

2015

PREPRINT 471

Manfred D. Laubichler and Jürgen Renn

Extended Evolution

Extended Evolution

Manfred D. Laubichler and Jürgen Renn

Authors' Note

The two papers in this preprint derive from the project on extended evolutionary theory—the development of a theory that captures the evolution of knowledge systems from genomes to science and technology. The first paper has been published online in the *Journal of Experimental Zoology, Part B: Molecular and Developmental Evolution* (9999:1–13); the second paper will be published in a forthcoming volume of the Springer series, *Vienna Circle Institute Yearbook*, edited by Friedrich Stadler.

Table of Contents

Extended Evolution: A Conceptual Framework for Integrating Regulatory Networks and Niche Construction.....	1
Abstract	1
1. <i>Introduction</i>	1
2. <i>Integrating Regulatory Networks with Niche Construction</i>	2
3. <i>The Problems of Homology and Innovation</i>	6
4. <i>A Model of Extended Evolution as Transformation of Complex Networks</i>	9
5. <i>The Origin of Eusociality as a Case of Extended Evolution</i>	14
6. <i>Conclusion: Innovation, Homology, and the Role of History</i>	23
<i>Acknowledgements</i>	26
<i>References</i>	27
Extended Evolution and the History of Knowledge.....	37
1. <i>Introduction</i>	37
2. <i>Cultural Evolution</i>	38
3. <i>The History of Knowledge as a Case of Extended Evolution</i>	40
4. <i>From Biological to Cultural Evolution</i>	45
5. <i>The Evolution of Language</i>	47
6. <i>The Neolithic Revolution</i>	52
7. <i>The Evolution of Writing Systems</i>	55
8. <i>The Dynamics of Cultural Evolution</i>	57
9. <i>Outlook</i>	58
<i>Acknowledgements</i>	61
<i>References</i>	61

Extended Evolution: A Conceptual Framework for Integrating Regulatory Networks and Niche Construction¹

Abstract

This paper introduces a conceptual framework for the evolution of complex systems based on the integration of regulatory network and niche construction theories. It is designed to apply equally to cases of biological, social and cultural evolution. Within the conceptual framework we focus especially on the transformation of complex networks through the linked processes of externalization and internalization of causal factors between regulatory networks and their corresponding niches and argue that these are an important part of evolutionary explanations. This conceptual framework extends previous evolutionary models and focuses on several challenges, such as the path-dependent nature of evolutionary change, the dynamics of evolutionary innovation and the expansion of inheritance systems.

1. Introduction

The debate over the adequacy of current evolutionary theory has again moved center stage.² In essence, this controversy is about how to integrate recent empirical and theoretical advances within evolutionary biology and related fields into the core of evolutionary theory and how to broaden its explanatory scope. These advances include insights from molecular and developmental biology that have led to the concepts of developmental and regulatory evolution and genomic regulatory networks³ and a deeper integration of ecological and evolutionary theory that has refocused attention on complex phenomena such as phenotypic plasticity or the idea of niche

¹ This paper is published in *J. Exp. Zool. (Mol. Dev. Evol.)* 9999:1–13, <http://onlinelibrary.wiley.com/doi/10.1002/jez.b.22631/epdf>

² Laland et al., 2014.

³ Davidson, 2001, Davidson, 2006, Materna and Davidson, 2007, Carroll, 2008, Shubin, 2008, Davidson, 2009, Davidson, 2011, Krakauer et al., 2011, Peter and Davidson, 2011, Peter et al., 2012, Ben-Tabou de-Leon et al., 2013.

construction with its focus on multiple inheritance systems.⁴ Another challenge has been to expand evolutionary explanations to human psychology, sociality, language, culture, technology, economics and medicine.⁵ Further debates involve patterns of evolutionary change,⁶ the causal mechanisms that generate phenotypic variation⁷ or the levels of selection.⁸ In all cases the question has been whether new data and concepts or new explanatory domains can be accommodated within the existing framework of evolutionary theory, or whether the core of evolutionary theory needs to be re-conceptualized or, at the very least, expanded.⁹

2. Integrating Regulatory Networks with Niche Construction

In this paper we discuss one particular challenge that, we argue, in light of these new insights requires a re-conceptualization of parts of evolutionary theory—the evolution of innovations within complex systems across scales.¹⁰ Innovation, the generation of novel characters or behaviors, as opposed to standard patterns of variation and adaptation, involves not only the transformation of regulatory systems, but also the kind of interactions between systems and their environment that have been described as niche construction.¹¹ Explanations of innovations require a detailed understanding of the generation of phenotypic variation that goes beyond referring to

⁴ Odling-Smee, 1995, Laland et al., 1999, Laland and Sterelny, 2006, Laland et al., 2008, Jeffares, 2012, Odling-Smee et al., 2013, Richerson and Christiansen, 2013, Buser et al., 2014.

⁵ Piaget, 1970, Carroll, 2004, Boyd and Richerson, 2005, Richerson and Boyd, 2005, Stearns and Koella, 2008, Nesse et al., 2010, Bowles and Gintis, 2011, Gluckman and Bergstrom, 2011, Ruse, 2013, Wimsatt, 2013.

⁶ Grant, 1999, Grant and Grant, 2008, Minelli, 2009, Erwin and Valentine, 2013.

⁷ Carroll, 2008, Peter and Davidson, 2015.

⁸ Okasha, 2008.

⁹ Pigliucci et al., 2010.

¹⁰ Wagner et al., 2000, Muller and Newman, 2005, Davidson and Erwin, 2010, Wagner, 2011, Wagner, 2014.

¹¹ Laland, Odling-Smee and Feldman, 1999, Laland et al., 2000, Odling-Smee et al., 2003, Erwin and Krakauer, 2004, Erwin, 2008, Laland, Odling-Smee and Gilbert, 2008, Odling-Smee, Erwin, Palkovacs, Feldman and Laland, 2013, Caporael et al., 2014.

mutation as the fundamental variation-generating mechanism¹² and that includes the specific features of regulatory networks at different scales—including changes to both the structure of these regulatory networks in form of rewiring genomic and other forms of interactions, the transformation of individual elements of these networks by means of mutations in a broad sense and the addition of new elements to the network¹³—as well as a more complex account of the interactions between systems and their various environments than is provided by an aggregate measurement of fitness. Rather we also need to understand how systems actively construct their relevant niches (or how technologies create demand) and how these constructed niches, in turn, affect the possibilities of future transformation of these systems. This last point captures the path-dependent nature of evolutionary change. Technically this is a question about the structure of search spaces for evolutionary dynamics.¹⁴ Of the competing views—one that defines a search space abstractly as the sum of all possible combinations at a particular level of the biological hierarchy, such as a sequence space for RNA or DNA molecules of a particular length or sum of all possible metabolic interactions within a particular pathway; the other that argues that in the case of complex systems the search space of future possibilities is actively constructed by the actions and properties of currently existing systems—we clearly argue for the latter. For us, within the current extended landscape of evolutionary biology the challenge of explaining evolutionary innovations thus translates into the need to integrate the complex transformations of regulatory networks and their elements mentioned above with niche construction perspectives.

¹² Khalturin et al., 2009, Jasper et al., 2015.

¹³ For a recent review see Peter and Davidson, 2015.

¹⁴ Barve and Wagner, 2013.

A focus on regulatory networks, such as gene regulatory networks, helped to discover causal mechanisms that control the development of specific phenotypic characters. Furthermore, comparative studies (of different species and of normal and pathological conditions) have shown how specific transformations of either regulatory network structures or individual elements within those networks are responsible for observed phenotypic variation.¹⁵ While many of these studies have focused on the genome, it has, however, also become clear that many contextual factors interact with the genome-based control circuits and thus contribute to the regulation of gene expression in a significant way.¹⁶ The specific nature of these interactions can, in principle, be traced outward from the genome and involves intra- and extracellular signaling pathways, metabolic and physiological networks, behavior and specific environmental factors that can all contribute to such regulatory cascades. In practice, however, detailed reconstructions of such extended causal networks are still rare and specific contextual effects are generally subsumed under a generalized environmental contribution to the partition of variance and in any case are considered to be a factor that is independent from the genomic, cellular or organismal system.

Niche construction theory,¹⁷ on the other hand, focuses on the ways systems actively shape or construct their environment. In this view, the niche is not something that exists out there in nature waiting to be discovered or filled by an organism. Furthermore, constructed niches often persist longer than any of their individual inhabitants, which allow these niches to store important hereditary and regulatory information. Niche construction theory thus

¹⁵ Carroll, 2000, Wagner, Chiu and Laubichler, 2000, Davidson, 2006, Carroll, 2008, Peter and Davidson, 2011, Davidson, 2014, Wagner, 2014.

¹⁶ Linksvayer et al., 2011, Linksvayer et al., 2012, Page, 2013.

¹⁷ Laland, Odling-Smee and Feldman, 1999, Laland, Odling-Smee and Feldman, 2000, Odling-Smee, Laland and Feldman, 2003, Erwin and Krakauer, 2004, Erwin, 2008, Laland, Odling-Smee and Gilbert, 2008, Odling-Smee, Erwin, Palkovacs, Feldman and Laland, 2013, Caporael, Griesemer and Wimsatt, 2014.

includes the notion of expanded and multiple inheritance systems (from genomic to ecological, social and cultural). This latter aspect has made the concept of niche construction especially attractive for theories of cultural evolution as it facilitates a more complex notion of inheritance and a closer link between evolutionary dynamics and learning.¹⁸ But most models of niche construction have treated these multiple inheritance systems as quasi-independent contributions to evolutionarily relevant variation, allowing only limited interactions between them. In part this is a consequence of the formal structure of variance decompositions (the famed Price equation) that is the foundation of much of niche construction theory. But it also reflects a tendency within niche construction theory to focus on multiple broadly defined factors and quantify their relative importance within evolutionary dynamics.

What both of these approaches are missing is a clearly defined conception of how systems at multiple scales interact with each other, where some are defined as internal to the organizational level of study and some are defined as context or environment. A precise definition of the nature of these interactions is, however, a prerequisite for a causal model of the evolution of complex systems and also for understanding innovation across scales. This requires us to clearly define the relevant elements of these systems and their properties. Without conceptual precision it will be impossible to define the measurements and metrics needed to turn integrative conceptual ideas into formal models and to specify the criteria for empirical validation. Another challenge is to trace the consequences of causal interactions at different scales through an iterative sequence of historical stages. The conceptual framework we propose here begins with a conceptual clarification of the

¹⁸ Odling-Smee, 1995, Laland, Odling-Smee and Feldman, 1999, Laland, Odling-Smee and Feldman, 2000, Boyd and Richerson, 2005, Laland, 2008, Laland, Odling-Smee and Gilbert, 2008, Boyd et al., 2011, Creanza et al., 2012.

properties of extended systems that include both regulatory and niche elements. In our conception, regulatory and niche elements are parts of an extended network of causal interactions. We then apply this conception to a specific problem—innovation—in the context of a specific well-documented example—the developmental evolution of eusociality. Comparing the extended networks at different stages of this evolutionary trajectory allows us then to reconstruct the co-evolutionary dynamics between different parts of these extended networks. For the case of genetic systems Linksvayer and Wade¹⁹ have proposed a model of indirect genetic effects that can be seen as a specific instance of such an extended model. It introduces an expanded conception of genetic effects that includes contributions from different individuals in the context of a behaviorally linked system, such as a colony of social insects or other socially interacting systems. Our framework allows us to go beyond the idea of indirect genetic effects in that it (1) includes a broader range of causal factors, including those that are often subsumed under ecological inheritance²⁰ and (2) applies to a much broader range of evolutionary phenomena—from genomic to social, cultural and technological.

3. The Problems of Homology and Innovation

The linked problems of, on the one hand, homology, or sameness of structures and behaviors across a wide range of species, social systems or cultures, and, on the other hand, innovation, i.e. the emergence and successful spread of novel structures, are some of the main challenges for any theory of phenotypic evolution. Homology has traditionally been seen as a consequence of genealogy and inheritance.²¹ Simply put, complex phenotypes

¹⁹ Linksvayer and Wade, 2009.

²⁰ Laland, Odling-Smee and Gilbert, 2008, Odling-Smee, Erwin, Palkovacs, Feldman and Laland, 2013.

²¹ Laubichler, 2000.

are the same because they inherited the same genes (or other types of hereditary information). This historical conception of homology does, however, not account for the observed patterns of sameness and stability as we often see more (gradual) divergence in genes or other parts of the hereditary material than in the resulting phenotypic characters. In response to these challenges a regulatory conception of homology was proposed that explains the stability of phenotypic characters through time as a consequence of conserved structures in regulatory developmental systems or networks.²²

In the context of this developmental view, conserved elements of regulatory networks (referred to in the literature either as kernels or character identity networks) establish the identity or sameness of specific characters or structures while other (more downstream) parts of the network allow for the adaption of these characters to specific functions.²³ These variants of recognizable characters are called character states. The reason for the existence of conserved parts of networks is found in the interdependencies between elements in these complex regulatory networks where changes to certain parts of the network would cause a large number of dramatic and often lethal consequences. The interdependent regulatory network architecture together with the historical accumulation of small changes (adaptations) that all depend on specific core elements of the networks thus account for the observed patterns of stability, path-dependency and canalization characteristic of all complex biological, social, cultural and technological systems.

This regulatory conception of homology provides an explanation for observed patterns of stability (sameness) across complex systems as well as for more specific features of complex networks, such as their modular and

²² Wagner, 1999, Wagner, Chiu and Laubichler, 2000, Wagner, 2007, Wagner, 2014.

²³ Davidson, 2006, Wagner, 2007, Davidson, 2009, Wagner, 2014.

hierarchical architecture and the path-dependent or canalized nature of change. Any explanation of stability or homology also provides implicitly an explanation of novelty. We define novelty as the emergence of a new character as opposed to the transformation of an existing character into a new character state. There are, of course, several ways how novelties can emerge. These are currently the subject of intense debates within developmental evolution. Most prominently is the argument about the importance of changes in coding vs regulatory regions.²⁴ As evidence exists that each type of change can play a role in specific instances of novelty,²⁵ in the context of our framework it is important to note that independent of the kind of mutation all of these, in various ways, ultimately contribute to a rearrangement of the underlying regulatory networks that control the development of characters.²⁶ Such a rearrangement can be caused by the addition of new elements (for instance through gene duplication or lateral gene transfer, if we focus on genomic systems) or by the emergence of new links and regulatory relationships among already existing elements. In any case, novelties (or inventions in the context of technological change) are understood as the consequence of a specific type of transformation of regulatory networks. In the context of evolution or history, the eventual fate of these novelties or inventions is determined by the selective conditions of the environment, markets or domains of implementation. Only a successful novelty or invention is then called an innovation sensu Schumpeter.²⁷

²⁴ Carroll, 2008, Laland, Odling-Smee and Gilbert, 2008, Davidson and Erwin, 2010, Davidson, 2011, Odling-Smee, Erwin, Palkovacs, Feldman and Laland, 2013, Davidson, 2014, Peter and Davidson, 2015.

