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Evolvability

A Unifying Concept in Evolutionary Biology?

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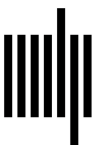
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2 **A History of Evolvability: Reconstructing and Explaining the Origination of a Research Agenda**

Laura Nuño de la Rosa

This is one of the main reasons why most practicing scientists don't end up working on things that are fundamental: Because they don't know the history of things.

—Russ Lande

This chapter addresses the origination of evolvability research with the aim of contributing more generally to the reconstruction and explanation of the recent history of evolutionary biology. I combine co-citation analysis and first-person reconstructions of the history of the field obtained from a series of interviews with evolutionary biologists who were and/or are currently active in evolvability studies. After a preliminary methodological reflection, I present a reconstruction of the multiple origins of evolvability research. In the last section of the chapter, I make use of cultural evolution theory to discuss two kinds of explanations that might account for this pattern: “Selectionist” explanations highlight aspects of the methodological and intellectual landscape that promoted the acceptability and diffusion of the evolvability perspective; “evolvability” explanations address the role of internal, theoretical developments involved in the origination and diversification of evolvability research. Although selectionist explanations have been largely explored, internal factors accounting for the evolvability of scientific concepts and theories remain relatively neglected. I argue that explaining the recent history of evolvability research from this perspective provides promising insights to our understanding of science dynamics.

2.1 Introduction

Although the idea of evolvability, as for almost every topic in evolutionary biology, can be traced back to Darwin, evolvability as a research program only emerged in the late 1990s. Compared to the concern with constraints, which remained steady throughout the 1990s and has fallen gradually over the past decade, the interest in evolvability underwent an exponential growth in the first half of the 2000s and has continued to increase after 2005 at a slower pace (see figure 2.1). Since the late 990s, evolvability research has increased and diversified in several domains of biology, being considered by some as one of the main “expanders” of the Evolutionary Synthesis (Pigliucci 2009).

This chapter addresses the historical origins of evolvability research with the aim of contributing more generally to the reconstruction and explanation of the recent history of evolutionary biology. Even more broadly, I aspire to shed some light on one of the most fascinating questions in the history of science, namely, “[b]y what processes do intellectual

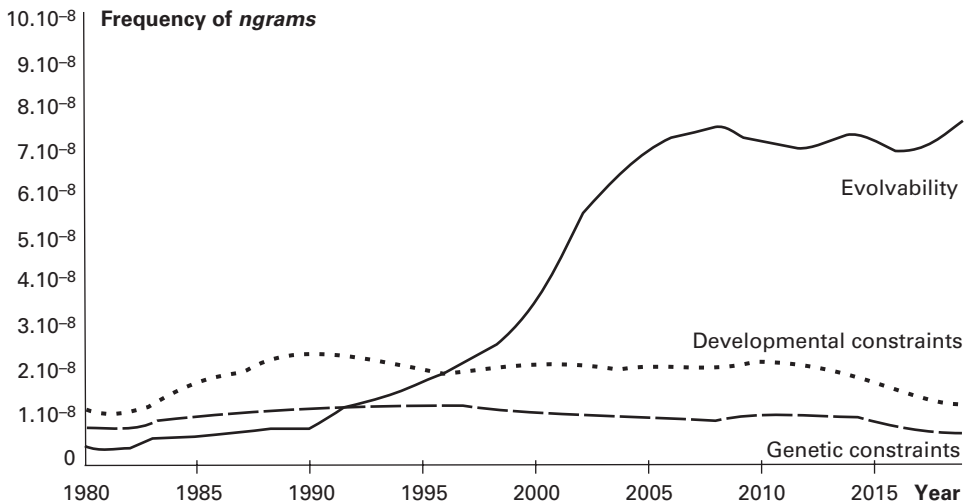


Figure 2.1

Graph charting the frequency of use of the phrases (*ngrams*) “evolvability,” “genetic constraints,” and “developmental constraints” in Google Books written in English between 1980 and 2019. The *y* axis corresponds to the number of times an *ngram* (e.g., *evolvability*) is used as compared to the total number of words (or two-word phrases) in all books published each year (*x* axis). This is the reason that the numbers in the *y* axis are so small, but what matters is the comparison between the frequencies of each phrase. Adapted from the graph generated by Google Books Ngram Viewer.

innovations originate, spread, and establish themselves within a scientific tradition?” (Toulmin 1967, 460).

Over the past few years, different bibliometric methods, including temporal reconstructions of citation landscapes and co-word analyses, have been employed for studying the dynamics of scientific fields (Chavalarias and Cointet 2013). Co-citation networks, where nodes correspond to cited references and links to co-citation relationships (Small and Griffith 1974), are particularly useful for analyzing and mapping the conceptual and dynamical structure of research agendas. In a previous work, I used co-citation analysis to study the interdisciplinary structure of evolvability research (Nuño de la Rosa 2017; see also Villegas et al., chapter 3).¹ I concluded that the evolvability research program shows a complex conceptual structure organized in six partly overlapping disciplinary clusters: complex network analysis, molecular evolution, quantitative genetics, population genetics, evo-devo, and macroevolutionary studies (see figure 2.2).

Although recent studies have looked at the early meanings and usages of the evolvability concept (Crother and Murray 2019), the origination of evolvability as a research program organized around a set of coordinated problem agendas (Brigandt and Love 2012) remains largely unexplored. To inquire into the generation of the clusters and the resulting interdisciplinary structure of evolvability research identified in my previous work, here I compare evolvability co-citation networks from different time periods (see figure 2.3 in section 2.3). Moreover, with the aim of interrogating the biographical, societal, and theo-

1. References to chapter numbers in the text are to chapters in this volume.

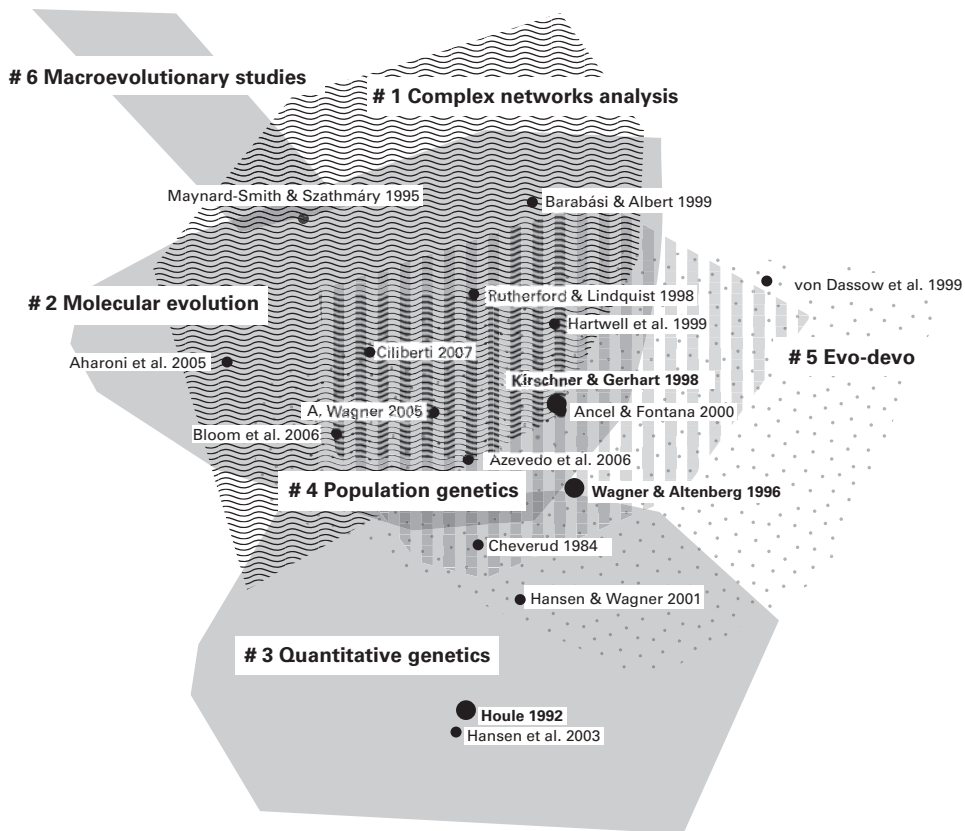


Figure 2.2

Evolvability co-citation network. Modified from Nuño de la Rosa (2017), Figure 3. Nodes represent the most co-cited publications within the network. Co-citation links have been removed. The clusters group publications linked together by a higher number of co-citation links. Bibliographic records were gathered from the Web of Science, based on a topic search for papers on “evolvability” or “evolutionary adaptability” published in English between 1970 and 2014. The data file, containing 1,039 full records and cited references, was imported to CiteSpace 3.9.R7 to map a single network. Check the Methods section in Nuño de la Rosa (2017) for more details.

