how developmental interactions and sustained evolvability can result in dynamical instabilities in body plan evolution. This serves as an example of how theoretical modeling, grounded in biological first principles, can yield insights into the factors driving this second order evolutionary concept.

Chapters 6, 7, and 11 elaborate on statistical relationships between proposed evolvability attributes such as mutation rate and actual adaptive capacity for variation. They feature mathematical models and theorems that lend quantitative rigor to the study of the ability to generate heritable variation, from equations for the rate of neutral evolution and variance-scaled evolvability metrics to formalizing multi-level selection using Price's equation. Chapter 11 stands out by investigating the connections between mutational robustness and evolvability through mathematical modeling. It defines mutational robustness as the likelihood that a random mutation has no effect on fitness. Analysis suggests that while flat, extended fitness peaks encourage robustness, they hinder adaptive modifications. Nevertheless, bridging distant genotypes on neutral networks can reconcile robustness with evolvability. This book underscores the dynamic integration of abstract hypotheses with biological principles in the investigation and analysis of evolutionary dynamics. The mathematics presented throughout the chapters delivers a conceptual foundation for evolvability, allowing one to derive non-intuitive results about how processes like selection, mutation, recombination, and genetic drift shape the ability to evolve across generations.

Chapters that delve into the synergy between genetics, development, and phenotypic expression, such as chapters 8 and 9, are especially aligned with biosemiotics angle. Chapter 8, by examining the genetic expression framework and emphasizing the roles of pleiotropy and epistasis in evolvability, challenges the traditional geno-centric viewpoint by highlighting the interpretative complexity the processing of DNA blueprint and other inheritable carriers of information, resonating with the context-sensitive understanding advocated by biosemiotics. Chapter 9 further explores the developmental basis for this evolutionary concept, emphasizing how developmental systems, through stochastic metastability, can navigate the balance between robustness and potential for change. Thereby, the authors illustrate the dynamic and non-linear nature of genetic and epigenetic influences on the diversity in observable characteristics. These chapters are good examples of the importance of developmental processes and the complex genotype–phenotype relationships in shaping evolutionary trajectories, offering an interpretation that bridges genetic determinism with the interpretative flexibility inherent in living systems that is not inconsistent with biosemiotic views on the interpretative nature of genetic and development (Favareau et al., 2017).

Beyond its core scientific content, the book also somewhat engages with deeper philosophical questions regarding evolvability by examining foundational issues like whether evolvability is better framed as a propensity, capacity, or disposition (de la Rosa & Villegas, 2022). There is also extensive debate about whether evolvability should be conceptualized as a cause or a product of evolution (Payne & Wagner, 2019). Some authors advocate viewing the ability for an organism to evolve as a selectable trait analogous to adaptation, while others argue it is more an outcome of various genetic and developmental properties (Jablonski, 2022).

Resolving these conceptual ambiguities has implications for the ontological status afforded to evolvability. The book thus establishes fertile ground for philosophers of biology seeking to analyze evolvability through the lens of causation, natural selection, and the units of evolutionary process and explanation (DiFrisco & Jaeger, 2019). The authors collectively demonstrate how research on the capacity for adaptive evolution can enrich philosophical interpretations on the mechanisms of evolution.

Exploring the variable aspects of evolvability further, an intriguing perspective comes from the fact that the themes presented in the book resonate with Deacon's (2010) view on the role of relaxed selective pressure in facilitating complex adaptations in the emergence of human language capabilities. Deacon suggests that evolutionary complexity can arise not solely through direct genetic determinants but also through a combination of social, cognitive, and environmental factors in a manner that resembles the multifaceted view of evolvability presented in the book, which points out the critical role of genetic, developmental, and ecological variables in the evolutionary process. Therefore, the book strengthens the hypothesis that evolvability can operate beyond strict genetic boundaries, underscoring that semiotic processes could have a significant impact on both biological and non-biological transformation of trajectories and changes in replicators' dynamics (Nowak, 2006).

This volume holds special relevance for scholars investigating the intersection of evolution and cognition as several chapters include a discussion on the mechanisms by which evolvability arises from the GP mapping process (Lacková, 2018). Understanding how inheritable information gets translated into hereditary characteristics and capabilities touches on fundamental questions about the nature of cognition and the evolution of cognitive complexity. Mapping the topological genotype and phenotypic spaces could shed light on the prerequisites for cognitive evolution and the emergence of intelligence (Schnell et al., 2021). By revealing the generative mechanisms underlying complexity in life sciences, the authors provide conceptual tools to investigate the evolutionary origins and constraints on cognitive architectures. Biologists interested in the evolution of morphological novelties and developmental innovations thus can gain key theoretical insights about evolvability's role in cognitive evolution from this integrative synthesis.