²⁵ Khalturin, Hemmrich, Fraune, Augustin and Bosch, 2009, Jasper, Linksvayer, Atallah, Friedman, Chiu and Johnson, 2015.

²⁶ Wagner, 2014, Peter and Davidson, 2015.

²⁷ Erwin, 2008, Davidson and Erwin, 2010, Krakauer, Collins, Erwin, Flack, Fontana, Laubichler, Prohaska, West and Stadler, 2011.

However, this relationship between novel variants and their selective environment can be quite complex, as we have to also account for the role of processes summarized under the general label of niche construction in this process. And most importantly, we need to be able to account for how transitions between regulatory states can actually be viable within specific evolutionary lineages, a problem that has not yet been fully resolved. Our conceptual framework suggests ways how an emphasis on the interactions between these two kinds of processes can contribute to a better understanding of the evolutionary dynamics of homology and innovation.

4. A Model of Extended Evolution as Transformation of Complex Networks

We, as others before,²⁸ have identified the integration of regulatory network and niche construction perspectives as one challenge for extending evolutionary theory and suggest that this requires a model that brings together regulatory and niche elements within one network of interacting causal factors. While others have done this for some specific cases and within the conceptual structure of either evolutionary genetics²⁹ or cultural evolution³⁰ our proposed perspective aims to bring evolutionary processes at all levels into one conceptual framework. We see this not as an exercise in grandiose theory or abstraction, but rather as a logical consequence of the internal dynamics of such integrated systems. One aspect of this is the role of coarse graining for theory development within biology.³¹ In the context of our proposed framework this implies to generalize from individual cases while at the same time provide enough specificity to be able to apply the framework to a number of specific cases. The extensions of the causal

²⁸ Erwin, 2008, Laland, Odling-Smee and Gilbert, 2008, Erwin, 2012, Andersson et al., 2014.

²⁹ Linksvayer, Fewell, Gadau and Laubichler, 2012.

³⁰ Laland, Odling-Smee and Gilbert, 2008, Andersson, Tornberg and Tornberg, 2014.

³¹ Krakauer et al 2012.

networks to include both internal and external (environmental) factors also allows us to focus on those cases that are characterized by multiple kinds of elements, such as cases of social and cultural evolution that include a number of different factors (biological, social, cultural). In this section we provide an abstract formulation of our framework that will be the basis of future modeling.

We begin by defining an internal system as a network of agents capable of persisting through time and reproducing its structure. The agents form the nodes of this network while their causal interactions constitute the links. Such systems may span multiple scales. Therefore an agent or node at one scale can be a network of agents at a different scale. Both persistence and reproduction typically require control and coordination of actions not only within and among the agents constituting the internal system, but also interactions between the system and other systems and their environment.

An extended network includes the environment as part of the network structure. All aspects of the environment that causally affect these interactions form the structured niche of the internal system. Together, system and structured niche constitute the extended regulatory network. The structured niche has itself a network structure induced by the primary network constituted by the internal system. Its nodes are those aspects of the environment that condition, mediate or become the target of actions, in short the environmental resources of the internal system. Its links are causal relations among these resources and between the resources and the internal network structures. Niches and environments are scale-dependent. The niche for an internal network at one scale can be part of the internal network at another scale. Therefore, from the system's perspective there are no absolute boundaries between an internal network and its environment. These distinctions are thus always process specific and also pragmatic. In modeling

a specific type of causal interaction it often makes sense to treat some aspects of these extended causal networks as internal or as context or environment.

Actions are regulated by the structure of the extended regulatory network and may be directed at the environment or at other agents changing their states so as to affect their actions. Actions realize functions related to the possible states of a system and its environment. Actions always involve environmental resources, constituting the material conditions or the targets of their realization. When actions are performed they change the environment in ways that are characteristic for the system and may thus be considered as an “externalization” of the system’s internal structures. But actions also do not leave the system itself indifferent and constantly change its internal structure. Therefore also the converse process takes place, an “internalization” of the environment. The internal structures of actors are the result of iterative (through evolutionary and individual time scales) transformations of such action networks.

We can illustrate this abstract notion of network dynamics in the context of models of evolution by natural selection, one prominent explanatory framework within present-day evolutionary theory. Here the agents correspond to individuals and the networks to populations. The internal structures of these agents include units of inheritance and the system of developmental interactions. The latter turns these agents into units of interaction and establishes the range of behaviors for each agent. Based on the internal complexity of these agents, they can also adapt their behaviors through interaction with the environment. The key regulative structure of interactions at the level of the population network is, however, selective reproduction. It includes the effects of random variation at the level of the internal genetic and developmental system and, as a consequence, heritability across generations. Interactions with the environment take multiple forms. These include the construction of individual niches through

interactions between possible internal states and environmental resources and conditions. As a consequence, internal states are externalized into the environment. It also includes selection among the units of inheritance in intergenerational transitions. In this case the interactions between individuals and their environment lead to a corresponding internalization of states in the sense that successful internal-environmental interactions become the foundation of the next generation.

Recasting the standard dynamics of natural selection this way allows us to see it as a special case of evolutionary network transformation. Regulatory structures in networks other than those directly involved in inheritance may also cross the boundary of individual and population-level interactions. This is captured by the idea of multiple inheritance systems within niche construction theory. In particular, regulatory network structures may expand by incorporating interactions with other units as well as features of the environment, or the extended network in our model. Due to the process we define as “externalization,” agents shape the range of possible interactions with their environment. They may do so not only by reproduction, but also by constructing niches, as well as by exploring their functional and behavioral potential (“exaptation”) which, in a given environment, is typically larger than the most immediate selected function, making it possible to react to newly emerging challenges. Within our model of extended networks these externalized factors can become an important part of the regulatory structures governing the behavior of agents and, if they are stable enough, also have substantial evolutionary consequences. These are captured by a complementary process we have described as “internalization,” where elements of the transformed environment may, under certain conditions, be integrated into an expanding regulatory structure that, in turn, shapes the interactions within the network. In biological evolution, this extension may at first happen, within a single generation, only at the developmental and

behavioral level. Still, it will enlarge the set of regulative networks on which natural selection can act, possibly turning a transient extended regulatory structure into a heritable feature.

The dynamics between externalization and internalization is particularly relevant for explanations of evolutionary innovations. Regulatory evolutionary changes of different kinds³² leading to genuine novelty or innovation can be explained as a consequence of the creation of additional regulatory modules or network transformations. Again, there are many concrete ways how this can actually be realized.³³ These often operate upstream of the highly canalized structures that control normal development and organismal function. Furthermore, the complex and hierarchical developmental and cellular systems can either amplify (“facilitate” sensu Kirschner and Gerhart³⁴) or suppress the variation induced by changes on the genomic level. One way in which such an additional module may have emerged is from a transient extended regulatory structure. Contingent circumstances and challenges to a network may indeed lead to a specific coordination of actions within the network that can be preserved at the developmental level of the agents within structured niches resulting from externalization and serving as scaffolding for the extended regulative structure sustaining such actions. The idea of scaffolding has been discussed especially in the context of cultural evolution³⁵ where the effects of constructed niches on evolutionary dynamics are often more straight forward and where the iterative and path-dependent nature of these processes is also quite visible. Our framework builds on these ideas, but identifies these features more closely as complex systems’ properties, which

³² Peter and Davidson, 2015.

³³ Carroll, 2008, Khalturin, Hemmrich, Fraune, Augustin and Bosch, 2009, Jasper, Linksvayer, Atallah, Friedman, Chiu and Johnson, 2015.

³⁴ Kirschner and Gerhart, 2005, Gerhart and Kirschner, 2007

³⁵ Caporael, Griesemer and Wimsatt, 2014

emphasizes the general dimension of these processes. An internalization of such action control by natural selection would then turn the transient extended regulatory structure into a heritable feature and at the same time decouple it from environmental constraints. In the following section we apply this framework to a number of evolutionary scenarios in the context of social evolution that illustrate these processes in general terms and suggest ways how these dynamics of externalization and internalization could be tested with concrete empirical data.

5. The Origin of Eusociality as a Case of Extended Evolution

There are many cases of evolutionary innovation that can serve as illustrations for our framework of extended evolution. However, the multiple sequences of evolutionary transitions leading to the emergence of a variety of eusocial systems provide particular compelling cases. Focusing on evolutionary trajectories rather than a single event better reveals the complex transformations of extended regulatory systems that result from the dynamics of externalization and internalization between regulatory systems and constructed niches that are the core of our model.³⁶ While all social systems involve cooperation and frequently division of labor, in the case of eusocial systems this also includes reproductive division of labor. The latter phenomenon has been a major challenge for evolutionary theory since Darwin.³⁷ Furthermore, social systems of various degrees of complexity have evolved several times and each time this process involved multiple steps that, we argue, show all the characteristics of the complex co-evolutionary dynamics that includes both externalization and internalization events.

³⁶ Wilson, 1971b, Wilson, 1971a, Wilson, 1985, Hölldobler and Wilson, 1990, Stearns, 1992, Page, 1997, Rueppell et al., 2004, Wilson and Holldobler, 2005a, Wilson and Holldobler, 2005b, Gadau et al., 2009, Hölldobler and Wilson, 2009, Amdam and Page, 2010, Nowak et al., 2010, Hölldobler and Wilson, 2011, Page, 2013.

³⁷ Wilson, 1971a, Wilson and Holldobler, 2005a, Hölldobler and Wilson, 2009, Nowak, Tarnita and Wilson, 2010, Page, 2013, West-Eberhard, 2014.

The multiple evolutionary trajectories from solitary insects to superorganisms with a complete reproductive division of labor contain different types of social systems that can be characterized by the way in which the regulatory mechanisms of development and behavior connect organisms to their niche.³⁸ These include (1) solitary species which interact with others only during courtship and mating; (2) subsocial species which care for their offspring; (3) communal species which share a nest but otherwise do not interact; (4) quasisocial species which cooperate during brood care; (5) semisocial species with cooperative brood care and reproductive division of labor and (6) eusocial species which are characterized by cooperative breeding, reproductive division of labor and overlapping generations within the nest. Within eusocial species we distinguish between primitively eusocial species, which do not show morphological caste differentiation and generally have some degree of flexibility in social roles, and highly eusocial species or superorganisms, which show considerable morphological caste differentiation and generally little flexibility in social roles.³⁹ To be clear, we are not saying that these stages represent a single evolutionary trajectory; rather we are using these different types of social systems as examples of different regulatory networks and the transitions between them as illustrations for the dynamics of internalization and externalization, especially as some of these transitions have been well studied and modeled in a way that is consistent with our overarching framework.⁴⁰

³⁸ Wilson, 1971a, Page, 1997, Fewell, 2003, Amdam et al., 2004, Linksvayer and Wade, 2005, Hughes et al., 2008, Gadau, Fewell and Wilson, 2009, Hölldobler and Wilson, 2009, Amdam and Page, 2010, Johnson and Linksvayer, 2010, Boomsma et al., 2011, Linksvayer, Fewell, Gadau and Laubichler, 2012, Linksvayer et al., 2013.

³⁹ Wilson, 1971a, Hölldobler and Wilson, 2009.

⁴⁰ Heinze et al., 1997, Amdam, Norberg, Fondrk and Page, 2004, Linksvayer, 2006, Patel et al., 2007, Gadau, Fewell and Wilson, 2009, Linksvayer et al., 2009, Linksvayer and Wade, 2009, Ihle et al., 2010, Johnson and Linksvayer, 2010, Wade et al., 2010, Linksvayer, Kaftanoglu, Akyol,

In the case of solitary and subsocial species, the niche does not include constructed structures while communal and quasisocial species live in constructed structures and are distinguished by the degree of social interactions that regulate their behavior. In the case of semisocial and primitively eusocial systems with no morphological caste differentiation, colonies live within constructed nests and division of labor is triggered by behavioral mechanisms such as simple dominance hierarchies (“behavioral regulation”).⁴¹ Highly integrated eusocial systems or superorganisms build the most elaborate nests or stable niches and are characterized by morphological caste differentiation, including reproductive division of labor, controlled by developmental mechanisms that operate through complex nutritional, hormonal and behavioral signaling networks that ultimately control gene expression (“developmental and physiological regulation”).⁴² Each type of social organization is thus characterized by specific interactions of regulatory systems with constructed niches.

These different social systems are marked, on the one hand, by an increasing internalization of the regulatory mechanism at the colony level, from contingent environmental and variable social conditions to stable genomic, developmental and niche-construction mechanisms and signals inherent to the colony. At the same time, the causes triggering the developmental differentiation of individual organisms are increasingly externalized into the social and ecological niches emitting regulatory signals originating from the state of the colony and the behavior of other individuals in the colony. Taken

Blatch, Amdam and Page, 2011, Linksvayer, Fewell, Gadau and Laubichler, 2012, Page et al., 2012, Flatt et al., 2013, Linksvayer, Busch and Smith, 2013.

⁴¹ Bertram et al., 2003.

⁴² Beshers and Fewell, 2001, Rueppell, Amdam, Page and Carey, 2004, Amdam et al., 2006, Page and Amdam, 2007, Patel, Fondrk, Kaftanoglu, Emore, Hunt, Frederick and Amdam, 2007, Linksvayer, Fondrk and Page, 2009, Amdam and Page, 2010, Ihle, Page, Frederick, Fondrk and Amdam, 2010, Johnson and Linksvayer, 2010, Leimar et al., 2012, Linksvayer, Fewell, Gadau and Laubichler, 2012.

together, these internalization and externalization mechanisms achieve an ever-higher integration of the colony. These dynamic transformations of regulatory control mechanisms constitute a conceptual model of possible evolutionary dynamics by which superorganisms could have emerged.

This example also highlights several central features of our model of extended networks of causally interacting agents. First, we see that the behavioral capacities of individuals, together with the environmental resources available to them, enable the construction of social and environmental niches. This leads in turn to an extension of the regulatory control structures governing their behavior. Second, these constructed niches represent a transitional extension of the regulatory control system involved in the emergence of an evolutionary innovation. Third, insofar as these extended systems are favored by natural selection we then observe a gradual internalization of these extended control systems into more stable (from an evolutionary point of view) hereditary and developmental structures. Taken together these steps provide us with a conceptual framework for explanations of evolutionary innovations that combines regulatory networks, niche construction and selection in the context of one model describing the transformations of extended networks.