retical processes generating this pattern, I combine quantitative bibliometric analysis with a series of in-depth interviews with evolutionary biologists who were and/or are currently active in evolvability studies. In alphabetical order, this chapter includes content from 25 interviews with Scott Armbruster, Steve Arnold, Richard Dawkins, Frietson Galis, Benedikt Hallgrímsson, Thomas Hansen, David Houle, Gene Hunt, Johannes Jaeger, Russ Lande, Lee Hsiang Liow, Michael Lynch, Joanna Masel, Mihaela Pavličev, Joshua Payne, Massimo Pigliucci, Christophe Pélabon, Arthur Porto, Peter Schuster, Arlin Stoltzfus, Jacqueline Sztepanacz, Masahito Tsuboi, Kjetil Voje, Andreas Wagner, and Günter P. Wagner. Most interviewees were participants of the project on evolvability that took place between 2019 and 2020 at the Centre for Advanced Study (CAS) in Oslo. Some of them (Arnold, Dawkins, Jaeger, Lande, Masel, Pigliucci, Schuster, Stoltzfus, and A. Wagner) were not directly involved in the CAS project but were interviewed either because of their historical role in the origination of evolvability research in different disciplinary areas or

because of their current work on evolvability-related issues. In what follows, content and literal excerpts from these interviews will be identified by placing each interviewee's surname in parentheses after the excerpts.

After a preliminary reflection on the advantages and drawbacks of quantitative bibliometric methods and qualitative interviews for studying the recent history of science (section 2.2), I present a historical reconstruction of the multiple origins of evolvability research (section 2.3). In section 2.4, I make use of some conceptual resources from cultural evolution theory to discuss two kinds of explanations that might account for the historical pattern leading to the origination of evolvability research: "Selectionist" explanations highlight aspects of the methodological and intellectual landscape that promoted the acceptability and diffusion of the evolvability perspective; "evolvability" explanations address the consequences for empirical research of internal, theoretical developments in evolutionary biology. Although selectionist explanations have been largely explored by cultural evolutionists, internal factors accounting for the evolvability of scientific concepts and theories remain relatively neglected. I argue that explaining the recent history of evolvability research from this perspective provides novel, promising insights to our understanding of science dynamics.

2.2 Some Methodological Reflections: From Ideas to People and Back

Bibliometric methods, in particular co-citation analysis, are particularly advantageous for reconstructing the history of research agendas. The most obvious merit is that they avoid subjective biases affecting first-person reconstructions of conceptual lineages. The virtuous decoupling of historical patterns from explanatory processes is particularly useful for circumventing theoretical biases in the philosophy of science, where historical narratives are often shaped to illustrate one's preferred approach (Chavalarias et al. 2022). Importantly, bibliometric methods also allow us to separate intellectual descent from conceptual convergence, or the emergence of the same research themes in different disciplinary environments. Co-citation networks are particularly useful in this regard, insofar as they include not only publications on our topic of interest but also the references cited in these publications, which permits reconstruction of the disciplinary background they belong to. Co-citation analysis is also a good sieve for separating intellectual traditions from mere historical precedence. The history of evolvability research abounds in cases of predecessors who did not have an influence in subsequent studies. Andreas Wagner refers to a paper on protein evolution (Lipman and Wilbur 1991) that preceded Peter Schuster and colleagues' work on neutral networks, but that he was unaware of when he started working on evolvability-related issues (A. Wagner). Frietson Galis's thinking on the evolvability of body plans was highly influenced by Rudy Raff (1996), although she later discovered that it was Klaus Sander (1983) who first characterized the phylotypic stage more than a decade earlier. Some of the precedent works that were neglected by a scientific community are often written by the same authors who are later acknowledged as the founders of the field. Günter Wagner's work is a good example. Although his article in *Evolution* (G. P. Wagner and Altenberg 1996) is widely perceived as a founding work on evolvability, he identifies a series of papers starting in 1981 (G. Wagner 1981) as his first work on the evolution of evolvability. As we will see in this chapter, many more earlier works can be identified as

precedents of evolvability-related ideas. However, when following the history of a scientific field rather than a specific idea, the question is not whether there are historical precedents of this idea, but rather when it became a well-identified research agenda: “Very often, the topics arrive early, but the question is whether they precipitate sustained research effort or not” (G. Wagner).

Finally, the dynamics of ideas are relatively independent of their individual carriers, and co-citation analysis allows us to detect wide patterns of usage of methodological and conceptual resources that are independent of the explicit purpose for which they were originally conceived. An illustrative example is the mutation (M-) matrix, a quantitative genetics parameter that describes the effects of new mutations on genetic variances and covariances (Jones et al. 2007). Although introduced in the 1980s in the field of quantitative genetics, the M-matrix is not even recognized by its users as a measure of the potential to evolve: “turning a science into ideology only works by simplifying things, not seeing things that go beyond your framework [...] you are doing it yourself even if you don’t want to” (G. Wagner). Another example is the separation between selection and the evolutionary response to selection in the multivariate version of the breeder’s equation introduced by Russ Lande and Steve Arnold in their seminal paper (Lande and Arnold 1983). This separation is interpreted in several interviews as a key step in evolvability research, but Lande and Arnold themselves highlight different aspects of their contribution to the topic (see section 2.4.2).

Notwithstanding their advantages, bibliometric methods also have serious flaws. First, many works are cited but not read. This leads to miscitations and propagation of “mutated memes,” as Conner and Lande (2014) warn about many references to the botanist Raissa Berg. Berg (1960) is one of the earliest proponents of a modularity hypothesis for the differential evolvability of floral and vegetative traits. She argued that floral traits were subject to stabilizing selection due to specialized pollination, leading to decoupling of the floral and vegetative traits into separate “correlation pleiades.” This claim is often mistakenly interpreted, according to Conner and Lande, as entailing that flowers are tightly integrated organs (but see Armbruster et al. 2014). Second, some papers are retrospectively magnified. There are plenty of “courtesy citations” to works perceived by scientific communities as important ancestors of a given idea, even when these works did not have a real influence. For instance, Andreas Wagner refers to Alberch (1991) as the “go-to” citation on early work on genotype-phenotype maps, a paper that he himself cites, even though he does not think it offers a clear treatment of the topic (A. Wagner). Moreover, even when citations are not mere courtesy, it is hard to know what their real influence was. For instance, in the introduction to their paper, Lande and Arnold (1983) present their measure of selection as a kind of response to Gould and Lewontin’s (1979) criticism of adaptationism. However, when asked about the influence of this criticism, Arnold denies that it played any role: “Gould and Lewontin 1979 didn’t acknowledge the fact that measuring selection is a way to tackle the adaptationist paradigm. It’s basically a rhetorical paper that enjoys and generates conversation, but not research” (Arnold). A further phenomenon that is hard to detect from mere citation patterns are rediscoveries. For instance, although modularity was a well-known topic in the zoological literature, it only became a topic of interest in plant evolution after the rediscovery of Berg’s work (Lande 1979, 1980). Lande’s citations of Berg’s works led Jim Cheverud to read Berg, and they caused Scott

Armbruster to write an article testing her ideas (Armbruster et al. 1999), which in turn brought Berg's thinking to the attention of more botanists (Cheverud, Armbruster).

