Introduction: Perspectives on Entangled Life

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Abstract Despite burgeoning interest in new and more complex accounts of the organism-environment dyad, biologists and philosophers of biology have paid little attention to the history of these ideas and to their broader deployment in the social sciences and in other disciplines outside biology. Even in biology and philosophy of biology, detailed conceptual models of the organism-environment relationship are still lacking. This volume is designed to fill these lacunae by providing the first multidisciplinary discussion of the topic of organism-environment interaction. It brings together scholars from history, philosophy, psychology, anthropology, medicine, and biology to discuss the common focus of their work: entangled life, or the complex interaction of organisms and environments.

In September 1978, a special issue of Scientific American was published, "devoted to the history of life on earth as it is understood in the light of the modern 'synthetic' theory of evolution" (1978, 47). Introduced by the zoologist Ernst Mayr, it comprised a series of articles by prominent scientists showing how that theory made sense of the history of life, from its origins to the emergence of modern human behavior. The final article in the issue, however, stood apart from the others. It offered an extended critique of a notion-adaptation-that was central to the theoretical perspective celebrated by the rest: a notion that had indeed been central to studies of the natural world even before evolution came onto the scene. The idea that the environment sets "problems" that organisms must "solve" was riddled with difficulties, according to geneticist Richard Lewontin (1978, 213). Organisms,

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Lewontin insisted, are not passively shaped by the selective forces resulting from changes in environments. Instead, they actively create those changes:

There is a constant interplay of the organism and the environment, so that although natural selection may be adapting the organism to a particular set of environmental circumstances, the evolution of the organism itself changes those circumstances. (215)

This article closing a special issue devoted to the "modern synthesis" of genetics and natural selection was in fact part of a broad intellectual movement in the late 1970s that began to question certain aspects of that very synthesis—a movement that insisted upon the importance of interaction between organism and environment during ontogeny, or the lifetime of the organism (e.g., Gould 1977; Lewin 1980; Bonner 1982).

Much of the recent interest among biologists in different models of the interaction of organism and environment can be traced back to the new perspectives that emerged in this period. Evolutionary-developmental biology, or "evo-devo," is now a hot topic. Evo-devo has a complex intellectual history going back at least to the nineteenth century, but many historians and practitioners see the modern resurgence of interest in development as a response to the late-1970s critique of the modern synthesis by Lewontin and others (Laubichler 2007; Müller 2007; Wagner 2007; for deeper roots, see Raff and Love 2004; Amundson 2005; and the other chapters in Laubichler and Maienschein 2007). By opening up the black box into which the modern synthesis placed ontogenetic processes, evo-devo explores the interaction of organism and environment at developmental rather than evolutionary timescales.

Lewontin's point about organisms modifying their environments inspired another recent research program in biology even more directly—niche construction. In "Niche-Constructing Phenotypes," the first outline of this approach, John Odling-Smee followed Lewontin in criticizing the modern synthesis for holding "autonomous events in the environment ... to be exclusively responsible for directing the course of evolution down nonrandom paths" (1988, 75). Odling-Smee went on to suggest that the organism-environment relationship—and adaptation itself—involves at least two processes:

Instead of natural selection's causing organisms to adapt to their environments, ... the constructive activities of phenotypes could cause their environments to become adaptive to themselves. More plausibly, ... the adaptive fit between organisms and their environments could be caused by both of these processes acting together. (77)

This idea of niche construction, and the related notion of ecosystem engineering, opened up new research directions in biology (Odling-Smee et al. 2003; Cuddington et al. 2007), and the resultant models of the relation between organism and environment have been extensively discussed by philosophers (Godfrey-Smith 2000, 2001; Sterelny 2001, 2005; Okasha 2005; Griffiths 2005; Barker 2008; Pearce 2011a).

But despite the burgeoning interest in new and more complex accounts of the organism-environment dyad by biologists and philosophers, little attention has been paid in the resulting discussions to the history of these ideas and to their deployment in disciplines outside biology—especially in the social sciences. Even in biology and philosophy, there is a lack of detailed conceptual models of the organism-environment relationship. This volume is designed to fill these lacunae by providing the first multidisciplinary discussion of the topic of organism-environment interaction.¹ It brings together scholars from history, philosophy, psychology, anthropology, medicine, and biology to discuss the common focus of their work: *entangled life*, or the complex interaction of organisms and environments.

This multidisciplinary approach is important for at least two reasons. First, it has the potential to reveal historical connections that are not apparent from the perspective of a single modern discipline. For example, when the notion of organism and environment as an interacting system was first articulated in the late nineteenth century, biology, psychology, and philosophy were much less isolated from one another than they are now (and certainly less so than they were in the 1970s). Historical investigation may thus help us recover the set of interdisciplinary problems to which the organism-environment framework was originally applied, and give us new ways of thinking about today's analogous problems. These roots and ramifications of the concept of organism-environment interaction can be traced through various historical periods. In the 1960s, notably, researchers in both psychology and anthropology independently championed "ecological" approaches to their respective sciences: ecological psychology and cultural ecology were both studying humans interacting with their environments, albeit at different levels of organization (Geertz 1963; Gibson 1966; Barker 1968; Rappaport 1968). Histories can connect disciplines, and connecting disciplines can in turn enrich our histories.