Our explanation builds on progress reached in recent years in the understanding of social and eusocial systems.⁴³ The starting point is the observation that the evolutionary trajectories leading to various social

⁴³ West-Eberhard, 1986, Gadau et al., 2000, Rueppell, Amdam, Page and Carey, 2004, Giray et al., 2005, Wilson and Holldobler, 2005b, Wilson and Holldobler, 2005a, Amdam and Seehuus, 2006, Wilson, 2006, Hunt et al., 2007, Nelson et al., 2007, Page and Amdam, 2007, Patel, Fondrk, Kaftanoglu, Emore, Hunt, Frederick and Amdam, 2007, Linksvayer, Fondrk and Page, 2009, Amdam and Page, 2010, Ihle, Page, Frederick, Fondrk and Amdam, 2010, Abbot et al., 2011, Linksvayer, Kaftanoglu, Akyol, Blatch, Amdam and Page, 2011, Strassmann et al., 2011, Dolezal et al., 2012, Kapheim et al., 2012, Linksvayer, Fewell, Gadau and Laubichler, 2012, Page, Rueppell and Amdam, 2012, Flatt, Amdam, Kirkwood and Omholt, 2013, Wilson and Nowak, 2014.

systems are built on the reproductive groundplan of solitary insects.⁴⁴ A solitary insect is characterized by a life cycle that goes through different physiological and behavioral stages from an embryonic and developmental to a foraging and finally a reproductive phase. Each of the stages of the reproductive groundplan is characterized by a unique state of genome activation as different gene batteries are expressed, corresponding to, among other things, ovarian activation and different behavioral programs.⁴⁵ The life cycle of a solitary insect thus corresponds to a sequence of internal network states responding to both external and internal signals. For instance, solitary insects need to have stored enough energy and resources and be able to assess the timing and other relevant environmental clues before they can begin to switch into the reproductive mode, triggering both behavioral and physiological programs that involve mating and egg-laying.

In case of eusocial insects, the same genomic regulatory circuits that characterize individual stages of the groundplan act as the building blocks for the social life in the colony or the superorganism.⁴⁶ Comparative studies have revealed how the transitions from solitary to social life (or from organism to superorganism) involve regulatory changes that transform the underlying reproductive groundplan from a sequential to a parallel mode.⁴⁷ Where solitary insects perform different behavioral tasks sequentially, the colony as a whole performs these tasks simultaneously based on new forms of coordination that regulate and modify the expression of ancestral genomic

⁴⁴ Amdam, Norberg, Fondrk and Page, 2004, West-Eberhard, 2005a, Amdam, Csondes, Fondrk and Page, 2006, Page and Amdam, 2007, Patel, Fondrk, Kaftanoglu, Emore, Hunt, Frederick and Amdam, 2007, Linksvayer, Fondrk and Page, 2009, Amdam and Page, 2010, Ihle, Page, Frederick, Fondrk and Amdam, 2010, Linksvayer, Kaftanoglu, Akyol, Blatch, Amdam and Page, 2011, Linksvayer, Fewell, Gadau and Laubichler, 2012, Page, Rueppell and Amdam, 2012.

⁴⁵ For a summary see Page, 2013.

⁴⁶ Amdam, Norberg, Fondrk and Page, 2004, Amdam and Page, 2010, Johnson and Linksvayer, 2010.

⁴⁷ Page, 2013.

and behavioral programs. The development and evolution of the superorganism thus involve an expansion and a rearrangement of the regulatory and action-coordination networks that control the development and behavior of individuals, including differential caste development and the activation of behavioral programs in response to colony level regulatory states.

On the basis of our theory of extended evolution, we can now make use of these insights, first to interpret these changes in terms of internalization and externalization processes, and second, as steps along an evolutionary trajectory. As mentioned above, on the level of the colony or the superorganism as a whole, we observe many regulatory elements that in case of solitary insects are variable external signals from the environment now originating from within the constructed and stabilized niches of the colony and the nest. We claim that these causally relevant elements regulating the actions of the colony have, in the context of evolutionary processes, become internalized into the constructed physical and social structures of these systems.

That this is a plausible perspective becomes clear when one considers the origin of the division of labor, including reproductive division of labor, based on dominance hierarchies. Such dominance hierarchies are a consequence of interactions between individuals within a specific ecological setting—a single nest.⁴⁸ There are ecological conditions that selectively favor aggregations of originally solitary individuals.⁴⁹ As a consequence, within this newly constructed social and environmental niche the regulatory network

⁴⁸ Beshers and Fewell, 2001.

⁴⁹ West-Eberhard, 1978, Wilson, 1978, Hölldobler and Wilson, 1990, Wilson and Hölldobler, 2005b, Hölldobler and Wilson, 2009, Hölldobler and Wilson, 2011.

governing the behavior of each individual is made up mainly of input from other individuals in form of social interactions.

In systems with developmental caste determination (which exhibit a close similarity to cellular differentiation within a complex organism,⁵⁰ the amount and the importance of signals internal to the colony increases. The regulatory state of the colony acting through linked behavioral, physiological, metabolic and cellular signaling networks that intersect with the core genomic networks regulating gene expression in the developing larvae controls caste differentiation. The developmental path of each individual is thus regulated by the colony as a whole resulting in a more stable but also more canalized social system. And finally in cases of genetic caste determination, many of those elements originally external to the individual but internal to the colony have been fully incorporated into the system of genomic regulation.⁵¹

As we have also mentioned above when analyzing the mechanisms involved in the regulation of colony-level behavior and function from the point of view of the individual insect inside the colony, we observe that along the evolutionary trajectory towards greater social integration relevant developmental causes are externalized into the social and ecological niches as regulatory signals originating from the state of the colony and the behavior of other individuals in the colony. In the case of developmental caste determination, for example, the signaling cascades that regulate gene expression with the developing larvae extend all the way into the network of social interactions in the colony that influence the feeding behavior of the nurse workers and subsequently the hormonal and physiological signaling cascades within the larvae (Fig 1).

⁵⁰ Page, 2013.

⁵¹ Julian et al., 2002.

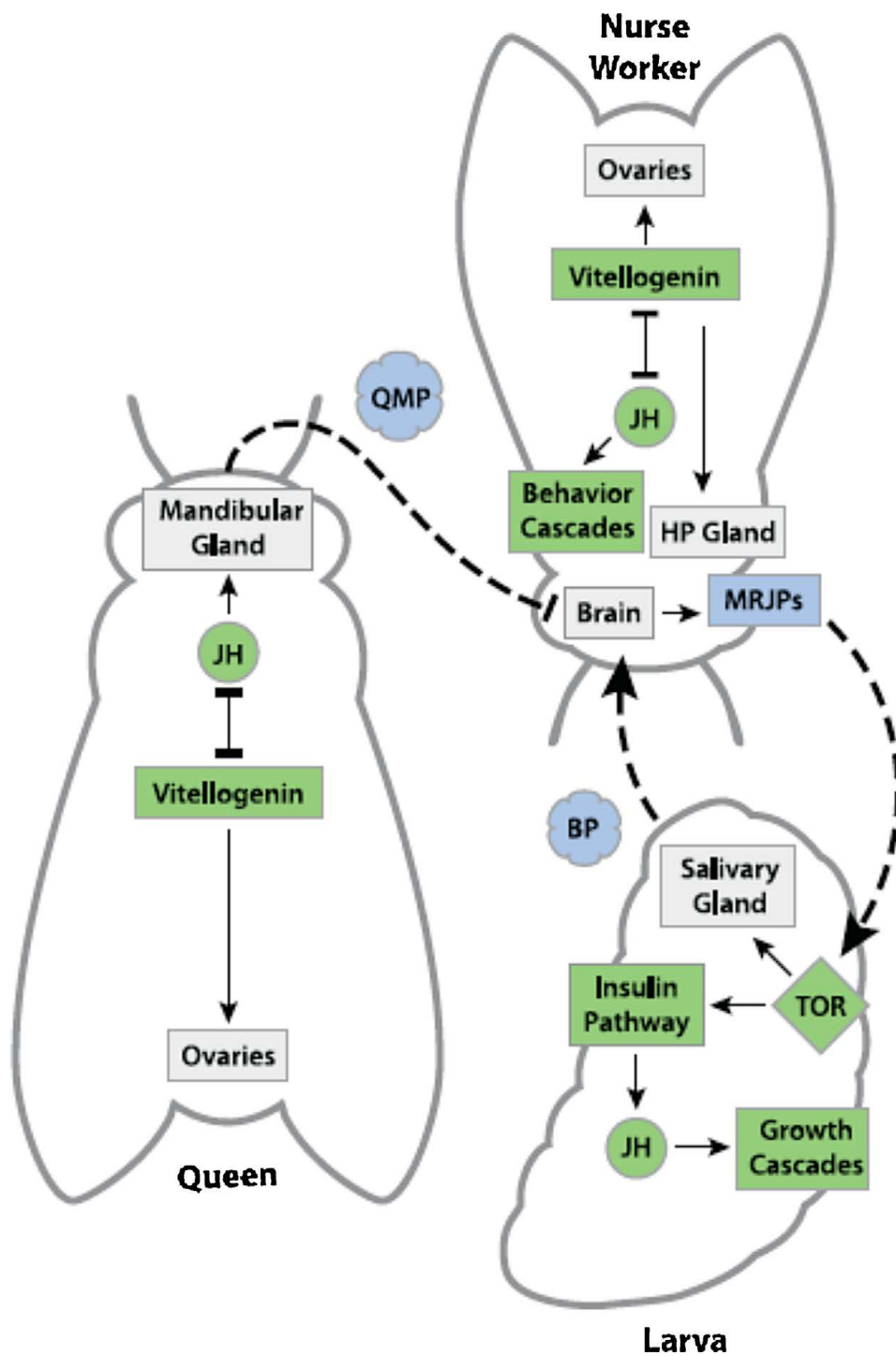


Fig 1: Extended Networks of Regulatory Control: A hypothetical Network of developmental control in the superorganism (reprinted with permission from Linksvayer et al 2012).

On the background of this classification of social systems in terms of internalization and externalization processes leading to an increasing integration of a colony, it now becomes possible to develop plausible evolutionary scenarios for the emergence of this interdependence. Given sufficient plasticity of the developmental and behavioral apparatus of individual organisms, any given niche may act as regulatory input for the individuals as well as for the colony as a whole. The development and reproductive behavior of the colony as a whole is thus governed both by its distributed genome and its extended regulatory system. This potential for integration is also the basis for the emergence of higher levels of selection. Multi-level selection processes can then, under the right conditions, favor increasingly integrated systems. In this context, mutations favoring stabilization of such initially plastic systems by internalization and externalization processes will be favored until a point of no-return in the evolutionary trajectory towards a superorganism is reached. As a consequence of increased integration of these extended regulatory systems, colonies become increasingly independent of variable environmental signals, which, in turn, enables them to succeed in a greater number of habitats. This evolutionary dynamics is enabled by internalization processes that encode and stabilize variable environmental conditions within the genome, the developmental apparatus and niche-construction behavior and externalization processes that create feed-back mechanisms making sure that individual developmental and behavioral processes can be flexibly adapted within a given niche.

Applying our theory of extended evolution to the case of social evolution thus accomplishes three objectives: We are able to provide an integrative explanatory framework for multiple kinds of empirical data and theoretical perspectives, we can derive the main innovative features of social systems as a consequence of the logic of extended evolution, and we can develop

consistent narratives for the emergence of social evolution as an evolutionary innovation.

6. Conclusion: Innovation, Homology, and the Role of History

Evolutionary and historical change proceeds in different modalities covering a whole spectrum of different types. Gradual change is arguably the predominant type. It involves the kind of “descent with modification” that ever since Darwin has been recognized as a universal principle of nature and culture. Gradual change is, however, not the only kind of historical change. In biological as well as cultural evolution we also observe patterns of discontinuous change, whether in form of major transitions, paradigm shifts, revolutions, or major innovations.⁵² Complementary to major transitions and innovations are patterns of extreme conservation and canalization that resist change for prolonged periods of time. Both types of phenomena are substantial challenges to a solely gradual and continuous conception of history and evolution.

Our focus on network transformation provides a framework for developing concrete explanations for discontinuous or major changes as well as canalization and can accommodate a wealth of comparative data about genomic and other regulatory networks across a wide range of species and characters.⁵³ These data have revealed a spectrum of different types of changes connected with phenotypic evolution that include: (1) slow and gradual divergence, mostly driven by changes in individual genes and (2) regulatory changes that represent transformations of network structures. In the case of genomes, the latter can be a consequence of genomic rearrangements or of nucleotide substitutions in regulatory regions. We thus

⁵² Buss, 1987, Maynard Smith and Szathmary, 1995, Davidson, 2006, Carroll, 2008, Calcott et al., 2011, Wagner, 2014.

⁵³ Peter and Davidson, 2015.

often have a good understanding of the endpoints of regulatory network transformations within different evolutionary trajectories, either gradual or discontinuous, at the phenotypic level. What we lack, especially in cases of discontinuous phenotypic evolution, is an understanding of the detailed dynamics of these evolutionary transformations.

The main problem here is to understand how large-scale rearrangements connected to evolutionary innovations can be viable within populations. Models that propose neutral or hidden genetic variation and gene duplication are among the few that even address this problem.⁵⁴ Others, such as Kirschner and Gerhart⁵⁵ or Caporael, Griesemer and Wimsatt⁵⁶, have also proposed models that can account for the viability of intermediate forms. In contrast to these specific models, our framework of extended evolution provides, from a more systems' theoretical perspective, a synthetic and dynamic perspective for the explanation of the discontinuity or innovation problem. Two features of our framework are relevant for the first part of the innovation challenge—the origin of novelty. Our framework explicitly recognizes that the horizon of possible states generated by complex extended networks is always larger than what is actually realized. Our framework relies on general insights into the structure and behavior of complex systems⁵⁷ that allow us to capture findings about hidden genetic variation and phenotypic plasticity⁵⁸. There are more possible phenotypic systems states, either as a consequence of the structure of individual regulatory networks or of the variational properties of populations than are realized at any given time. But these properties alone do not yet explain the actual

⁵⁴ Kimura, 1994, Roughgarden, 1996, Hartl, 2011, Lesk, 2012.

⁵⁵ Kirschner and Gerhart, 2005.