A second group of limitations of bibliometric methods has to do with how scientific knowledge is transmitted. Citations do not reflect the transmission of exact copies of ideas but interpretations of them. This is a well-known shortcoming of meme-like models of cultural evolution (Sterelny 2006): The transmission of information is not about copying but about inferential reconstruction, and reconstructions are highly biased by a multiplicity of psychological and social factors. Therefore, cultural transmission, including the transmission of scientific ideas, can be highly inaccurate. Nonetheless, many factors have been shown to enhance the reliability of cultural transmission, from group size (Henrich and Boyd 2002) to epistemic scaffolds, such as well-designed specialized vocabularies (Sterelny 2006). In science dynamics, both the increase in size of scientific communities and the epistemic scaffolding that accompanies the institutionalization of disciplines promote the reliability of transmission of scientific ideas. However, when scientific fields are nascent, the small size of the disciplinary community and the lack of epistemic scaffolds make bibliometric methods poor tools for reconstructing the origination of a field. This situation can linger for decades in some fields. This is the case, according to Joanna Masel, for theoretical population genetics, which still lacks mentors and an acceptable textbook that would serve the purpose of training people in a common background (Masel).

Finally, just as fossils are imprints of ecological interactions, very often citations are just traces of true intellectual exchanges. Many anecdotes from our interviews illustrate this point, such as that of the day when Steve Arnold, one of the founders of evolutionary quantitative genetics, met Pere Alberch, one of the originators of evolutionary developmental biology:

I remember being at a party [. . .] when Pere Alberch had come to give a seminar in Chicago. We both had a few drinks, and he started attacking evolutionary quantitative genetics. So I started beating him about this, and he got very heated. My feeling was that he didn't understand my field, whereas I understood his field and its limitations rather more vividly than he did. So we were in each other's faces, battling for our approaches. *I think this captures the essence more than the subtleties of who is referencing whom.* (Arnold, my emphasis)

Asking the very actors who were involved in the origination of our field of interest seems like a natural choice to interpret and complement the information obtained by citation analysis. Although the list of interviewed evolutionary biologists referred to above is by no means exhaustive, I believe it is a fair representation of the individual "carriers" of the evolvability program. Interviewees include the authors of some of the seminal works of evolvability research identified by co-citation analysis, as well as biologists from a variety of disciplinary approaches (paleontology, evolutionary genetics, evo-devo, molecular evolution, evolutionary computing, and systems biology) and taxonomic specialties (molecular, plant, and animal evolution). Nonetheless, two important biases in the choice of people need to be acknowledged. First, quantitative geneticists are clearly overrepresented compared to biologists with other backgrounds. Second, senior and male scholars have a disproportionately higher representation compared to female and young biologists. The first bias is inherited from the composition of the members of the CAS project and is partly compensated for by interviews with biologists who visited the CAS and a few who were external to the project. The second bias is attributable to the historiographical

nature of the interviews project. Although partially mitigated by including younger and women researchers when considering the totality of topics covered in the interviews, the historiographical aims of this chapter impede the correction of this bias.

2.3 The Multiple Origins of Evolvability Research

Phylogenetic approaches to the history of science attempt to reconstruct patterns of conceptual descent with modification that are assumed to be independent of mechanisms explaining these patterns (Lennox 2001). Patterns of conceptual descent include not only genealogical intellectual relationships but also the tempo of conceptual change, which, just like organic evolution, shows periods of stasis and change.

A preliminary comparison of co-citation networks of evolvability works published in different time periods delivers a good first approximation to the origination of evolvability research (see figure 2.3). Concerning the tempo, a clear explosion of interest in evolvability occurred in the early 2000s, as shown by the burst in citations in the 5 years separating the two networks (see also figure 2.1). Regarding the pattern of conceptual descent, the origins of evolvability studies seem as heterogeneous as the agenda itself, although interdisciplinary exchanges appear to have been crucial in its expansion and diversification. Figure 2.3a, comprising references cited from 1990 to 2000, shows a clear dominance of quantitative genetics research on evolvability. The 1992 article by David Houle occupies the center of the network, connected to a cloud of works on heritability in quantitative genetics (Mousseau and Roff 1987; Falconer 1989; Messina 1993) on the left, and two closely linked papers (G. Wagner and Altenberg 1996; Kirschner and Gerhart 1998) on the right. In figure 2.3b, covering the period between 2000 and 2005, the developmental evolutionary approach to evolvability, represented by G. Wagner and Altenberg 1996 and Kirschner and Gerhart 1998, has moved to the center, while quantitative genetics publications on evolvability are displaced to the right, indicating that they no longer represent the central conceptual framework in evolvability research. In turn, there is an explosion of connections to new disciplinary fields, including computational evolution (Kauffman 1993; Altenberg 1994) and neutral networks (Schuster et al. 1994; Huynen et al. 1996; van Nimwegen et al. 1999; Ancel and Fontana 2000) on the left, and canalization (G. Wagner et al. 1997; Rutherford and Lindquist 1998; Rutherford 2000), molecular evolution and evo-devo (von Dassow and Munro 1999; von Dassow et al. 2000) on the right.

Historical roots differ, depending on the disciplinary context. Evolvability means different things (Pigliucci 2008; Brigandt et al., chapter 4) and plays different roles (Villegas et al., chapter 3) in evolutionary biology. This plurality reflects the historical reconstructions of the origination of each disciplinary approach to evolvability, as well as the perceptions of how evolvability studies relate to classical work in evolutionary biology. In turn, this heterogeneity in evolvability research reflects the heterogeneity of biology as a discipline. Steve Arnold points out this issue when asked about the different views of evolution endorsed by quantitative geneticists and evolutionary molecular biologists: “It’s probably asking too much that the generalizations coming out of evolutionary quantitative genetics are going to find a receptive ear in molecular evolution circles [. . .] we are literally talking different languages, and literally thinking about different empirical systems” (Arnold).