A significant strength of the book is the expertise of its contributors. The chapters feature original contributions from prominent academics who have shaped the modern study of evolution. This gives the book significant weight and influence within the field. The chapters achieve an effective balance between abstract modeling, concrete data analysis, and historical context. While covering an expansive intellectual terrain, the book is not without limitations. Some chapters seem overly focused on abstract conceptual principles without clear connections to empirical data or testable hypotheses. A few chapters also suffer from dense mathematical formalism that may limit accessibility to a wider audience. Additional synthesis between chapters highlighting the interconnections between concepts and additional chapters on software implementation (Watanabe, 2023) would have been valuable. Furthermore, expanding the disciplinary outlook beyond evolutionary biology/ecology/genetics to other disciplines, such as medical oncology (Takamatsu et al., 2020), economics (Cochrane & Maclaurin, 2012), linguistics (Deacon,

2010, as mentioned; Winter, 2014), and biosemiotics (Hoffmeyer, 2008), may have enriched the discussion of evolvability.

An example of how the concept of evolvability is deeply intertwined with the principles of biosemiotics is the argument that the emergence of new or modified sign relations in agents plays a pivotal role in evolutionary processes (Sharov & Tønnessen, 2021, Chapter 8). Rather than adhering to the gene-centric angle, this perspective promotes an agency-centric approach, where organisms and their subagents actively interpret genetic information (Sharov, 2021). This approach is not unreasonable because organisms, by actively interpreting hereditary information within an intricate network of gene-environment relations, could exercise a form of biological agency that enables adaptive evolutionary changes, reflecting a non-deterministic flexibility or freedom of choice in the sentence that organisms can interpret the signal based on its context (Kull, 2023), that contrasts with the fixed laws governing physical systems. For example, evolutionary adaptations may emerge from the interpretative plasticity of organisms, where changes at the phenotypic level drive evolutionary shifts. Therefore, adaptations in evolutionary biology could be viewed as a semiotic phenomenon, where the success of an organism ("semiotic fitness") is not merely a matter of survival and reproduction but rather its competence in interpreting and understanding "genotype-envirotype" linkages. How does the interpretative activity of organisms influence evolutionary transformations? In what ways do semiotic interactions between organisms and their environments contribute to evolutionary innovations? Clearly, a more integrated approach to understanding the evolutionary dynamics that encompass not just biological but also semiotic processes could enable us to better understand evolution (Hendlin, 2021).

The edited book could benefit from the inclusion of standpoints on how semiotics, based on Conrad's hierarchical adaptability theory (Conrad, 1983; Ulanowicz, 2002), could enhance the understanding of evolvability by looking at the connection between adaptability and adaptation. For example, consideration of not just genetic and phenotypic diversities but also the systemic and environmental factors that facilitate evolutionary change aligns well with the book's theme of evolvability. Furthermore, Conrad and Ulanowicz's emphases on the interconnectedness and the emergent properties of ecological networks aligns with the book's principles of exploring GP maps, while the quantifying of adaptability through conditional entropy and connectivity could offer new methods for assessing evolvability and deepen the exploration of the capacity to generate variation by showcasing how a system-level attribute such as adaptability may contribute to evolutionary potential. Finally, the book's approach to evolvability could also gain further depth by addressing the idea that the ability of an organism to generate heritable characteristics could be affected by different types of stability (for example, equilibria that are m-stable but not locally δ-stable may lead to polymorphism and exhibit a greater spectrum of evolutionary dynamics over time), which could be analyzed in the context of game theory (Li, 2023).

In conclusion, the edited book offers fresh viewpoints on how evolution shapes the capacity for future evolution. The collection of essays presents a rich synthesis of the current state of evolvability research while also posing provocative questions that drive the field forward. While the question posed in the title remains open,

this volume makes a compelling case for the potential of evolvability as a unifying concept. By merging deep scientific inquiry with philosophical reflection, the book reminds us of how "*evolution is cleverer than [we] are*" (Dennett & McKay, 2006).

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Declarations

Ethics Approval and Consent to Participate This article did not involve any human participants or animals.

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