⁵⁶ Caporael, Griesemer and Wimsatt, 2014.

⁵⁷ Holland, 2012.

⁵⁸ West-Eberhard, 2005b.

evolutionarily stable transformations of phenotypes and especially not how those transitioning populations can be stable enough for such a transformation to be successful.

Here our conceptualization of the dynamics of externalization and internalization offers a possible answer. Realizing that elements of the constructed niche are part of the extended regulatory network for any phenotypic trait and also that these niches can provide stable hereditary information suggests how such transformations can happen, and, as we have seen in our example of social insects, actually did happen. The externalization of parts of the regulatory network into the constructed social or environmental niche enables not only the further exploration of phenotypic states, it also stabilizes emerging new characters throughout transitional phases, as constructed niches can serve as scaffoldings providing stable patterns of heredity. It is important to note here that constructed niches are not only distant structures in the external environment, but that these also include developmental and social contexts that can be as close to the genome as the cytoplasm or maternal behavior. While externalization processes contribute to the transition between network states and therefore also to character transformation, internalization processes then subsequently lead to the increasing stabilization of the new characters and their extended regulatory networks. Selection of favorable variants plays an important role in both cases. But selection and random variation alone do not provide a sufficient explanation for these transitions; the specific structures of regulatory networks and their constructed niches, as well as the dynamics of their transformation through externalization and internalization, are an essential part of the explanation of evolutionary novelties as we have seen in our discussion of the evolution of eusociality.

Cast that way, our framework then presents the evolutionary sequences leading to eusociality as a sequence of network transformations that pass

through a sequence of steps that, while differing in their individual features, include the following stages: (a) the network of a solitary insect responding to internal states and external cues; (b) a semi-social phase with reproductive division of labor maintained by behavioral interactions; and (c) a highly eusocial state with reproductive division of labor and morphological caste differentiation generated by developmental regulation.

The main addition of our framework of extended evolution to explanations of phenotypic evolution lies in emphasis of the dynamic sequence of transformations that connect regulatory networks to their respective niches. Focusing on these transformations may yield mechanistic explanations for the dynamics of evolutionary change that include internal—genomic, developmental, organismic, but also, in cases of cultural evolution, cognitive and institutional—factors and environmental elements. All these factors are linked through a causal network generating phenotypes and their variants.

Finally, our framework offers, as we have seen, an explanation for the related challenges of homology and innovation. An extended conception of regulatory networks that involves both internal and niche elements, as well as the dynamics of externalization and internalization explains not only the stability of developmental systems but also the possibility of transitions between stable states. Connecting our framework to population genetics models suggests a possible explanation of how populations can actually cross valleys in Wrightian fitness landscapes.

Acknowledgements

We would like to thank Jochen Büttner, Lindy Divarci, Doug Erwin, Sascha Freyberg, Christoph Rosol, Matthias Schemmel, Florian Schmaltz, Matteo Valleriani, Sander van der Leeuw, and the members of the Laubichler Lab, especially Guido Caniglia, Erick Peirson, Valerie Racine. MDL acknowledges NSF grants SES 1243575 and SES 1127611. The authors declare no conflict of interest.

References

- Abbot P, Abe J, Alcock J, Alizon S, Alpedrinha JA, Andersson M, Andre JB, van Baalen M, Balloux F, Balshine S, Barton N, Beukeboom LW, Biernaskie JM, Bilde T, Borgia G, Breed M, Brown S, Bshary R, Buckling A, Burley NT, Burton-Chellew MN, Cant MA, Chapuisat M, Charnov EL, Clutton-Brock T, Cockburn A, Cole BJ, Colegrave N, Cosmides L, Couzin ID, Coyne JA, Creel S, Crespi B, Curry RL, Dall SR, Day T, Dickinson JL, Dugatkin LA, El Mouden C, Emlen ST, Evans J, Ferriere R, Field J, Foitzik S, Foster K, Foster WA, Fox CW, Gadau J, Gandon S, Gardner A, Gardner MG, Getty T, Goodisman MA, Grafen A, Grosberg R, Grozinger CM, Gouyon PH, Gwynne D, Harvey PH, Hatchwell BJ, Heinze J, Helanterä H, Helms KR, Hill K, Jiricny N, Johnstone RA, Kacelnik A, Kiers ET, Kokko H, Komdeur J, Korb J, Kronauer D, Kummerli R, Lehmann L, Linksvayer TA, Lion S, Lyon B, Marshall JA, McElreath R, Michalakis Y, Michod RE, Mock D, Monnin T, Montgomerie R, Moore AJ, Mueller UG, Noe R, Okasha S, Pamilo P, Parker GA, Pedersen JS, Pen I, Pfennig D, Queller DC, Rankin DJ, Reece SE, Reeve HK, Reuter M, Roberts G, Robson SK, Roze D, Rousset F, Rueppell O, Sachs JL, Santorelli L, Schmid-Hempel P, Schwarz MP, Scott-Phillips T, Shellmann-Sherman J, Sherman PW, Shuker DM, Smith J, Spagna JC, Strassmann B, Suarez AV, Sundstrom L, Taborsky M, Taylor P, Thompson G, Tooby J, Tsutsui ND, Tsuji K, Turillazzi S, Ubeda F, Vargo EL, Voelkl B, Wenseleers T, West SA, West-Eberhard MJ, Westneat DF, Wiernasz DC, Wild G, Wrangham R, Young AJ, Zeh DW, Zeh JA, Zink A. 2011. Inclusive fitness theory and eusociality. *Nature* 471:E1-4; author reply E9-10.
- Amdam GV, Csondes A, Fondrk MK, Page RE, Jr. 2006. Complex social behaviour derived from maternal reproductive traits. *Nature* 439:76-78.
- Amdam GV, Norberg K, Fondrk MK, Page RE, Jr. 2004. Reproductive ground plan may mediate colony-level selection effects on individual foraging behavior in honey bees. *Proceedings of the National Academy of Sciences of the United States of America* 101:11350-11355.
- Amdam GV, Page RE. 2010. The developmental genetics and physiology of honeybee societies. *Animal behaviour* 79:973-980.
- Amdam GV, Seehuus SC. 2006. Order, disorder, death: lessons from a superorganism. *Advances in cancer research* 95:31-60.
- Andersson C, Tornberg A, Tornberg P. 2014. An evolutionary developmental approach to cultural evolution. *Current anthropology* 55:154-163, 171-154.
- Barve A, Wagner A. 2013. A latent capacity for evolutionary innovation through exaptation in metabolic systems. *Nature* 500:203-206.

- Ben-Tabou de-Leon S, Su YH, Lin KT, Li E, Davidson EH. 2013. Gene regulatory control in the sea urchin aboral ectoderm: spatial initiation, signaling inputs, and cell fate lockdown. *Developmental biology* 374:245-254.
- Bertram SM, Gorelick R, Fewell JH. 2003. Colony response to graded resource changes: an analytical model of the influence of genotype, environment, and dominance. *Theoretical population biology* 64:151-162.
- Beshers SN, Fewell JH. 2001. Models of division of labor in social insects. *Annual review of entomology* 46:413-440.
- Boomsma JJ, Beekman M, Cornwallis CK, Griffin AS, Holman L, Hughes WO, Keller L, Oldroyd BP, Ratnieks FL. 2011. Only full-sibling families evolved eusociality. *Nature* 471:E4-5; author reply E9-10.
- Bowles S, Gintis H. 2011. *A cooperative species : human reciprocity and its evolution*. Princeton: Princeton University Press.
- Boyd R, Richerson PJ. 2005. *The origin and evolution of cultures*. Oxford ; New York: Oxford University Press.
- Boyd R, Richerson PJ, Henrich J. 2011. Rapid cultural adaptation can facilitate the evolution of large-scale cooperation. *Behavioral ecology and sociobiology* 65:431-444.
- Buser CC, Newcomb RD, Gaskett AC, Goddard MR. 2014. Niche construction initiates the evolution of mutualistic interactions. *Ecology letters*.
- Buss LW. 1987. *The evolution of individuality*. Princeton, N.J.: Princeton University Press.
- Calcott B, Sterelny K, Szathmáry Er. 2011. *The major transitions in evolution revisited*. Cambridge, Mass.: MIT Press.
- Caporael LR, Griesemer JR, Wimsatt WC. 2014. *Developing scaffolds in evolution, culture, and cognition*. MIT Press.
- Carroll J. 2004. *Literary Darwinism : evolution, human nature, and literature*. New York: Routledge.
- Carroll SB. 2000. Endless forms: the evolution of gene regulation and morphological diversity. *Cell* 101:577-580.
- Carroll SB. 2008. Evo-devo and an expanding evolutionary synthesis: a genetic theory of morphological evolution. *Cell* 134:25-36.
- Creanza N, Fogarty L, Feldman MW. 2012. Models of cultural niche construction with selection and assortative mating. *PloS one* 7:e42744.
- Davidson EH. 2001. *Genomic regulatory systems : development and evolution*. San Diego: Academic Press.

- Davidson EH. 2006. *The regulatory genome : gene regulatory networks in development and evolution*. Burlington, MA ; San Diego: Academic.
- Davidson EH. 2009. Developmental biology at the systems level. *Biochimica et biophysica acta* 1789:248-249.
- Davidson EH. 2011. Evolutionary bioscience as regulatory systems biology. *Developmental biology* 357:35-40.
- Davidson EH. 2014. The uncommon roles of common gene regulatory factors in the genomes of differentiating cells. *The EMBO journal* 33:1193-1194.
- Davidson EH, Erwin DH. 2010. Evolutionary innovation and stability in animal gene networks. *Journal of experimental zoology Part B, Molecular and developmental evolution* 314:182-186.
- Dolezal AG, Brent CS, Holldobler B, Amdam GV. 2012. Worker division of labor and endocrine physiology are associated in the harvester ant, *Pogonomyrmex californicus*. *The Journal of experimental biology* 215:454-460.
- Erwin DH. 2008. Macroevolution of ecosystem engineering, niche construction and diversity. *Trends in ecology & evolution* 23:304-310.
- Erwin DH. 2012. Novelty that change carrying capacity. *Journal of experimental zoology Part B, Molecular and developmental evolution* 318:460-465.
- Erwin DH, Krakauer DC. 2004. Evolution. Insights into innovation. *Science* 304:1117-1119.
- Erwin DH, Valentine JW. 2013. The Cambrian explosion : the construction of animal biodiversity.
- Fewell JH. 2003. Social insect networks. *Science* 301:1867-1870.
- Flatt T, Amdam GV, Kirkwood TB, Omholt SW. 2013. Life-history evolution and the polyphenic regulation of somatic maintenance and survival. *The Quarterly review of biology* 88:185-218.
- Gadau J, Page RE, Jr., Werren JH, Schmid-Hempel P. 2000. Genome organization and social evolution in Hymenoptera. *Die Naturwissenschaften* 87:87-89.
- Gadau Jr, Fewell J, Wilson EO. 2009. *Organization of insect societies : from genome to sociocomplexity*. Cambridge, Mass.: Harvard University Press.
- Gerhart J, Kirschner M. 2007. The theory of facilitated variation. *Proceedings of the National Academy of Sciences of the United States of America* 104 Suppl 1:8582-8589.
- Giray T, Giovanetti M, West-Eberhard MJ. 2005. Juvenile hormone, reproduction, and worker behavior in the neotropical social wasp *Polistes*

- canadensis. *Proceedings of the National Academy of Sciences of the United States of America* 102:3330-3335.
- Gluckman PD, Bergstrom CT. 2011. Evolutionary biology within medicine: a perspective of growing value. *Bmj* 343:d7671.
- Grant PR. 1999. *Ecology and evolution of Darwin's finches*. Princeton, N.J.: Princeton University Press.
- Grant PR, Grant BR. 2008. *How and why species multiply : the radiation of Darwin's finches*. Princeton: Princeton University Press.
- Hartl DL. 2011. *Essential genetics : a genomics perspective*. Sudbury, Mass.: Jones and Bartlett Publishers.
- Heinze J, Puchinger W, Holldobler B. 1997. Worker reproduction and social hierarchies in *Leptothorax* ants. *Animal behaviour* 54:849-864.
- Holland JH. 2012. *Signals and boundaries : building blocks for complex adaptive systems*. Cambridge, Mass.: MIT Press.
- Hölldobler B, Wilson EO. 1990. *The ants*. Cambridge, Mass.: Belknap Press of Harvard University Press.
- Hölldobler B, Wilson EO. 2009. *The superorganism : the beauty, elegance, and strangeness of insect societies*. New York: W.W. Norton.
- Hölldobler B, Wilson EO. 2011. *The leafcutter ants : civilization by instinct*. New York: Norton.
- Hughes WO, Oldroyd BP, Beekman M, Ratnieks FL. 2008. Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* 320:1213-1216.
- Hunt GJ, Amdam GV, Schlipalius D, Emore C, Sardesai N, Williams CE, Rueppell O, Guzman-Novoa E, Arechavaleta-Velasco M, Chandra S, Fondrk MK, Beye M, Page RE, Jr. 2007. Behavioral genomics of honeybee foraging and nest defense. *Die Naturwissenschaften* 94:247-267.
- Ihle KE, Page RE, Frederick K, Fondrk MK, Amdam GV. 2010. Genotype effect on regulation of behaviour by vitellogenin supports reproductive origin of honeybee foraging bias. *Animal behaviour* 79:1001-1006.
- Jasper WC, Linksvayer TA, Atallah J, Friedman D, Chiu JC, Johnson BR. 2015. Large-scale coding sequence change underlies the evolution of postdevelopmental novelty in honey bees. *Molecular biology and evolution* 32:334-346.
- Jeffares B. 2012. Thinking tools: acquired skills, cultural niche construction, and thinking with things. *The Behavioral and brain sciences* 35:228-229.
- Johnson BR, Linksvayer TA. 2010. Deconstructing the superorganism: social physiology, groundplans, and sociogenomics. *The Quarterly review of biology* 85:57-79.