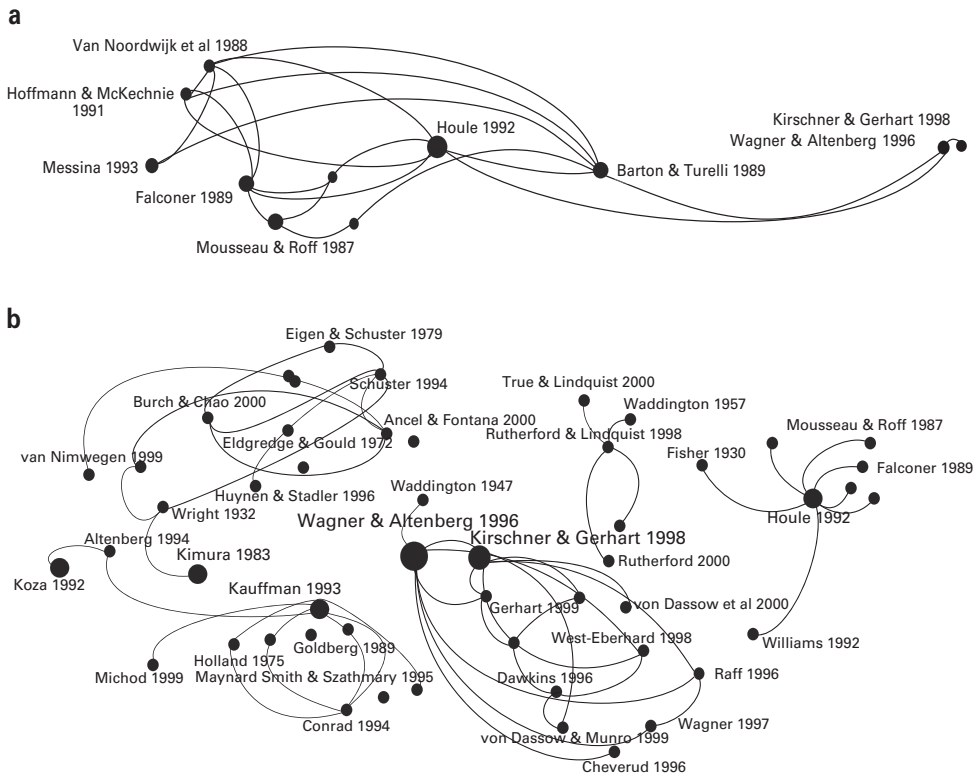


Figure 2.3

Co-citation networks on evolvability. Nodes correspond to cited references and edges to co-citation links. Bibliographic records were gathered from the Web of Science based on a search for publications containing “evolvability” in their title, keywords, or abstract, and published in English between 1990 and 2005. Full records and cited references were downloaded. This datafile was imported into VOSviewer, version 1.6.17 to build and visualize the co-citation networks. Figure 2.3a corresponds to works published between 1990 and 2000 with more than five citations, and cited references. Figure 2.3b corresponds to publications between 2000 and 2005 with more than seven citations, and cited references. Only the main nodes and a few representative co-citation links are shown. Navigable networks can be found in the book’s online resources.

In considering evolvability as the ability of populations to respond to selection, evolutionary geneticists tend to see a clear continuity between themes discussed in classical population genetics and what is now called evolvability. In her interview, theoretical population geneticist Joanna Masel recognizes some of the classical work of the founders of population genetics (e.g., Fisher’s on genetic linkage or the red queen hypothesis on the evolution of sex) as works on “the challenges to rapid adaptation.” Although these works emphasized sex rather than other concepts currently related to evolvability (e.g., robustness or modularity), they were still works on “the limits to the rate of adaptation,” which Masel interprets as limits to evolvability. According to Stoltzfus, this early identification of evolvability with rapid adaptation was influenced by the belief that the age of the earth might be much younger than the current estimate of 4.5 billion years. This was “one reason why Haldane and Fisher believed that evolution would take place based on abundant standing variation: it’s faster” (Stoltzfus).

From the perspective of a quantitative geneticist such as David Houle, research on evolvability concerns the more general question of “what are the conditions under which

evolution is possible?” In this view, “the intellectual tradition of what is now evolvability” also includes classical works in population genetics:

When I wrote the 1992 paper I thought these were things that everybody was already thinking about. I would trace the ancestry of that back to Fisher and Wright at least [. . .]. What are the conditions under which evolution is possible? Wright’s shifting balance theory, for example, is in that sense about evolvability: he had this idea about the combination of internal states, population states and selective environment that would enable new things to come about in evolution. Fisher similarly worked on that [. . .]. For example, Fisher microscope models: how to approach an optimum? This is kind of about evolvability. (Houle)

From this perspective, “far from being something that was ignored,” evolvability is “something that wasn’t named evolvability in the past” (Houle). In particular, Houle links the origins of his work on evolvability to his early interest in heterosis, or the problem of the advantage of being a heterozygote. He interprets this interest as “a component of a larger problem,” namely, the maintenance of genetic variation: “Implicitly (or explicitly, depending on how you want to see it), that connects to the issue of what we now call evolvability, because without genetic variation, you don’t have any ability to evolve at all.” Houle recalls that at the time he started his PhD, there was an important controversy over the maintenance of variation in life-history traits. According to the famous table in Falconer’s textbook in quantitative genetics (showing up in our network in the 1989 edition; see figure 2.3), life-history traits were less heritable than morphological traits and therefore were regarded as less responsive to selection. In thinking of fly wings, Houle noticed that wings did not vary much and that the concepts of heredity and evolvability were not the same thing. This led him to introduce a new mean-standardized measure of evolvability, defined as the ability of populations to respond to selection (Houle 1992). Why he decided to call this ability “evolvability” did not rely on him being aware of other uses of the term. He did not know about Dawkins’s paper (1988), although he recalls that Stuart Kauffman visited his university when he was a graduate student and he might have heard the word (Houle).

Houle’s definition and measure of evolvability has become the central reference for evolutionary quantitative geneticists (see figure 2.3b). In the view of the interviewees in this field, the ability of populations to respond to selection is not a new topic of research but instead a new measure of such a capacity: “a way of scaling genetic variance, and not necessarily [. . .] a thing in itself” (Sztepanacz). In Christophe Pélabon’s view, the interest in evolvability was already present in the work on heritability, insofar as heritable traits were those considered to respond to selection. According to him, the novelty of evolvability does not come from the idea of evolvability itself but rather from the recognition “that traits can differ in their evolvability.” Pélabon quotes Mousseau and Roff (1987), an important node in our network (see figure 2.3a), as one of the first works to deal with this issue. Although Mousseau and Roff discussed heritability and therefore used a poor method of standardization, Pélabon thinks that the question that traits differed in their ability to respond to selection was already present in that paper. Furthermore, if one includes the maintenance of variation in the definition of evolvability, previous works on such phenomena as mutational meltdown (Gabriel and Lynch 1993), or the inability of populations to maintain themselves due to the accumulation of deleterious mutations, might also be considered as precedents of evolvability research (Lynch).

Paleontologists (Hunt, Liow) and quantitative geneticists working at the intersection of micro and macroevolution (Porto, Tsuboi, Voje) were all interested in constraints early in their careers and see the latter as the flip side of evolvability. The idea that species and clades differ in their intrinsic ability to evolve is also regarded as an old idea in macroevolutionary studies (see Jablonski, chapter 17). Nonetheless, some of the publications identified as seminal works of this approach are perceived by some evolutionary geneticists as endorsing a very different view of evolution. In this regard, the key reference showing up in our network is Eldredge and Gould (1972) on punctuated equilibrium (see figure 2.3b). Researchers working on macroevolutionary scales see evolvability as a core component of the punctuated-equilibrium hypothesis, “in that an increase in evolvability during speciation allows new species to appear, while species that have emerged seem to have rather low evolvability, since they are not changing at all” (Voje). Two other recurrent works in our interviews with paleontologists are Vermeij (1973) on the role of dimensionality for the evolutionary “versatility” of body plans, and Lloyd and Gould (1993) on species selection on variability.

Younger evolutionary geneticists working on macroevolution tend to perceive “a natural continuity” between classical evolutionary genetics and current studies on evolvability. Masahito Tsuboi associates evolvability with the interest in “how genetic variation arises in the first place,” a concern that has not been much addressed in evolutionary genetics but was present early on (Tsuboi). In contrast, biologists endorsing a mechanistic understanding of evolvability do not recognize clear precedents in evolutionary genetics. This is true for Massimo Pigliucci, who does not see any intellectual ancestor of evolvability research in classical population genetics. Molecular evolutionist Arlin Stoltzfus argues that mutational biases in the introduction of variation were neglected in classical evolutionary genetics. However, the received view of evolution as selection shifting gene frequencies from abundant variation in gene pools, started to collapse with the irruption of comparative genetics in the 1960s. In this regard, Stoltzfus identifies an important mechanistic shift in the 1980s, when biologists “began to think about evolution like mutationists, and to treat evolution as a Markov chain of mutation-fixation events.” This new way of thinking and modeling evolution led to the emergence of molecular evolution, an approach that “was absolutely not predicted” by standard theory (Stoltzfus). This “shift to mutationism” is interpreted as an instance of what H. Allen Orr (2002) has called the “curious disconnect” between the mathematical models and the verbal theory of evolutionary genetics (Stoltzfus; see also Stoltzfus 2012, 2017).