- Julian GE, Fewell JH, Gadau J, Johnson RA, Larrabee D. 2002. Genetic determination of the queen caste in an ant hybrid zone. *Proceedings of the National Academy of Sciences of the United States of America* 99:8157-8160.
- Kapheim KM, Smith AR, Ihle KE, Amdam GV, Nonacs P, Weislo WT. 2012. Physiological variation as a mechanism for developmental caste-biasing in a facultatively eusocial sweat bee. *Proceedings Biological sciences / The Royal Society* 279:1437-1446.
- Khalturin K, Hemmrich G, Fraune S, Augustin R, Bosch TC. 2009. More than just orphans: are taxonomically-restricted genes important in evolution? *Trends in genetics : TIG* 25:404-413.
- Kimura M. 1994. *Population genetics, molecular evolution, and the neutral theory : selected papers*. Chicago: University of Chicago Press.
- Kirschner M, Gerhart J. 2005. *The plausibility of life : resolving Darwin's dilemma*. New Haven: Yale University Press.
- Krakauer DC, Collins JP, Erwin D, Flack JC, Fontana W, Laubichler MD, Prohaska SJ, West GB, Stadler PF. 2011. The challenges and scope of theoretical biology. *Journal of theoretical biology* 276:269-276.
- Laland K, Uller T, Feldman M, Sterelny K, Muller GB, Moczek A, Jablonka E, Odling-Smee J, Wray GA, Hoekstra HE, Futuyma DJ, Lenski RE, Mackay TF, Schluter D, Strassmann JE. 2014. Does evolutionary theory need a rethink? *Nature* 514:161-164.
- Laland KN. 2008. Exploring gene-culture interactions: insights from handedness, sexual selection and niche-construction case studies. *Philosophical transactions of the Royal Society of London Series B, Biological sciences* 363:3577-3589.
- Laland KN, Odling-Smee FJ, Feldman MW. 1999. Evolutionary consequences of niche construction and their implications for ecology. *Proceedings of the National Academy of Sciences of the United States of America* 96:10242-10247.
- Laland KN, Odling-Smee J, Feldman MW. 2000. Niche construction, biological evolution, and cultural change. *The Behavioral and brain sciences* 23:131-146; discussion 146-175.
- Laland KN, Odling-Smee J, Gilbert SF. 2008. EvoDevo and niche construction: building bridges. *Journal of experimental zoology Part B, Molecular and developmental evolution* 310:549-566.
- Laland KN, Sterelny K. 2006. Perspective: seven reasons (not) to neglect niche construction. *Evolution; international journal of organic evolution* 60:1751-1762.

- Laubichler MD. 2000. Homology in development and the development of the homology concept. *American Zoologist* 40:777-788.
- Leimar O, Hartfelder K, Laubichler MD, Page RE, Jr. 2012. Development and evolution of caste dimorphism in honeybees - a modeling approach. *Ecology and evolution* 2:3098-3109.
- Lesk AM. 2012. *Introduction to genomics*. Oxford ; New York: Oxford University Press.
- Linksvayer TA. 2006. Direct, maternal, and subsocial genetic effects on individual and colony traits in an ant. *Evolution; international journal of organic evolution* 60:2552-2561.
- Linksvayer TA, Busch JW, Smith CR. 2013. Social supergenes of superorganisms: do supergenes play important roles in social evolution? *BioEssays : news and reviews in molecular, cellular and developmental biology* 35:683-689.
- Linksvayer TA, Fewell JH, Gadau J, Laubichler MD. 2012. Developmental evolution in social insects: regulatory networks from genes to societies. *Journal of experimental zoology Part B, Molecular and developmental evolution* 318:159-169.
- Linksvayer TA, Fondrk MK, Page RE, Jr. 2009. Honeybee social regulatory networks are shaped by colony-level selection. *The American naturalist* 173:E99-E107.
- Linksvayer TA, Kaftanoglu O, Akyol E, Blatch S, Amdam GV, Page RE, Jr. 2011. Larval and nurse worker control of developmental plasticity and the evolution of honey bee queen-worker dimorphism. *Journal of evolutionary biology* 24:1939-1948.
- Linksvayer TA, Wade MJ. 2005. The evolutionary origin and elaboration of sociality in the aculeate Hymenoptera: maternal effects, sib-social effects, and heterochrony. *The Quarterly review of biology* 80:317-336.
- Linksvayer TA, Wade MJ. 2009. Genes with social effects are expected to harbor more sequence variation within and between species. *Evolution; international journal of organic evolution* 63:1685-1696.
- Materna SC, Davidson EH. 2007. Logic of gene regulatory networks. *Current opinion in biotechnology* 18:351-354.
- Maynard Smith J, Szathmáry Er. 1995. *The major transitions in evolution*. Oxford ; New York: W.H. Freeman Spektrum.
- Minelli A. 2009. *Perspectives in animal phylogeny and evolution*. Oxford ; New York: Oxford University Press.

- Muller GB, Newman SA. 2005. The innovation triad: an EvoDevo agenda. *Journal of experimental zoology Part B, Molecular and developmental evolution* 304:487-503.
- Nelson CM, Ihle KE, Fondrk MK, Page RE, Amdam GV. 2007. The gene vitellogenin has multiple coordinating effects on social organization. *PLoS biology* 5:e62.
- Nesse RM, Bergstrom CT, Ellison PT, Flier JS, Gluckman P, Govindaraju DR, Niethammer D, Omenn GS, Perlman RL, Schwartz MD, Thomas MG, Stearns SC, Valle D. 2010. Evolution in health and medicine Sackler colloquium: Making evolutionary biology a basic science for medicine. *Proceedings of the National Academy of Sciences of the United States of America* 107 Suppl 1:1800-1807.
- Nowak MA, Tarnita CE, Wilson EO. 2010. The evolution of eusociality. *Nature* 466:1057-1062.
- Odling-Smee FJ. 1995. Niche construction, genetic evolution and cultural change. *Behavioural processes* 35:195-205.
- Odling-Smee FJ, Laland KN, Feldman MW. 2003. *Niche construction : the neglected process in evolution*. Princeton: Princeton University Press.
- Odling-Smee J, Erwin DH, Palkovacs EP, Feldman MW, Laland KN. 2013. Niche construction theory: a practical guide for ecologists. *The Quarterly review of biology* 88:4-28.
- Okasha S. 2008. *Evolution and the levels of selection*. Oxford ; New York: Clarendon Press ; Oxford University Press.
- Page RE. 2013. *The spirit of the hive : the mechanisms of social evolution*. Cambridge, MA: Harvard University Press.
- Page RE, Jr. 1997. The evolution of insect societies. *Endeavour* 21:114-120.
- Page RE, Jr., Amdam GV. 2007. The making of a social insect: developmental architectures of social design. *BioEssays : news and reviews in molecular, cellular and developmental biology* 29:334-343.
- Page RE, Jr., Rueppell O, Amdam GV. 2012. Genetics of reproduction and regulation of honeybee (*Apis mellifera* L.) social behavior. *Annual review of genetics* 46:97-119.
- Patel A, Fondrk MK, Kaftanoglu O, Emore C, Hunt G, Frederick K, Amdam GV. 2007. The making of a queen: TOR pathway is a key player in diphenic caste development. *PloS one* 2:e509.
- Peter IS, Davidson EH. 2011. Evolution of gene regulatory networks controlling body plan development. *Cell* 144:970-985.
- Peter IS, Davidson EH. 2015. *Genomic Control Process: Development and Evolution*. Amsterdam: Academic Press.

- Peter IS, Faure E, Davidson EH. 2012. Predictive computation of genomic logic processing functions in embryonic development. *Proceedings of the National Academy of Sciences of the United States of America* 109:16434-16442.
- Piaget J. 1970. *Genetic Epistemology*. New York: Columbia University Press.
- Pigliucci M, Müller G, Konrad Lorenz Institute for Evolution and Cognition Research. 2010. *Evolution, the extended synthesis*. Cambridge, Mass.: MIT Press.
- Richerson PJ, Boyd R. 2005. *Not by genes alone : how culture transformed human evolution*. Chicago: University of Chicago Press.
- Richerson PJ, Christiansen MH. 2013. *Cultural evolution : society, technology, language, and religion*. MIT Press.
- Roughgarden J. 1996. *Theory of population genetics and evolutionary ecology : an introduction*. Upper Saddle River, NJ: Prentice Hall.
- Rueppell O, Amdam GV, Page RE, Jr., Carey JR. 2004. From genes to societies. *Science of aging knowledge environment : SAGE KE* 2004:pe5.
- Ruse M. 2013. *The Cambridge encyclopedia of Darwin and evolutionary thought*. Cambridge England ; New York: Cambridge University Press.
- Shubin N. 2008. *Your inner fish : a journey into the 3.5-billion-year history of the human body*. New York: Pantheon Books.
- Stearns SC. 1992. *The evolution of life histories*. Oxford ; New York: Oxford University Press.
- Stearns SC, Koella JC. 2008. *Evolution in health and disease*. Oxford ; New York: Oxford University Press.
- Strassmann JE, Page RE, Jr., Robinson GE, Seeley TD. 2011. Kin selection and eusociality. *Nature* 471:E5-6; author reply E9-10.
- Wade MJ, Wilson DS, Goodnight C, Taylor D, Bar-Yam Y, de Aguiar MA, Stacey B, Werfel J, Hoelzer GA, Brodie ED, 3rd, Fields P, Breden F, Linksvayer TA, Fletcher JA, Richerson PJ, Bever JD, Van Dyken JD, Zee P. 2010. Multilevel and kin selection in a connected world. *Nature* 463:E8-9; discussion E9-10.
- Wagner A. 2011. *The origins of evolutionary innovations : a theory of transformative change in living systems*. Oxford ; New York: Oxford University Press.
- Wagner GnP. 2014. *Homology, genes, and evolutionary innovation*. Princeton: Princeton University Press.
- Wagner GP. 1999. A research programme for testing the biological homology concept. *Novartis Foundation symposium* 222:125-134; discussion 134-140.

- Wagner GP. 2007. The developmental genetics of homology. *Nature reviews Genetics* 8:473-479.
- Wagner GP, Chiu C-H, Laubichler MD. 2000. Developmental Evolution as a Mechanistic Science: The Inference from Developmental Mechanisms to Evolutionary Processes. *American Zoologist* 40:819-831.
- West-Eberhard MJ. 1978. Temporary queens in metapolybia wasps: nonreproductive helpers without altruism? *Science* 200:441-443.
- West-Eberhard MJ. 1986. Animal behavior: experimental behavioral ecology and sociobiology. *Science* 231:64-65.
- West-Eberhard MJ. 2005a. Developmental plasticity and the origin of species differences. *Proceedings of the National Academy of Sciences of the United States of America* 102 Suppl 1:6543-6549.
- West-Eberhard MJ. 2005b. Phenotypic accommodation: adaptive innovation due to developmental plasticity. *Journal of experimental zoology Part B, Molecular and developmental evolution* 304:610-618.
- West-Eberhard MJ. 2014. Darwin's forgotten idea: The social essence of sexual selection. *Neuroscience and biobehavioral reviews* 46P4:501-508.
- Wilson EO. 1971a. *The insect societies*. Cambridge, Mass.,: Belknap Press of Harvard University Press.
- Wilson EO. 1971b. Social insects. *Science* 172:406.
- Wilson EO. 1978. Ecology of ants and termites. *Science* 201:337.
- Wilson EO. 1985. The sociogenesis of insect colonies. *Science* 228:1489-1495.
- Wilson EO. 2006. Genomics: how to make a social insect. *Nature* 443:919-920.
- Wilson EO, Holldobler B. 2005a. Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences of the United States of America* 102:13367-13371.
- Wilson EO, Holldobler B. 2005b. The rise of the ants: a phylogenetic and ecological explanation. *Proceedings of the National Academy of Sciences of the United States of America* 102:7411-7414.
- Wilson EO, Nowak MA. 2014. Natural selection drives the evolution of ant life cycles. *Proceedings of the National Academy of Sciences of the United States of America* 111:12585-12590.
- Wimsatt WC. 2013. Articulating babel: An approach to cultural evolution. *Studies in history and philosophy of biological and biomedical sciences*.

Extended Evolution and the History of Knowledge⁵⁹

1. Introduction

This paper provides a framework for analyzing the history of knowledge from the perspective of extended evolution, a conceptual framework that analyzes evolutionary processes as transformations of extended regulatory network structures and is designed to apply to a whole range of phenomena, from genome and biological to cultural and technological evolution. All of these phenomena can be seen as a form of extended knowledge evolution. Our framework is thus inspired by Ernst Mach, a scientist turned historian and philosopher who developed a distinctly evolutionary conception of knowledge. For Mach the dynamics of highly structured systems of knowledge, such as science, was a logical outgrowth of the evolutionary roots of human cognition. He focused specifically on the role of memory—information from genomes to cultural traditions in present-day terminology—and emphasized how all life forms extract “knowledge” or information through a continuous process of trial and error. In consequence of these processes of knowledge acquisition, tested “hypotheses” become incorporated into the (genetic or cultural) make-up or memory of each species. In the case of human culture Mach’s ideas about the cultural transmission of shared or collective memories and the role of institutions in that process are indeed an early version of what we call cultural evolution today.⁶⁰

⁵⁹ This paper will be published in a forthcoming volume of the Springer series, *Vienna Circle Institute Yearbook*, edited by Friedrich Stadler.

⁶⁰ Mach 2011.

The proposal of extended evolution is a conceptual framework for the evolution of complex systems based on the integration of regulatory network and niche construction theories.⁶¹ It applies equally to cases of biological, social and cultural evolution. A general feature of this framework is the transformation of complex networks through the linked processes of externalization and internalization of causal factors between regulatory networks and their corresponding niches. Externalization refers to the stable or lasting transformation of niches (biological, cultural, social and technological) through the actions of systems, whereas internalization captures those processes that lead to the incorporation of stable features of the environment(s) into the regulatory structures governing the actions of systems. These processes extend previous evolutionary models and focus on several challenges, such as the path-dependent nature of evolutionary change, the dynamics of evolutionary innovation and the expansion of inheritance systems.⁶²

2. Cultural Evolution

Cultural processes do not suspend biological evolution but interact with it. The extent to which cultural processes themselves are subject to an evolutionary logic has been controversially discussed. There are in any case striking parallels between biological and cultural history. The history of human societies is a hereditary process involving populations in which cultural information is transmitted with variations from one generation to the next. Human societies come into being and disappear, competing with each other for resources. In spite of these parallels, it is notoriously difficult

⁶¹ Laubichler and Renn 2015.

⁶² Laubichler and Renn 2015.

to define what cultural information is, what counts as variation and what the units of selection in cultural evolution are.⁶³

Cultural evolution, on the other hand, clearly displays features that have gained prominence in recent developments of evolutionary theory, such as niche construction and the role of complex regulatory networks. Human societies transform their environments by means of their material culture which forms a “niche” and decisively shapes their evolution. Human societies do not just vary randomly, but in ways that are governed by hierarchically organized internal structures regulating the behavior of their members. From this perspective, cultural information is stored in these regulative structures as well as in the material culture that supports them. The structures govern variation and the units of selection at the hierarchical level at which they are effective.

Cultural evolution even suggests more precisely how complex regulatory networks interact with niche construction. Niches do not just affect fitness landscapes but extend the system itself by providing crucial regulatory effects. At the same time, the transformation of the environment by human societies constitutes a transformation of their informational organization. While current discussions no longer focus on reducing cultural evolution to a neo-Darwinian model that demands a particulate character or the blindness of cultural evolution, they do emphasize classical Darwinian concepts, such as transmission, variation, selection, drift and migration,⁶⁴ and not the transformation of regulative structures that are otherwise central to the social sciences and cultural history. Institutions are primarily studied with regard to the behavioral mechanisms that enable them, and with regard to their consequences for group selection processes. Niche construction, on the

⁶³ Richerson and Christiansen 2013.

⁶⁴ Mesoudi 2011.

other hand, has become increasingly relevant to discussions about cultural evolution.⁶⁵ Both niche construction and regulatory structures are indeed key factors in the study of certain episodes, for example when considering the role of the domination of fire or the invention of lethal weapons for human sociality.⁶⁶ However, so far this has not yet led to a general approach that deals with their ongoing evolutionary interaction.

3. The History of Knowledge as a Case of Extended Evolution

We consider cultural evolution as a special case of extended evolution.⁶⁷ Here, the interaction between cognition and tradition as regulatory structures and their external representations as part of the material culture form the niche that plays a key dynamical role.⁶⁸ More precisely, from this perspective, cultural evolution deals with embedded networks of actors, actions and their results (see Figure 1).

A crucial aspect of such a network is its capability to learn: the actors are assumed to have an internal, cognitive structure that governs the coordination of their actions and that in turn can change as a result of a reflection on their actions. The encoded experience of the actors constitutes their knowledge. Actions are always embedded in a larger network that includes other actors and the environment, and also a material and social culture resulting from prior actions. Action networks can generate systemic structures that we designate as institutions, regulating the actions that preserve these structures. The material and social culture corresponds, in biological terms, to a niche that has been constructed by a species

⁶⁵ Jeffares 2012; Laland 2008; Laland et al 2000; Mace and Holden 2005; Mesoudi et al 2004; Odling-Smee 1995; Read 2014; Richerson and Boyd 2005; Richerson and Christiansen 2013; Wimsatt 2013.

⁶⁶ Bowles and Gintis 2011.

⁶⁷ Laubichler and Renn 2015.

⁶⁸ Damerow 1996, 2000.

transforming its environment in such a way as to affect its own living conditions.

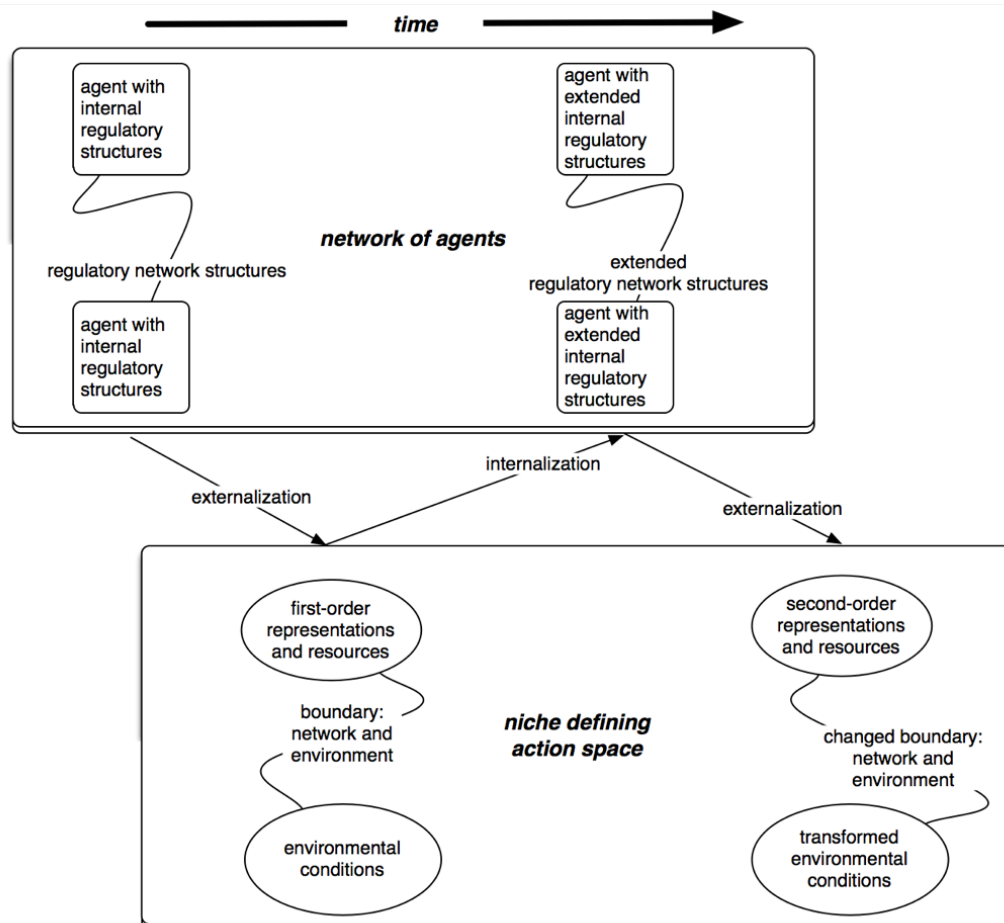


Fig.1.tiff: Networks of agents evolve, including their internal regulatory structures and niches. The niche itself has a network structure induced by the primary network. Its nodes are those aspects of the environment that condition, mediate or become the target of actions, in short the environmental resources and conditions of the internal system. The extended network, including the environment, defines an action space that shapes possible innovations, canalizes the evolutionary process and delimits the structure of the inheritance system.

The material means are that part of the context employed by the actor to reach the goal of an action. They comprise, in particular, the tools available to a given culture and the useful material resources found in the environment. They also constrain the range of actions that are possible in a given situation, thus defining a horizon of possibilities for actions. In dealing with challenges to the preservation of its actors and systemic structures, a network of actors can transform them into an enrichment and reorganization of its regulative structures. Such innovations are possible because the horizon of possibilities inherent in a given material context is larger than anticipated by any given set of actors, a principle that may be considered as a non-teleological version of Hegel's cunning of reason or a phylogenetic version of Vygotsky's "zone of proximal development."⁶⁹

Knowledge and institutions are two important regulative structures that govern actions within such a network.⁷⁰ We will first discuss knowledge, then institutions. Knowledge is, as mentioned above, encoded experience. Based on experience, it is, at the same time, the capacity of an individual, a group or a society to solve problems and to anticipate appropriate actions. In short, knowledge is a problem-solving potential. But it is not just a mental structure. It also involves material and social dimensions that play a crucial role in determining what actions are possible and legitimate in a given historical situation. Knowledge may be shared within a group or a society. Material artifacts such as instruments or texts may be used in learning processes organized by societal institutions, allowing individuals to appropriate the shared knowledge.

The social and material dimensions of knowledge are hence critical for understanding its transmission from one generation to the next. We

⁶⁹ Damerow 1996; Lock 2000; Vygotsky 1978.

⁷⁰ Renn 2014, 2015a.

designate the societal structures governing its production, dissemination and appropriation as the knowledge economy of a society. For most of human history, this knowledge economy was not supported by specialized institutions such as schools or universities. Knowledge was rather transmitted from generation to generation as part of a society's self-reproduction by raising children and involving them in labor processes and various cultural activities.⁷¹

Institutions are here defined as a means of reproducing the social relations existing within a given group or society and, in particular, collaborative roles and the societal distribution of labor. The coordination of individual actions mediated by institutions often presupposes behavioral norms and belief systems such as habits, religion, law, morality or ideology. Institutions represent the potential of a society or a group to coordinate the actions of individuals and to interact with their environment. In the most general sense, institutions can be conceived as encoded collective experience, which results in sets of shared behaviors connected by cognitive, social and material links.

As an "action potential" institutions therefore bear close relations to knowledge as we have defined it, but there are also important differences. While there is no knowledge without the mental anticipation of actions, institutions must largely regulate cooperative behavior without such direct mental anticipation of collective actions and their consequences. Nevertheless, institutions involve knowledge on various levels and must embody and transmit this knowledge in the sense of the capacity of individuals to anticipate actions that are compatible with the coordination regulated by institutions. In addition, institutions must also transmit knowledge on social control and on how to resolve conflicts. And finally, institutions form the basis for the knowledge economy of a society. The

⁷¹ Renn 2012.

history of knowledge must therefore be studied in close conjunction with the history of institutions in this broader sense.

All contexts of action may serve as an external representation of the two key regulative structures we have been considering: knowledge and institutions. Such external representations can be used to share and transmit but also to transform these regulative structures. We have already seen that external representations such as artifacts, tools and texts play a key role in the societal transmission of knowledge; they may also serve as the means of actions performed in order to process and transform knowledge, such as tables or computers.

As for institutions, all kinds of material aspects—persons, animals, places, artifacts, symbols or rituals—can become part of their external, material representation. They then represent a normative social order, defining a field of actions that is compatible with the regulations of an institution. The coordination of individual interactions can be partly discharged to handling the external representations of an institution, such as following a command chain, dealing with paperwork in an administration, exchanging goods for money on the market, or applying written law to a violation of norms.

We thus recognize two essential, complementary features of the model of cultural evolution we are proposing: the role of complex regulative network structures such as knowledge and institutions, and niche construction such as the creation and transmission of a material culture that includes the external representations of these regulative structures. The crucial point now for understanding the evolutionary dynamics of this system is the fact that this niche construction not only depends on complex regulative structures but also in turn shapes them. In the following, we will consider some important turning points in human cultural evolution to assess the current discussions on these turning points from the vantage point of our framework.

4. From Biological to Cultural Evolution

The conceptual framework of extended evolution is general enough not to force upon us a premature distinction between biological and cultural evolution, nor to reduce the latter to a metaphorical generalization of the former. An embedded network of actors, actions and their results may describe a population of our prehuman ancestors just as well as they describe a human society. The relevant regulative structures and environments will be different, but the concept is wide enough to allow for the identification of processes connecting one with the other in an evolutionary continuum.

The evolutionary mechanism giving rise to specifically human ways of thinking is often described in terms of distinct thresholds, involving ecological circumstances that drive humans into more cooperative ways of life and foster adaptations for dealing with problems of social coordination. In his recent book *A Natural History of Human Thinking* (2014) Michael Tomasello emphasizes the cooperative nature of human thinking. He postulates two key evolutionary steps. In the first step, a novel type of small-scale collaboration in human foraging led to socially shared joint goals and joint attention, creating a possibility for individual roles and perspectives within *ad hoc* situations. In the second step, which is characterized by growing human populations competing with each other, humans developed collective intentionality, enabling them to construct a common cultural ground by means of shared cultural conventions, norms, and institutions. The evolutionary mechanism is described in terms of ecological circumstances driving humans into more cooperative ways of life and fostering adaptations for dealing with problems of social coordination.

Against the background of extensive empirical studies involving comparisons between children and apes, Tomasello identifies the specific cognitive abilities emerging in these two evolutionary steps, which are designated as

joint and collective intentionality, respectively. Joint intentionality is characterized by the fact that humans can conceptualize the same situation under different perspectives, that they can make recursive inferences about each other's intentional states and that they can evaluate their own thinking with respect to the normative perspectives of others. Collective intentionality extends joint intentionality to include a conventional dimension of these cognitive capabilities which are now broadly shared within a culture and no longer a matter of ad hoc situations.

In this picture, specific forms of human thinking thus become first the presupposition and then the consequence of human culture. Less emphasis, on the other hand, is given to the evolving results of human thinking in the form of knowledge, institutions and material culture emerging and accumulating from human interactions with their environment over time. Instead of postulating two distinct evolutionary steps leading from biological to cultural evolution, our model rather suggests a continuously working feedback mechanism in which the ecological circumstances cited by Tomasello as evolutionary driving forces are themselves partly created by the regulative structures of human evolution through niche construction. More than Tomasello, we would therefore like to emphasize the material aspect of human actions, not only their instrumental but also their representational aspects, which are crucial for the transmission and transformation of the evolving regulative structures. Material representations of thinking, for instance, may function as external memory, as catalysts for the emergence of different perspectives and as triggers for reflection, and thus affect all the dimensions of thinking processes mentioned by Tomasello.

5. The Evolution of Language

The difference between an assumption of such distinctive evolutionary steps and the perspective of extended evolution becomes strikingly clear when we turn to our first example, the problem of the origin of language and more generally of communicative structures among actors. These structures arise in collaborative situations and depend on the specific constellation, size and ensuing challenges of the relevant communities. Even before the first proto-linguistic communication systems came into being there must have existed some regulative patterns of cooperation such as situative action coordination mediated by visual and other material clues. At least 1.8 million years ago, at the time of *Homo habilis*, these regulative structures had already been shaped by a shared material culture of tool use and transmission. Communication systems, including gestures, pointing, facial expressions, pantomiming, and much later vocalizations, initially would have only marginally supported such regulative structures without representing the full range of cooperative possibilities.⁷² Rather, they may have begun as sporadic, domain-specific and highly context-dependent communicative interactions, which complemented other regulative structures and inherited their “meaning” from these structures.

While communication systems presuppose certain cognitive capabilities on the side of the actors, such as joint attention, they also affect the development of these capabilities by opening up an explorative space in the Vygotskian sense discussed above.⁷³ This space exists precisely because communication systems constitute, like the underlying material culture, external representations of regulative structures that typically have a larger horizon of applicability than that given by their initial purpose or circumstances of

⁷² Dediu and Levinson 2013.

⁷³ Lock 2000; Damerow 2000.

application. This opens up the possibility for an iterative process of language evolution, resulting in the layered structure of the human communication system that we actually observe today, which comprises gestures, facial expressions, pointing, pantomiming and vocalizations, all as part of one integrated multi-modal system of human communication. In a path-breaking paper, Levinson and Holler⁷⁴ have suggested that this multi-modal system is indeed the result of a superposition of evolutionary layers. But what kind of evolution could produce such a layered structure?

Tomasello refers to the famous treatment of *major transitions* in evolution by Maynard Smith and Szathmáry⁷⁵, pointing out that “humans have created genuine evolutionary novelties via new forms of cooperation, supported and extended by new forms of communication. ... And humans have done this twice, the second step building on the first.”⁷⁶ For Maynard Smith and Szathmáry, the major transitions involve changes in the way information is stored and processed, listing as the three main possibilities duplication and divergence, symbiosis and epigenesis. Their own evolutionary account of language, for example, involves the explanation of the genesis of grammatical structures by genetic assimilation, essentially turning cultural into biological inheritance.