In the field of population genetics, Mihaela Pavličev has recently argued that there were some parallel attempts in the 1980s to integrate physiological and developmental mechanisms with evolutionary theory (see Pavličev 2016 and references therein). However, these early attempts did not leave a mark in population genetics and faded from view in the 1990s.

Thomas Hansen describes the field of quantitative genetics when he moved to the University of Oregon in 1992 as “a field in expansion,” where there was a lot of enthusiasm, “because people had started to do field studies of selection, and there were expectations around the ability to study the effect of genetic constraints.” However, he also “perceived it as narrow, in the sense that where variation came from was not problematized, and mutations were not studied that much.” Moreover, studies of mutations “were mostly estimating

mutational variances, which is descriptive work. There wasn't much theory around how the properties of mutations are generated, or what the consequences of them are" (Hansen).

The neutral networks approach to evolvability is represented in the co-citation network by several papers from the mid-1990s (Schuster et al. 1994; Huynen et al. 1996; Ancel and Fontana 2000; Burch and Chao 2000), in which the ability to evolve is modeled as the accessibility of phenotypes in mutational neighborhoods (see figure 2.3b). Interviewees working in this field (Schuster, Payne, A. Wagner) agree on referring to Sewall Wright's landscapes as originating a new way of looking at evolution, but they identify in the "molecular evolution" a turning point in the understanding of the genotype-phenotype map. According to Peter Schuster, one of the founders of this approach, classical molecular biology perished in the late 1970s and was progressively replaced by a much more complex view of the genotype-phenotype relationship. Schuster refers to his work and that of his collaborators as being instrumental in introducing the genotype-phenotype mapping as an intermediate bridge not included in Wright's model (Schuster). Younger scholars in computational evolution, such as Josh Payne, agree with this view:

The seeds of evolvability research were planted by Sewall Wright and John Maynard Smith. I think that concepts like genotype spaces and adaptive landscapes that are so central to evolvability research have been around for some time, but I don't think that they were really thinking about evolvability the way that we think evolvability now: the ability of mutation to bring phenotypic variation [...] that's part of what they were thinking of, but it wasn't what was driving the research. (Payne)

This reconstruction is clearly reflected in the network (figure 2.3b, bottom-left), where Wright (1932) and Maynard Smith and Szathmáry (1995) are important nodes that connect publications endorsing a neutral networks approach to evolvability. In turn, this cluster is peripherally connected to a paper by Eigen and Schuster (1979) representing one of the oldest subclusters of the network, namely, studies on evolvability in the field of the origins of life. In this context, the capacity to evolve is seen as a key condition for the successful origination of life as we know it. In the late 1970s, debates on the conditions for autocatalysis and self-enhancement for life origination were followed by debates on the requirements for biotic entities to undergo Darwinian evolution. In this context, Eigen and Schuster's work on the error threshold (Eigen 1971; Eigen and Schuster 1979) can be read as work on evolvability, namely, what the limits of mutation rates are that make Darwinian evolution possible (Schuster).

In the fields of evolutionary systems biology and evolutionary developmental biology, evolvability is seen as dependent on the internal properties of developmental systems. In the co-citation network, the field of evo-devo is represented by works on the developmental determinants of evolvability (Kirschner and Gerhart 1998; West-Eberhard 1998), and the role of developmental modularity (Raff 1996; von Dassow and Munro 1999; von Dassow et al. 2000) and integration (Cheverud 1996) (see figure 2.3b). In her interview, Fritson Galis agrees that evolvability issues were "definitely" present before the 1990s, but she recognizes a different set of ancestors of evolvability research. She refers to William Bateson on structural variation, Waddington and Schmalhausen on developmental plasticity, stabilizing selection, and genetic assimilation, Vermeij (1973) on the versatility of body plans, and Raff (1996) on the effect of developmental modularity on their conservation and variability. Johannes Jaeger associates his interest in developmental evolvability with

his frustration with reductionist views of development and evolution, and he recalls Kauffman (1993) and Goodwin (1994) as his major inspirations for an alternative, structuralist approach to evolvability.

Evolutionary biologists working at the intersection of evolutionary genetics and developmental evolution identify the “organismal perspective” advanced by Rupert Riedl as a major influence on their thinking on evolvability:

the core deficit [of population genetics] was the complete elimination of the theoretical importance of the organism, basically screening off everything that has to do with the organism so collapsing into one single parameter, fitness, on the one hand, and leaving it open at the lower level, at the genome, that is, genome and fitness. (G. Wagner)

Riedl’s book *Order in Living Organisms: A System Theory of Evolution* (1978) does not show up in our network, but recurrently turns up in the interviews as a major influence for “a small group of people that were either connected to or inspired by Riedl’s ideas” (G. Wagner). In this context, Wagner interprets the work that he, together with a few other people (including Jim Cheverud), were doing in the 1980s as an attempt to build a “conceptual infrastructure” or a “theoretical framework” that covered the gap between population genetics and organismal biology (G. Wagner). Günter Wagner, Andreas Wagner, and Mihaela Pavličev had Riedl as a professor during their graduate studies at the University of Vienna, and they all recall his lectures as being both unclear and inspiring. In his interview, Cheverud recalls having been highly influenced by Riedl’s ideas. Cheverud read Riedl’s book before writing his paper on morphological integration (Cheverud 1982), and the publication of that paper inaugurated his relationship with G. Wagner, with whom he has collaborated ever since. In this theoretical context, the link between evolvability and *internal selection* is regarded as distinctively crucial. In Pavličev’s view, the original idea that modularity enhances evolvability (as formulated in G. Wagner and Altenberg 1996 but dating back to Olson and Miller 1958 and Riedl 1978) “included function” into the definition of evolvability (Pavličev). Modularity was not only conceived in terms of dimensionality, or the number of traits affected by mutations, but also referred to how mutations in functional modules were more likely to be selected than those breaking the function. According to Pavličev, “this aspect has been dropped in later usage of modularity, treating only the variational part, the reduced dimensionality that can be exposed to any kind of external selection.” Yet, in contrast to external selection, internal selection is predictable, as it is dependent on the organismal structure: “there are unconditionally deleterious and likely advantageous or neutral directions.” Therefore, “evolvability should include internal selection. Without it, we are measuring variation or variability, essentially selectability” (Pavličev). Frietson Galis’s work on the role of negative pleiotropic effects in constraining the evolvability of body plans (starting in Galis 1999) aligns with this perspective.

Finally, several interviewees from different disciplinary areas locate the novelty of evolvability research in issues related not to evolvability itself, but to its evolution. For instance, when Richard Dawkins first wrote about the evolution of evolvability (Dawkins 1988), he saw it “as a heresy,” an exception to his “emphasis on microevolutionary pressures.” Although he now thinks that he “was wrong about it being heretical,” Dawkins related the heresy to what he then interpreted as group selection when it was actually “clade selection” (Williams 1992). In his view, the heterodoxy of evolvability had nothing to do with the role of constraints in evolution:

I am perfectly happy with the idea that in what I called biomorph land [. . .] some corridors are harder to go down than others [. . .]. So if you think there is a controversy between internalist and externalist thinking, then that is my concession to internalism, but I never thought of it as a concession, because I think that it was obvious. (Dawkins)

Joanna Masel also emphasizes lineage selection as a recent expansion of the classical frame of evolutionary theory that was developed in connection with the evolution of evolvability in the early 2000s, a topic to which she contributed (Masel and Bergman 2003).