Such an argument may fit well with the concept of human cognitive evolution being characterized by major evolutionary transitions, as is assumed by Tomasello⁷⁷ who claims that language “plays its role only fairly late in the process. ... Language (he says) is the capstone of uniquely human cognition and thinking, not its foundation.” Dediu and Levinson⁷⁸, on the other hand,

⁷⁴ Levinson and Holler 2014.

⁷⁵ Maynard Smith and Szathmáry 1995.

⁷⁶ Tomasello 2014, 141.

⁷⁷ Tomasello 2014, 127.

⁷⁸ Dediu and Levinson 2013.

argue “that recognizably modern language is likely an ancient feature of our genus pre-dating at least the common ancestor of modern humans and Neanderthals about half a million years ago.” According to their view, human evolution is a more protracted and reticulated process, involving both vertical and horizontal processes of gene-cultural coevolution and leading to the multi-layered regulatory structure of the human communication system observed today.

In our view, it is precisely the combination of regulatory networks and niche construction that may account for this structure. The evolution of human communication systems is thus governed by the same dynamics that is at the forefront of an emerging new synthesis in evolutionary theory. The process must have started from some contingent ecological context that constituted an external scaffolding for human social interactions, such as conditions favoring collective foraging or hunting. These initially fragile social interactions must have involved some context-dependent signaling, for instance, by means of gestures mimicking actions. The next step would then be a gradual exploration and extension of this situative action coordination, including a discovery of new possibilities such as the ritualization and conventionalization of gestures. The point is that this exploration effectively changed the environment in which social interactions took place, creating a new niche with feedback on the action coordination itself, in particular, on the possibilities for anticipating, by means of communicative acts, the articulation of goals of actions and hence the separation of their planning and execution, as well as the division of labor.

As a consequence, actions were then performed in a new context, accompanied by an ever more extended communication system. As we have emphasized, this extension of the communication system enriched the possibilities of action coordination. The enhanced coordination may also be considered as an internalization of the contingent external conditions of

social interaction-which are now turned into intrinsic properties of this interaction. In short, what may have been initially sporadic, situation-dependent signals within an originally only marginal communication process were eventually transformed into elements of a more and more self-sustaining system of communication, comprising for instance conventionalized gestures that are used outside of immediate action contexts. These elements hence receive their meaning not only from the contexts of action in which they are being applied but also from their role in the emerging communicative system. One immediate effect of such an internalization of external contexts is the stabilization of the originally fragile social scaffolding that originally may have been highly dependent on the contingent external conditions, for instance, specific ecological conditions.

A further consequence of the exploration of the inherent potential of an incipient communication system is the bootstrapping of developmental possibilities that can only be exploited under appropriate external conditions. This is what is designated in psychology as Vygotsky's zone of proximal development, that is, the difference between what an actor can do spontaneously without help and what the actor can do with support from a favorable environment.⁷⁹ This difference is not only familiar from children but also from acculturated apes brought into a human environment. In our case, however, the environment favoring ontogenetic development must, of course, be itself constructed in the course of historical evolution as a cultural niche. In agreement with argument by Lock and Damerow⁸⁰, we claim that in the evolution of populations, systems of external representation provide the conditions for the elaboration of implications that correspond functionally to Vygotsky's zone of proximal development in individual learning.

⁷⁹ Vygotsky 1978; Smith et al. 1997.

⁸⁰ Lock 2000; Damerow 2000.

Following Peter Damerow⁸¹, we further assume that on the level of the individual, action coordination is ruled by cognitive structures that are built up in ontogenesis through interaction with the environment and, furthermore, that these cognitive structures are shaped by the material means of actions. Indeed, the material means available in a given situation determine not only a horizon of possibilities for actions but also what is generic about an action, that is, what can be transferred from one context to another, thus shaping the cognitive structures emerging from their usage. Under this assumption, the construction of a cultural niche encompassing both material means for interacting with the environment and an external system of communication represented by bodily signals must in turn affect the cognitive structures acquired by individuals during their development.

This then is the beginning of a further step in the bootstrapping process. Because the relation between material means and external representations of thinking and communication, on the one hand, and cognitive structures on the other is, of course, not one-sided, with the actions forming the basis and cognition following suit. Newly developed cognitive structures may in turn enable an improvement of the material means of actions employed; similarly these cognitive structures can be represented in communication processes by new kinds of external representations, thus giving rise to an iterative, albeit highly path-dependent evolutionary process that generates cognitive structures of ever greater generality, in the sense of an increasing decontextualization.

It is quite conceivable that such an iterative evolution can indeed account for the emergence of the multimodal system of human communication of which modern language forms the capstone. It is, in any case, a characteristic feature of the process we describe here that new layers do not replace earlier

⁸¹ Peter Damerow 1996.

ones but are rather integrated with the pre-existing layers in an ever more extended regulative architecture. Witness the fact, for instance, that our vocal language continues to be accompanied by body language. But rather than illustrating this in detail for the example of language, we now turn to much more recent periods of history to demonstrate the generality of our model of cultural evolution.

6. The Neolithic Revolution

Our second example deals with the so-called Neolithic Revolution.⁸² Just as there were probably many pathways leading to early communication systems, there were certainly also many routes to food production in different parts of the world. Here we will concentrate on the emergence of food production in the Fertile Crescent around 10,000 BC. Developed agriculture is a comprehensive subsistence strategy involving intensive human labor. It represents an economic system by which human societies produce a large part of their food and other conveniences from domesticated plants and animals. Domesticated plants such as cereals are adapted to human nutritional needs and even rely on human intervention for their reproduction.

Long before humans began to sow harvested seeds, they practiced various forms of landscape management, for instance, cultivating wild cereals and pulses by tilling the soil. In the way that we dealt earlier with proto-languages, we will now deal with predomestication cultivation. Unlike fully developed agriculture, predomestication cultivation in the sense of the manipulation of wild plants and animals did not in itself constitute a complete subsistence strategy but only one component of such a strategy. It evidently existed for a very long time in human history but played only a

⁸² Renn 2015a, 2015b.

more or less marginal role for food production, in the same way that early communication systems must have initially played a rather marginal role in human cooperation. And this role was certainly not motivated by the later outcomes of domestication but constituted an activity with its own rationale and dynamics. Predomestication cultivation offers an example of the principle mentioned earlier that the horizon of applications of given means is always larger than the intentions for which they had been originally employed. This may even apply literally to some of the instruments employed in early farming, which had earlier been used for other purposes.

At least in the Fertile Crescent there were several reasons why predomestication cultivation did not remain marginal, in particular, the contingent ecological conditions that encouraged sedentariness. Sedentariness favored the extension of cultivation practices bound to local environments. Given the investment of labor in cultivation practices, such local predomestication cultivation practices in turn stabilized sedentariness, thus creating what Dorian Fuller has aptly called the “labor traps” along the protracted trajectories leading to domestication.⁸³ This mutual reinforcement of sedentariness and cultivation is similar to the stabilization effect of the development of a prelinguistic communicative system that was pointed out earlier. It constitutes a kind of resonance effect between external conditions and the internal structure of the evolving system. In any case, there was initially no guarantee that predomestication cultivation would lead necessarily to domestication proper. Only at some points along some trajectories may “tipping points” (Fuller) have been reached that then drove the further development in a particular direction, whereas other trajectories may have been aborted or remained in intermediate stages. Contingent

⁸³ Fuller et al. 2010, 2011.

external circumstances had thus been transformed into conditions for the internal stability and further development of a society.

We can also see an analogue to the process of decontextualization by the internalization of external conditions mentioned earlier for language evolution. Eventually, domesticated crops were no longer bound to the local contexts in which their ancestors were originally found but spread into other areas and ultimately across the world. Such globalization effects—also important to the evolutionary history of languages—may have helped to emancipate the incipient domestication processes from the variety of local contexts in which they took place. Since cultivation was part of a network activity taking place in an extended geographical area (and not just in a small core region as traditionally assumed), migration and exchange among different sedentary communities eventually contributed to a diversification and enrichment of cultivars at any specific location. The resulting recontextualization of cultivation may also have helped to separate wild from cultivated populations, thus contributing to a process by which human-defined plant or animal populations were ultimately transformed into biologically defined populations. We also briefly mention here another element of the co-evolutionary and niche construction dynamics of the Neolithic Revolution, namely the co-evolution of disease and society in the context of emerging trade networks and agricultural practices. The emerging constructed niche of agricultural and sedentary societies reaching new levels of population density facilitated the evolution of a number of infectious diseases, which in turn had a huge effect on the regulative structures of these societies.⁸⁴

⁸⁴ Diamond 1998; McNeill 1976.

7. The Evolution of Writing Systems

Our third example, also based on the work of Peter Damerow, deals with what has often been called the urban revolution that is associated with the emergence of writing in southern Mesopotamia in the second half of the fourth millennium BC.⁸⁵ Urbanization is of course based on the Neolithization process we have just described. In this period the modest accounting techniques that had been developed earlier in the context of the rural economy of Babylonia were extensively exploited in the administrations of emerging city-states. These modest accounting techniques correspond to the predomestication cultivation practices in our previous example and to precursors of linguistic communication in our first example. Among the traditional accounting techniques were small clay tokens of different shapes serving as symbolic representations of objects and used for representing and controlling their quantities, but also seals representing certain administrative acts. The exploration of these given means, which served as external representations of administrative knowledge, in the context of an expanding economy eventually led to a transformation of the traditional symbolic culture. The potential of existing tools of symbolic representation was exploited to its limits, with the effect of stabilizing the economies of the emerging city-states. The exploration of the potential of these tokens led, for instance, to a proliferation of the number and shapes of the clay counters, which had originally been used only in small quantities in the context of rural communities.

A critical turning point was when these two elements of the traditional accounting techniques—the counters used for keeping track of the quantities of the administered objects and the seal impressions documenting administrative acts—were represented within a single medium: the clay

⁸⁵ Damerow 2012, Renn 2015b.

tablets serving as the earliest medium of writing. Two initially separate accounting techniques thus became integrated in a new form of external representation whose enormous potential could and was explored in the sequel. The so-called numero-ideographic tablets, representing an early stage of proto-writing, became the starting point for the exploration of new forms of information storage and processing in the archaic period of Babylonian society. The tablets could hold more information than the earlier administrative techniques and that information could be more flexibly and efficiently structured. As in the evolution of language, we thus see that the exploration of a system of representation could act as the population-level analogue of Vygotsky's zone of proximal development.

The next step in the development of writing was again shaped by the fundamental property of external representations, that the range of their possible applications is larger than the specific goals for which they had initially been introduced. The potential of early proto-writing to represent mental constructions in fact reached far beyond the limited field of application within Babylonian administration for which this technique had originally been introduced. In its most developed form, achieved after about a thousand years of historical development, it also included the possibility to represent spoken language. Writing in the modern sense thus emerged from a representational system that was originally developed without this goal in mind, just as domestication resulted from cultivation practices originally pursued without this aim. Such novel possibilities typically occur only as a side effect of mainstream applications. And it is also characteristic that the foundational role of these marginal applications as being constitutive of a new stage is only realized once a new perspective is introduced, often triggered by a new external context.

One such context was education. Indeed, the growing complexity of the proto-writing system required institutional support for its transmission from

generation to generation. But schooling implies a separation of the cognitive means of administration from their immediate context of application and thus opens up a perspective in which the potential of these cognitive means could be explored independently from the constraints of their application to solve concrete administrative problems. The role of education provides a good example for the emancipation of a system of knowledge from its embedding within concrete contexts of application. But there were also other factors that may have similarly acted toward a recontextualization of the existing system of proto-writing, such as the spread of the system across cultural boundaries. Thus a more reflective perspective on this system was introduced favoring the discovery that it was possible to repurpose proto-writing to represent language.

8. The Dynamics of Cultural Evolution

Against the background of these three very different examples we can now summarize our model of cultural evolution. What we have been describing are networks of human actions that include a given material and social culture. This cultural niche results from prior actions and constitutes, together with other environmental conditions and the internal organization of the actors, the regulative structure governing the network. The evolution of a networked population consists in its dealing with outside challenges to its preservation and that of its systemic structures. In the process, such external challenges may be internalized, that is, transformed into elements of the internal network structure.

The cognitive structures of individual actors are generated by reflecting on environmentally embedded actions. They represent the cognitive dimension of an action potential that we designate as knowledge. Knowledge itself may be externally represented and is thus shareable within a knowledge economy. While innovations may be triggered by external challenges, they

become possible first because the horizon of possibilities associated with given means and external representations is always larger than the goals pursued by any given set of actors, and second because the context or the results of actions may become a source of new means of action and new external representations which then enable new forms of action coordination.

The evolution of a networked population may lead to the establishment of new patterns of interaction and new forms of internal, cognitive organization of the actors. On the individual level, new regulative structures arise because the reflection on actions with external representations may generate knowledge of a higher order of abstraction than the knowledge to which the external representation originally referred. The results of such reflections may then again be externally represented, thus generating context and path-dependent chains of abstractions of increasing order. On the population level, new regulative structures may emerge from the introduction of new means or from the exploration of given means, typically triggering both new forms of social organization and new forms of knowledge. Such new patterns of interaction are typically layered in the sense that the introduction of a new pattern does not lead to the complete eclipse of earlier patterns, which are rather integrated into the subsequent layers.

9. Outlook

Given the subject of this volume we have chosen our examples mainly from the domain of cultural evolution. But the conceptual framework we suggest is more general and provides a new perspective on all evolutionary processes—biological and cultural. To briefly illustrate how an integrated perspective on regulatory networks and niche construction applies more generally, we conclude with one particular example from biology: the

evolution of eusocial insects.⁸⁶ The evolution of these complex societies has long puzzled evolutionary theorists, mainly because of their remarkable reproductive division of labor, with a majority of the individuals not reproducing at all. But how can natural selection, favoring reproductive success, lead to giving up one's reproductive potential? In the last decades theorists have focused on models, either kin or group selection, to address this question. But this is not the crucial question. The more fundamental question is: how do we get any division of labor and differentiation into different caste types? And how does this work, given that all individuals in a colony have more or less the same genome? And how can such systems be the product of evolution?

The problem of the evolution of such a superorganism is the same as the problem of the evolution of any multicellular organism with different cell types, namely the problem of developmental regulation and niche construction.⁸⁷ Organisms (super or normal) develop from simple beginnings (a fertilized egg or a mated queen) and gradually differentiate into complex systems (a complex multicellular organism or a fully differentiated colony). At each step this process is controlled by a regulatory system, anchored in the genome, but extending outward and closely connected to co-constructed niches. This regulatory apparatus—more than 90% of the genome, speaking of administrative overhead—processes input, both internal and external, and assures a predictable developmental trajectory as well as the maintenance of system states.

For example, ant colonies have a fixed percentage of soldiers. Removing those—changing the niche for the brood caregivers—triggers a signal cascade that begins at the level of social interactions (reduced encounters

⁸⁶ Laubichler and Renn 2015; Hölldobler and Wilson 2009; Page 2013.

⁸⁷ Laubichler and Renn 2015.

with soldiers), then goes to the brain that processes the social signals and changes the behavior accordingly. The freshly laid larvae are now fed differently, which then triggers physiological processes and cellular signal cascades that ultimately change gene expression profiles so that soldiers hatch instead of other caste types. And this happens until the normal ratio of soldiers is restored. Not all the information of this regulatory system thus resides inside the genome; rather the various niches provide crucial regulatory effects, which are themselves the product of co-evolutionary dynamics. To highlight the inclusion of this external part into an extended regulatory system we refer to this phenomenon, which may also have played a role at the origin of life, as “externalization” or “endaptation” in contrast to the familiar concept of exaptation which designates the repurposing of existing characters.

These remarkable phenomena of differentiation are a consequence of the regulatory developmental potential of complex inheritance systems, including genomes and their external parts, which, as we now know, greatly influence the course of evolution by determining what kind of variation can be introduced into the system. This developmental evolution perspective accounts for the path-dependent and thus historical nature of evolution by analyzing the properties of complex inheritance systems and their interactions with a nested layer of co-constructed niches, from genomes to cultures. It focuses on explaining the origin of variation as a consequence of the properties of these complex systems.⁸⁸

Evolutionary theory is thus no longer based on “change in allele frequencies” but follows the same logic of extended evolution that we have summarized on the basis of our cases of cultural evolution. Our perspective, based on

⁸⁸ Laubichler and Renn 2015.

networks and contexts, hopefully overcomes Mach's worry about the relation between biological and cultural evolution:

Here we wish simply to consider the growth of natural *knowledge* in the light of the theory of evolution. For knowledge, too, is a product of organic nature. And although ideas, as such, do not comport themselves in all respects like independent organic individuals, and although violent comparisons should be avoided, still if Darwin reasoned rightly, the general imprint of evolution and transformation must be noticeable in ideas also.⁸⁹

Acknowledgements

This paper is based on a talk given by one of us (J.R.) at the international conference "Integrated History and Philosophy of Science – &HPS5," held at the University of Vienna from June 26–29, 2014. We are grateful to Friedrich Stadler for giving us the opportunity to present our approach on this occasion. The paper is based on earlier publications of the authors on related themes listed in the references. We would like to thank Sascha Freyberg, Matthias Schemmel and Matteo Valleriani for helpful discussions from which many of the ideas presented here have emerged. We are especially grateful to Lindy Divarci who carefully edited the text.

References

- Bowles, Samuel, and Herbert Gintis. 2011. *A Cooperative Species: Human Reciprocity and Its Evolution*. Princeton: Princeton University Press.
- Damerow, Peter. 1996. *Abstraction and Representation: Essays on the Cultural Evolution of Thinking*. Boston Studies in the Philosophy of Science, vol. 175. Dordrecht: Kluwer Academic Publishers.
- Damerow, Peter. 2000. How can discontinuities in evolution be conceptualized? *Cultural Psychology* 6 (2): 155–160.
- Damerow, Peter. 2012. The Origins of Writing and Arithmetic. In *The Globalization of Knowledge in History*, ed. Jürgen Renn, 153–173. Studies 1: Max Planck Research Library in the History and Development of Knowledge. Berlin: Edition Open Access.

⁸⁹ Mach 1986, 218.

- Dediu, Dan, and Stephen C. Levinson. 2013. On the antiquity of language: the reinterpretation of Neandertal linguistic capacities and its consequences. *Front Psychol* 4: 397.
- Diamond, Jared M. 1998. *Guns, Germs, and Steel: The Fates of Human Societies*. New York: Norton.
- Fuller, Dorian Q., Robin G. Allaby, and Chris Stevens. 2010. Domestication as Innovation: The Entanglement of Techniques, Technology and Change in the Domestication of Cereal Crops. *World Archeology* 42 (1): 13–28.
- Fuller, Dorian Q., George Wilcox, and Robin G. Allaby. 2011. Cultivation and Domestication Had Multiple Origins: Arguments against the Core Area Hypothesis for the Origins of Agriculture in the Near East. *World Archeology* 43 (4): 628–652.
- Hölldobler, Bert and Edward O. Wilson. 2009. *The Leafcutter Ants: Civilization by Instinct*. New York: W.W. Norton.
- Jeffares, Ben. 2012. Thinking tools: acquired skills, cultural niche construction, and thinking with things. *Behav. Brain Sci.* 35 (4): 228–229.
- Laland, Kevin N., et al. 2008. EvoDevo and niche construction: building bridges. *J Exp Zool B Mol Dev Evol* 310 (7): 549–566.
- Laland, Kevin N., et al. 2000. Niche construction, biological evolution, and cultural change. *Behav Brain Sci* 23 (1): 131–146; see also the discussion on pp. 146–175.
- Laubichler, Manfred, and Jürgen Renn. 2015. Extended evolution: A conceptual framework for integrating regulatory networks and niche construction. *J. Exp. Zool. (Mol. Dev. Evol.)* 9999:1–13, <http://onlinelibrary.wiley.com/doi/10.1002/jez.b.22631/epdf>
[A version of this paper is included in this preprint.]
- Levinson, Stephen C. and Judith Holler. 2014. The origin of human multimodal communication. *Philosophical Transactions of the Royal Society B*.
- Lock, Andrew J. 2000. Phylogenetic Time and Symbol Creation: Where Do Zopeds Come From? *Culture & Psychology* 6 (2): 105–129.
- Mace, Ruth, and Clare J. Holden. 2005. A phylogenetic approach to cultural evolution. *Trends Ecol Evol* 20 (3): 116–121.
- Mach, Ernst. 1986. *Popular Scientific Lectures*. La Salle, Ill.: Open Court.
- Mach, Ernst. 2011. *Erkenntnis und Irrtum. Skizzen zur Psychologie der Forschung. Ernst Mach Studienausgabe*. Berlin: Xenomoi Verlag.

- Maynard Smith, John, and Eörs Szathmáry. 1995. *The Major Transitions in Evolution*. Oxford: Oxford University Press.
- McNeill, William. 1976. *Plagues and Peoples*. New York: Anchor Books Doubleday.
- Mesoudi, Alex et al. 2004. Perspective: is human cultural evolution Darwinian? Evidence reviewed from the perspective of the Origin of Species. *Evolution* 58 (1): 1–11.
- . 2011. *Cultural Evolution: How Darwinian Theory Can Explain Human Culture and Synthesize the Social Sciences*. London: University of Chicago Press.
- Odling-Smee, John. 1995. Niche construction, genetic evolution and cultural change. *Behav Processes* 35 (1–3): 195–205.
- Page, Robert E. 2013. *The Spirit of the Hive: The Mechanisms of Social Evolution*. Cambridge, Mass.: Harvard University Press.
- Read, Dwight W. 2014. The substance of cultural evolution: Culturally framed systems of social organization. *Behav Brain Sci* 37 (3): 270–271.
- Renn, Jürgen, Ed. 2012. *The Globalization of Knowledge in History*. Studies 1: Max Planck Research Library in the History and Development of Knowledge. Berlin: Edition Open Access.
- Renn, Jürgen. 2014. The Globalization of Knowledge in History and its Normative Challenges. *Rechtsgeschichte/Legal History* (22): 52–60.
- Renn, Jürgen. 2015a. From the History of Science to the History of Knowledge – and Back. *Centaurus* (57): 37–53.
- Renn, Jürgen. 2015b. Learning from Kushim about the Origin of Writing and Farming. *Grain Vapor Ray. Textures of the Anthropocene*. K. Klingan, A. Sepahvand, C. Rosol and B. M. Scherer. Cambridge, MA: MIT Press: 241–259.
- Renn, Jürgen, Manfred D. Laubichler, and Helge Wendt. 2014. Energietransformationen zwischen Kaffee und Koevolution. In *Willkommen im Anthropozän! Unsere Verantwortung für die Zukunft der Erde, Katalog zur Sonderausstellung am Deutschen Museum*, eds. Nina Möllers, Christian Schwägerl, and Helmuth Trischler, 81–84. Munich: Deutsches Museum.
- Richerson, Peter J., and Morten H. Christiansen. 2013. *Cultural Evolution: Society, Technology, Language, and Religion*. Strungmann Forum Reports. Cambridge, MA: MIT Press.
- Richerson, Peter J., and Robert Boyd. 2005. *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press.

- Smith, Leslie, Julie Dockrell, and Peter Tomlinson. 1997. *Piaget, Vygotsky and Beyond: Future Issues for Developmental Psychology and Education*. New York: Routledge.
- Tomasello, Michael. 2014. *A Natural History of Human Thinking*. Cambridge MA: Harvard University Press.
- Valleriani, Matteo. 2010. *Galileo Engineer*. Boston Studies in the Philosophy of Science, vol. 269. Dordrecht: Springer.
- Vygotsky, Lev S. 1978. *Mind in Society. The Development of Higher Psychological Processes*. Cambridge MA: Harvard University Press.
- Wimsatt, W. C. 2013. Articulating babel: An approach to cultural evolution. *Stud Hist Philos Biol Biomed Sci* 44 (4): 563–571.

MAX-PLANCK-INSTITUT FÜR WISSENSCHAFTSGESCHICHTE

Max Planck Institute for the History of Science

Preprints since 2013 (a full list can be found at our website)

- 437** Jürgen Renn **Schrödinger and the Genesis of Wave Mechanics**
- 438** Pietro Daniel Omodeo **L'iter europeo del matematico e medico scozzese Duncan Liddel**
- 439** Irina Tupikova & Klaus Geus **The Circumference of the Earth and Ptolemy's World Map**
- 440** Pietro Daniel Omodeo und Jürgen Renn **Das Prinzip Kontingenz in der Naturwissenschaft der Renaissance**
- 441** Horst Kant und Jürgen Renn **Eine utopische Episode – Carl Friedrich von Weizsäcker in den Netzwerken der Max-Planck-Gesellschaft**
- 442** William G. Boltz and Matthias Schemmel **The Language of 'Knowledge' and 'Space' in the Later Mohist Canon** (TOPOI – Towards a Historical Epistemology of Space)
- 443** Stefano Bordoni **Looking for a Rational Thermodynamics in the late XIX century**
- 444** Sonja Brentjes and Jürgen Renn **The Arabic Transmission of Knowledge on the Balance**
- 445** Horst Nowacki **Archimedes and Ship Design**
- 446** Matthias Schemmel **Elements of a Historical Epistemology of Space** (TOPOI – Towards a Historical Epistemology of Space)
- 447** Martin Thiering and Wulf Schiefenhövel **Spatial Concepts in Non-Literate Societies: Language and Practice in Eipo and Dene Chipewyan** (TOPOI – Towards a Historical Epistemology of Space)
- 448** Jürgen Renn **Einstein as a Missionary of Science**
- 449** Hubert Laitko **Der Ambivalenzbegriff in Carl Friedrich von Weizsäckers Starnberger Institutskonzept**
- 450** Stefano Bordoni **When Historiography met Epistemology.** Duhem's early philosophy of science in context
- 451** Renate Wahsner **Tausch – Allgemeines – Ontologie oder Das Auseinanderlegen des Konkreten und seine Aufhebung**
- 452** Jens Høyrup **Algebra in Cuneiform.** Introduction to an Old Babylonian Geometrical Technique
- 453** Horst Nowacki **Zur Vorgeschichte des Schiffbauversuchswesens**
- 454** Klaus Geus and Mark Geller (eds.) **Esoteric Knowledge in Antiquity** (TOPOI – Dahlem Seminar for the History of Ancient Sciences Vol. II)
- 455** Carola Sachse **Grundlagenforschung. Zur Historisierung eines wissenschaftspolitischen Ordnungsprinzips am Beispiel der Max-Planck-Gesellschaft (1945–1970)**
- 456** David E. Rowe and Robert Schulmann **General Relativity in the Context of Weimar Culture**
- 457** F. Jamil Ragep **From Tūn to Turun: The Twists and Turns of the Tūsi-Couple**
- 458** Pietro Daniel Omodeo **Efemeridi e critica all'astrologia tra filosofia naturale ed etica: La contesa tra Benedetti e Altavilla nel tardo Rinascimento torinese**
- 459** Simone Mammola **Il problema della grandezza della terra e dell'acqua negli scritti di Alessandro Piccolomini, Antonio Berga e G. B. Benedetti e la progressiva dissoluzione della cosmologia delle sfere elementari nel secondo '500**

- 460** Stefano Bordoni **Unexpected Convergence between Science and Philosophy: A debate on determinism in France around 1880**
- 461** Angelo Baracca **Subalternity vs. Hegemony – Cuba's Unique Way of Overcoming Subalternity through the Development of Science**
- 462** Eric Hounshell & Daniel Midena **“Historicizing Big Data” Conference, MPIWG, October 31 – November 2, 2013** Report
- 463** Dieter Suisky **Emilie Du Châtelet und Leonhard Euler über die Rolle von Hypothesen. Zur nach-Newtonschen Entwicklung der Methodologie**
- 464** Irina Tupikova **Ptolemy's Circumference of the Earth** (TOPOI – Towards a Historical Epistemology of Space)
- 465** Irina Tupikova, Matthias Schemmel, Klaus Geus **Travelling along the Silk Road: A new interpretation of Ptolemy's coordinates**
- 466** Fernando Vidal and Nélia Dias **The Endangerment Sensibility**
- 467** Carl H. Meyer & Günter Schwarz **The Theory of Nuclear Explosives That Heisenberg Did not Present to the German Military**
- 468** William G. Boltz and Matthias Schemmel **Theoretical Reflections on Elementary Actions and Instrumental Practices: The Example of the Mohist Canon** (TOPOI – Towards a Historical Epistemology of Space)
- 469** Dominic Olariu **The Misfortune of Philippus de Lignamine's Herbal or New Research Perspectives in Herbal Illustrations From an Iconological Point of View**
- 470** Fidel Castro Díaz-Balart **On the Development of Nuclear Physics in Cuba**