The conceptual roots of evolvability research cannot be attributed to a common intellectual descent. Instead, parallel roots lead to what is still not regarded as a single concept. Nonetheless, interdisciplinary exchanges did play an important role in the explosion and diversification of evolvability studies in the 2000s. There were many precedents in attempting to set up this interdisciplinary research agenda. The 1989 Dahlem Conference included a group discussion on the evolution of evolvability (Arnold et al. 1989). The discussion was coordinated by Steve Arnold and included people as diverse as Pere Alberch, Vilmos Csányi, Richard Dawkins, Sharon B. Emerson, Bernd Fritzsche, Tim J. Horder, John Maynard Smith, Matthias J. Starck, Elisabeth Vrba, Günter Wagner, and David Wake. The group report included almost every topic that later has been discussed in the evolvability literature, from the role of developmental constraints to levels of selection. However, the ideas discussed did not precipitate an alternative research front until the 2000s. A series of books published in the mid-1990s (Maynard Smith and Szathmáry 1995; Dawkins 1996; Raff 1996) seem to have played an important role in this regard. They all show up in the co-citation network (see figure 2.3b) and are acknowledged by at least one of our interviewees (Hansen) to have been influential in his thinking on evolvability.

More local, interdisciplinary interactions concern relationships between paleontology and quantitative genetics, between computer science and molecular evolution, and between theoretical chemistry and neutral network models. Jim Cheverud (1982, 1988) describes the novelty of his early work on morphological integration as the result of bridging phenotypic studies on integration from paleontology (Olson and Miller 1958) with agricultural studies. When asked about his major influences at that time, Cheverud refers to authors from different specialties, including Berg, Gould, Riedl, and Lande and Arnold, with whom he interacted in the early 1980s in the Chicago area. Another area of disciplinary overlap, reflected in the collaborations among Peter Schuster, Günter Wagner, Peter Stadler, and Andreas Wagner, was that between theoretical chemistry and molecular evolution. In turn, the emergence of evolutionary approaches in engineering and computer science acted as the enabling factor for evolvability becoming a research agenda. In the field of evolutionary engineering, G. Wagner points to Ingo Rechenberg's (1973) book as one of the earliest attempts to solve the evolvability problem. Rechenberg was a German aircraft engineer who developed an evolutionary method based on random changes for solving complex optimization problems. This method included "a feedback loop that optimizes the evolvability of that device." According to Wagner, the founders of evolutionary genetic programming reached the same conclusion:

you can successfully use random change as a way to improve things if and only if the variational process is tuned appropriately to solve these problems. So evolvability is not a trivial state of any replicating and varying system but needs to be built into the system in order [for evolution] to be possible. (G. Wagner)

In contrast to evolutionary engineering, computer science is significantly represented in the co-citation network (figure 2.3b) as an influential cluster of publications on genetic programming (Holland 1975; Goldberg 1989; Koza 1992) constituting the intellectual base for computational studies on evolvability (Kauffman 1993; Altenberg 1994). This ascendancy is manifest in Richard Dawkins's seminal work (Dawkins 1988). In his interview, Dawkins admits that he was highly influenced by his attendance of an Artificial Intelligence workshop in Los Alamos in 1987, where he met Chris Langton, Stuart Kauffman, and Craig Reynolds.

2.4 Explaining the Origination of Evolvability Research

My analysis of the origination pattern of evolvability research shows that there were historical precedents of almost all relevant components of the evolvability research agenda, but they did not precipitate into such an agenda until the 2000s. This pattern of “conceptual lag” is not unique to evolvability research. Other approaches, such as eco-evo-devo (Love 2015) were also drafted in the late 1970s–early 1980s but did not crystallize as research agendas until 20 years later. Why did these new perspectives have to wait two decades to be pursued as core research programs in evolutionary biology? Which factors determine scientists' choices among available intellectual variants? (Toulmin 1967).

To answer this question, I will apply conceptual tools from cultural evolution theory as they have recently been applied to epistemic evolution and in particular to science dynamics (Richerson et al. 2013; Mesoudi et al. 2013; chapters 2–4 in Love and Wimsatt 2019; Fadda 2021). Cultural evolution theory applies models and metaphors drawn from evolutionary biology to explain the evolution of culture, including the history of science. Nonetheless, my use of these conceptual tools for explaining the origin and diversification of evolvability research will be intentionally metaphorical. I do not consider evolvability as a cultural replicator, nor do I endorse a population approach to the differential reproduction of cultural variants (Richerson and Boyd 2005). There are substantial differences between theoretical and biological variation (Thagard 1980) that I will not discuss here. From my perspective, the main advantage of evolutionary philosophies of science is that they allow us to offer integrated accounts of traditionally opposed perspectives of science, namely, internalist narratives based on the rationality of scientific progress and externalist reconstructions of the social norms governing scientific communities (Fadda 2021). In what follows, I embrace evolutionary explanations as loose analogies that help organize the many factors at play in the origination of evolvability research into two broad, nonmutually exclusive, explanatory kinds, namely, (1) “selectionist” explanations, and (2) “evolvability” explanations. While the former have been largely explored by evolutionary epistemologists, I will advance a novel internalist approach for the origination of evolvability research that might be generalizable to other episodes in the history of science.

2.4.1 Selection Criteria and the Dynamics of the Academic Landscape

Evolutionary epistemologists have mainly looked at science as a selection process (Hull 2001). Selection criteria concern the epistemic standards of what scientists find acceptable, and changes in these standards often depend on changes in the intellectual landscape that foster the acceptability of new theoretical perspectives. Interviewees appeal to several factors

transforming the intellectual landscape for the acceptability of the evolvability perspective and moving it from theoretical debates to empirical studies. These factors include the incorporation of new and simpler model systems, such as prions, RNA molecules, or minimal genetic networks (Masel); the development of new molecular methods for engineering proteins in the late 1990s and early 2000s (A. Wagner); the discovery of genetic similarities between regulatory genes in the 1990s and the establishment of phylogenetic methods in the 1980s (G. Wagner); and the development of computational technologies since the early 1990s (A. Wagner). All these methodological innovations “helped forge an experimental, empirical paradigm that was meeting a field that was ready to move in that direction” (G. Wagner).

Changes in epistemic standards concern how conceptual innovations meet novel technological and conceptual niches, but dissemination of scientific ideas also depends on social criteria that bias their selection by individual scientists. In cultural evolution, “context biases” refer to sociological factors, such as the status or prestige of individuals, or the frequency of ideas in a given community, that play a role in the dissemination of ideas (Fadda 2021). For instance, prestige biases appeal to the disposition of individuals to instantiate the practices of successful individuals. A clear example of the role of academic status and social prestige of scientists in the acceptance and dissemination of evolvability ideas is that of Günter Wagner. As mentioned above, before the publication of his article with Altenberg in 1996, Wagner had written a series of papers on evolvability starting in 1981. However, as he himself recognizes, the fact that these papers were published “in an obscure place and by an obscure person” might explain why the basic idea did not make an impression in the field (G. Wagner). In contrast, several interviewees refer to Wagner moving to Yale in 1991 (Galis), gaining a MacArthur fellowship a year later (Cheverud) or publishing that paper in the well respected journal *Evolution* as playing a key role in the reception of evolvability ideas.

“Conformist biases” refer to the tendency to adopt the most common practice in a given population (Boyd and Richerson 1985). The use of heritability instead of evolvability as a measure of the potential to respond to selection is a good example of “intellectual inertia” in evolutionary quantitative genetics (Houle, Hansen). As a structured set of methodological and conceptual practices, conformist biases align with the kind of sociological factors that explain the ideological consistency of scientific communities during normal periods of science (Kuhn 1970). In turn, when a field is in a state of crisis, conformist biases are less likely to be followed, while new concepts and paradigms are more prone to proliferate (Thagard 1980). It might be argued that the proliferation of evolvability studies in the 2000s was enhanced by the critical interrogation of the foundations of the Modern Synthesis that started to grow on several disciplinary grounds in the late 1980s (see section 2.3).

Dialectical styles play an important role in the construction of scientific consensus. In his celebrated book on the origins of population genetics, Provine (1974, 25) argued that if Mendelians and biometricians had worked with, instead of against each other, the mathematical synthesis between Mendelian inheritance and natural selection attained by population genetics might have occurred 15 years earlier. Can the same be said about population geneticists and evo-devoists, or between micro- and macroevolutionists in the 1970s and early 1980s? Many of our interviewees agree that the clash between microevolutionists and paleontologists after the publication of the punctuated equilibrium hypothesis (Eldredge and Gould 1972) made integration a difficult enterprise. Mihaela Pavličev also points to

dialectical styles as one of the factors accounting for the disappearance of mechanistic approaches in population genetics after the attempts made in the 1980s: “there were very powerful, present, people in the field that were probably very strongly advocating for their own approach to the questions” (Pavličev).

Dialectical styles do not characterize all members of opposite sides. For instance, Jim Cheverud’s collaborators (Pavličev, Porto, and G. Wagner) agree that his nonconfrontational style facilitated synthesis. Nonetheless, the relationship between paleontologists and evolutionary biologists is no longer regarded as contentious as it was in the 1970s: “the relationship is a little more either benign neglect in terms of evolutionary theory and among paleontologists to a little bit more of people cooperative and interested on both sides” (Hunt); “I think that, more and more, graduate students come to know something about the fossil record as well as quantitative approaches in biology” (Liow). Regarding the conflict between organismal and statistical approaches to evolution, many young researchers are simply unaware of the existence of such a conflict (Pavličev). Massimo Pigliucci resorts to Plank’s principle of generational replacement (Kuhn 1970, 151) to account for the resistance of evolutionary biologists to study evolvability, which he regards as a core component of the Extended Synthesis:

Most of the people that are resistant to the Extended Evolutionary Synthesis are what I would consider at this point the old guard: Michael Lynch [. . .] Doug Futuyma, Jerry Coyne [. . .]. All of these people are still among the major critics of the Extended Synthesis and they’re all on their way out in terms of their influence on the field and in terms of their careers. New generations come in, and now it’s easy for the new students to talk about plasticity, niche construction, and evolvability. It’s kind of like a second nature because they grew up with that literature and they don’t see it as problematic. (Pigliucci)

Another populational factor in the spread of scientific ideas concerns the institutional “maturation” of ideas. When asked about the explosion of interest in evolvability in the mid-1990s, Pigliucci argues that scientific ideas need some time to mature, reaching a threshold when suddenly, enough researchers start working on new research topics.

It may have a snowball effect when these students start to work on the topic and later start an academic career, request funding for that sort of stuff, and eventually they themselves are called by granting agencies to adjudicate grants, so they tend to fund that kind of research. So it takes about 20 years for that kind of development to occur. (Pigliucci)

The publication of reviews and popular science books on evolvability-related issues (see section 2.3) might have triggered this snowball effect in younger generations of evolutionary biologists.

2.4.2 From Conceptual Constraints to Evolvability of Theoretical Components

Together with selectionist explanations, evolution of culture theorists have pointed to the importance of constraints internal to practices, behaviors, or ideas accounting for the evolution of cultural variants. “Content biases” concern epistemic preferences of scientists based on what are perceived as theoretical virtues of scientific ideas (Fadda 2021). As opposed to context biases, they comprise *intrinsic* properties, such as simplicity or generality, that make some cultural items more prone to be copied than others. Independently of the academic status of their carriers, the success of some papers boosting research in evolvability notably depended on the clarity with which ideas that had been previously advanced were formulated.

This was the case of G. Wagner and Altenberg's 1996 paper or that of A. Wagner (2008) on the relationship between robustness and evolvability, a link already hinted at by previous works (e.g., Schuster et al. 1994) (Payne). In quantitative genetics, Houle and Hansen also had to publish the same ideas in more digestible ways (Hansen et al. 2011) to propagate the mean-standardized measure of evolvability in their scientific community (Hansen). In contrast, other concepts and tools, such as mutation matrices, have met greater resistance to being incorporated into the methodological repertoire of evolutionary biologists because of the intrinsic difficulties associated with their estimation. Massimo Pigliucci believes that, compared to plasticity, evolvability itself is a more difficult concept, and he speculates this might explain why it took longer to become a research agenda: "evolvability is less easy to grasp at a conceptual level, it has been explored for less time than plasticity, there are different types and levels of evolvability, and [it] is far more difficult to study empirically, especially in macroevolutionary-leaning aspects of the evolvability question." Notwithstanding its complexities, Pigliucci argues that evolvability has other internal, theoretical virtues related to *generality* that might explain its late but resounding success as a fundamental concept in evolutionary biology:

I think evolvability plays a particularly interesting role, partly because it is such a high-level concept that can be applied widely, while none of the other concepts actually work the same way. You don't talk about phenotypic plasticity of a clade, or epigenetic inheritance between species. Niche construction gets closer because it can actually expand to different levels, but evolvability is really such a broad concept that it can expand on everything, from within population variation to major transitions: that's pretty much the entire span of evolutionary biology. So that's one reason why I think it is a fundamental concept. (Pigliucci)

In what might be interpreted as a population approach to "cultural evolvability," Mesoudi et al. (2004) cite a study showing that more heterogeneous teams of researchers make more discoveries than do teams composed of scientists with similar disciplinary backgrounds. They interpret this increase in scientific productivity as resulting from the ability of heterogeneous scientific communities to generate more variation in research outputs on which selection can act. In our case, interactions of researchers from different disciplinary backgrounds seem to have been instrumental in the diversification of evolvability research, as described in section 2.3. As I have argued elsewhere (Nuño de la Rosa 2017), overlapping disciplinary areas in evolvability research act as "trading zones" (Galison 1999) of concepts and methodologies that are later translated and operationalized in different disciplinary specialties.

Together with the structure of scientific communities, internal determinants of science development play an important role in the proliferation and diversification of research agendas. Some cultural evolution theorists have explored how links between social practices might confer different cultural evolvabilities on these practices (Sterelny 2006). Some practices (e.g., those related to social interaction) tend to be strongly associated, whereas others (e.g., technological and craft skills) tend to evolve in a more modular way, insofar as they can be adopted without influencing one another. Philosophers of science have also paid attention to the role of integration between scientific concepts and resulting patterns of conceptual covariation (Brigandt 2013; Love 2015). The ability of the evolvability conceptual framework to connect related concepts in evolutionary biology seems to have been crucial in the dissemination of evolvability ideas. For instance, David Houle believes that

the accidental use of the same word in different disciplinary contexts (e.g., computer science and quantitative genetics) had a great effect in this regard. Johannes Jaeger comes to a similar conclusion: “it’s good to have a term like that because, even if it means different things to different people, it focuses people on certain types of questions.” In each disciplinary field, evolvability is also seen as a “meta-concept,” insofar as it connects many related concepts into a unified research agenda. Benedikt Hallgrímsson regards it this way for the field of evo-devo:

Evolvability as a concept is sort of a meta-evo-devo concept, because it needs to refer to robustness, integration, modularity, constraints, and all these core concepts of evolutionary developmental biology; and it makes sense to use it because there are some times when you want to refer to the collection of all those things, so you talk about evolvability. Or you want to refer to the connections of all those things and how they relate to the nondevelopmental determinants of evolvability, such as population genetics concepts. (Hallgrímsson)

Connections among concepts determine how they are transmitted through time and across disciplinary contexts. Just like traits, concepts not only travel in clusters, but during their journey, they also individuate in different theoretical contexts:

You can take every concept in modern biology [. . .] and trace it back. What you find is that the concept exists in different contexts, I guess changed and reinterpreted by the context it has every time. [. . .] People that conceptualize new things are often not the best people to define it in a concrete way, because when things are first articulated, they are fuzzy and poorly connected to other concepts. Then we refine them, and we interpret them as time goes on. (Hallgrímsson)

The emergence of evolvability research in the field of quantitative genetics offers an exemplary case study to investigate the individuation of a scientific concept in a given disciplinary background. In his interview, Thomas Hansen identifies “two events or theoretical developments in evolutionary biology that set the stage for the study of evolvability as something separate from selection” (see also Hansen and Pélabon 2021). The first event had to do with the separation of *selection from inheritance* in Fisher’s Fundamental Theorem of 1930 (see Frank 2012). In Darwin’s original formulation, selection and inheritance were deeply entangled. The Modern Synthesis inherited this view, and the implication of Fisher’s theorem passed unnoticed until Price reinterpreted it in the early 1970s, making the separation between selection and transmission explicit: “What this [separation] allows is that we can theoretically and empirically study selection without bothering about inheritance, which is something that we really couldn’t do before” (Hansen).

The second, and independent, event was the separation between *selection and constraints* in quantitative genetics introduced by Lande and Arnold (1983) when they wrote the response to selection as the G-matrix multiplied by the selection gradient, operationalized as multiple regression: “This provided two tools to study both variation and selection in the field. So people could go out and estimate selection gradients in the field without worrying about genetics at all. And at the same time, you can study the G-matrix independently of the selection, which typically happened in the lab, and later also in actual populations” (Hansen). Given that in Houle’s (1992) definition of evolvability, the G-matrix is what determines evolvability in the short term, the separation between the G-matrix and the selection gradient was a fundamental step in the autonomization of evolvability as a

research agenda. According to Hansen, it was this separation that “really facilitated the study of evolvability as a separate entity.”

As already mentioned, neither Lande nor Arnold interpret their article in these terms. When asked about the novelty of their contribution, they both highlight the extension of the breeder’s equation to multiple characters and the measure of selection as multiple regression. Neither of them refers to the implications of this measure for the separation between selection and constraints, a distinction that, according to Lande, he had previously introduced (Lande 1979, 1982). This is again an example of theoretical developments that are not consciously intended by their creators: “In developing a way to measure selection, they just happen to set things up in a way that made it possible to study evolvability” (Hansen). Indeed, in using variance standardization of traits, Lande and Arnold reintroduced the correlation between the selection gradient and the G-matrix, leading to a paradoxical situation: “Since everybody copied their approach, we got a situation where the theory was conceptually correct but was empirically implemented in a way that had all the old problems. This is what David [Houle] and the rest of us have been trying to straighten out with the mean-standardizations” (Hansen).

From this perspective, the mean-standardized measure of evolvability is not “just one of several measures” (Lande) of a theory that was already at work. Instead, it results from a theoretical reinterpretation in the evolvability framework that takes into account the centrality of scale in evolutionary biology. This argument needs to be understood within the more general framework relating meaning and measurement in biological theory (Houle et al. 2011; Houle and Pélabon, chapter 6). From this perspective, the life of scientific concepts can be understood as the result of a transition from verbal models to measurement. Hansen and Houle (2008) identify the lack of such a theory as one of the reasons that evolvability has received relatively little attention until recently. Recent work on evolvability has been precisely “about creating this theoretical context for it to be meaningful and operational” (Hansen). For instance, the move from constraints to evolvability in the work on *Dalechampia* (Hansen et al. 2003a,b) depended on the operationalization of ideas that had been previously formulated in a vague manner. An example is *conditional evolvability*, which was used “as a method for quantifying evolutionary modularity, which was a very important concept in the 1990s but [. . .] was rather vague” (Hansen).

The modularity of theoretical components can be applied to further distinctions accounting for the autonomous development of evolvability as a research agenda. In particular, the *separation between the G-matrix and the M-matrix* in quantitative genetics can be interpreted as a third event in theoretical decoupling that allowed evolvability to be studied independently of selection. In classical evolutionary theory, the mutational input was treated as a fixed parameter, while evolvability research is precisely interested in understanding how mutational effects and mutation rates evolve:

I think the connection between evo-devo and evolutionary quantitative genetics came through that: because we need the genotype-phenotype [GP] map to study mutational effects. [. . .]. If we think about the GP map as an abstract mathematical function, as you move around in this landscape, mutational effects will change. Basically, a change in the effect of mutations is the same as a change in the effect of the difference between two alleles that segregate in a population. This is determined by the GP map and therefore we need to mathematicize the GP map and put it into the theoretical population genetics framework. (Hansen)

In this context, a further conceptual distinction that has contributed to the independent study of the variational determinants of evolvability has been that between *biological and statistical epistasis*. While biological epistasis refers to the dependency of the phenotypic effects of mutations on the genetic context, statistical epistasis refers to the statistical deviation from additivity in a given population. This conceptual distinction arose gradually in the early 1990s, starting with Cheverud and Routman (1996). Since then, Hansen, G. Wagner, and collaborators (e.g., Hansen et al. 2006) have worked on elucidating the effects of epistasis on the selection response. In this regard, the individuation of the epistasis concept is again regarded as resulting from it becoming a meaningful concept that can be appropriately measured and integrated with population genetics theory:

In classical population genetics theory [epistasis] is largely something to average over, because the main concern was the changing gene frequency or the change in the mean of a character under natural selection, and there the influence of epistasis is small. [. . .] However, if you think that variational properties of organisms change in evolution, you want to know how they do it, and thus there has to be fundamentally a question of how epistatic effects and other forms of context-dependency contribute to and are involved in evolutionary change at the population genetic level. [. . .] How to properly define epistasis is the problem of how to define a quantitative concept, which is measurement theory. (G. Wagner)

I have argued that the modularization of theoretical components accounts for the autonomous development of evolvability as a research agenda, at least in quantitative genetics. But why evolvability instead of constraints? As mentioned in section 2.1, the ascendancy of evolvability in the 1990s coincides with the decline, or at least the stasis, of constraints (see figure 2.1). However, Ingo Brigandt (2015) has argued that we should not interpret this pattern as a replacement but rather as a transformation of the concern with constraints into a research program on evolvability. From this perspective, evolvability was instrumental in overcoming the vigorous debate between constraints and selection that predated evolutionary biology in the 1980s and 1990s. By emphasizing the positive side of constraints, from the prevention to the facilitation of change, evolvability played an important role in dissolving this dichotomy (Love 2015). Our interviewees agree that constraints and evolvability are two sides of the same coin and that research on constraints can be easily translated into research on evolvability. However, they perceive evolvability as a more productive framework: “Even if one can literally map almost everything from evolvability back into that framework, it’s been, I think, just a better way of thinking about it” (Hunt). Younger scholars working on microevolutionary studies of macroevolutionary variation agree: Although evolutionary geneticists working on macroevolutionary timescales were convinced that phenotypic variation would eventually be found in every dimension, “the idea that there are dimensions in which evolution proceeds faster was very attractive” (Porto). Therefore, the theoretical decoupling of evolvability from selection was not a mere autonomization: It required the integration of evolvability into a common theoretical context where selection was a key explanatory component. Studies on the evolution of evolvability played a crucial role in this integration of evolvability in evolutionary theory, insofar as they opened up the possibility of explaining evolvability as a result of selection (Okasha 2018).

The origination and diversification of an interdisciplinary research agenda such as evolvability is a complex episode in science dynamics. Only a simultaneous consideration of explanatory approaches can do full justice to the multidimensional phenomena involved in

cultural evolution (Love and Wimsatt 2019). An evaluation of the relative weight of the external social and internal theoretical factors involved in the origination of evolvability research is beyond the scope of this chapter, but I believe the major factors in play have been at least outlined here. In particular, I have argued that the individuation of scientific concepts in different theoretical contexts, as well as the modularization of theory components, played an important role in enabling the independent development and diversification of evolvability research. I hope to have persuaded the reader that biological studies on evolvability have promising metatheoretical consequences for the understanding of science itself.

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