Second, bringing researchers from different disciplines together fosters both collaboration and cross-fertilization. As Alan Love has argued, multidisciplinary research is prompted by "complex problem domains that elude scientific explanations arising from specific disciplinary approaches" (2008, 876; cf. Mitchell 2009). When phenomena are complex—and the interaction of organisms and environments surely qualifies—the theories and techniques of individual sciences tend to be inadequate to the challenges of describing, explaining, and intervening on those phenomena. When methods and concepts developed in different disciplinary contexts are combined, however, such difficulties may be met more successfully: a diversity of tools makes problems more tractable. Philosophers have also argued that including a variety of perspectives tends to improve the results of scientific inquiry, since it expands the range of possible interpretations of and approaches to particular problem areas (Wylie 1992; Okruhlik 1994; Longino 2002). (There is reason to suppose that this might be especially true for topics—such as organism-environment interaction—that are deeply interwoven with values and assumptions about human

¹It collects several papers presented in the "Organism-Environment Interaction: Past, Present, and Future" section of the *Integrating Complexity: Environment and History* conference at Western University, 7–10 October 2010. The conference was the off-year workshop of the International Society for the History, Philosophy, and Social Studies of Biology, and was funded by the Rotman Institute of Philosophy and the Social Sciences and Humanities Research Council of Canada. For a brief report of the conference, see Pearce (2011b).

life and human society.) Biologists, social scientists, and philosophers may be able to share insights from their local viewpoints so as to clarify their respective models of organism-environment interaction, and perhaps even develop novel collaborative models.

A final aim of this volume is to show scholars in different disciplines that they really are dealing with similar types of conceptual and empirical problems, despite their apparently divergent goals. Over the last several decades, there has been a quiet revolution across a wide range of fields of study: simplistic understandings of the relation between organism and environment have been increasingly rejected in favor of sophisticated models. Niche construction, evo-devo, nature/nurture, developmental systems, genotype x environment, political ecology, plasticity, feedback effects, affordances-these are among the characteristic concepts of the new approach. But researchers employing these concepts often do not engage with one another's work, and thus do not realize that they are all tackling the same problem: How should we understand organism-environment interaction? This lack of communication is a missed opportunity. The main goal of this volume is thus to convince biologists, philosophers, and social scientists that they are often struggling in the same conceptual thicket even though the foliage they see is different. Identifying the shared object-organism-environment interaction-is the first step to finding a wav out.

The volume is divided into three main parts: Historical Perspectives, Contested Models, and Emerging Frameworks. The first part explores the origins of the modern idea of organism-environment interaction in the mid-nineteenth century and its development by later psychologists and anthropologists. In the second part, a variety of controversial models—from mathematical representations of evolution to model organisms in biomedical research—are discussed and reframed in light of recent questions about the interplay between organisms and environment. Finally, the third part investigates several new ideas that have the potential to reshape key aspects of the biological and social sciences.

Today, the idea of organism-environment interaction is ubiquitous. But in the opening chapter, Trevor Pearce shows that this idea, at least in its modern form, dates only to the mid-nineteenth century. It was the philosophers Auguste Comte and Herbert Spencer who first paired the terms 'organism' and 'environment' as part of an account of the nature of life. This dichotomy went on to frame late-nineteenth-century discussion in biology, psychology, and philosophy, specifically the 1890s debates over the causal factors of evolution and the philosophical program of pragmatists like John Dewey.

Christopher Green takes a closer look at a key moment in these 1890s debates: the origins of the idea that environment-induced modifications can pave the way for similar heritable variations—what came to be called the "Baldwin Effect." Green argues that debates about the future of the hundreds of thousands of immigrants who entered the United States each year were an essential part of the context for James Mark Baldwin's much-debated proposal. Arguments over the possibility of improving the lot of these often-destitute immigrants lay in the background of biological debates between neo-Lamarckians and neo-Darwinians over the nature of the organism-environment relationship in evolution. The next two chapters move to the twentieth century, exploring the history of ecological approaches to psychology and anthropology. Harry Heft links the ecological psychology of James J. Gibson and Roger G. Barker to the radical empiricism of William James and his student Edwin B. Holt. In particular, Holt's notion of action as "out-reaching, outgoing, inquiring, examining, and grasping" laid the groundwork for the modern idea of situated action. Thinking of most behavior as situated helps connect Gibson's "affordances" and Barker's "behavior settings," two important accounts of the relation between organism and environment in human action. The latter account moves beyond consideration of individual organisms in interaction with their individual environments to look at the complex interactions that connect multiple participants, objects, and structures to comprise a functionally-integrated behavior setting, in analogy with the interactions among organisms and abiota that comprise an ecosystem.

As mentioned above, ecological approaches emerged in the 1960s not only in psychology but also in anthropology. After reviewing the origins and development of ecological anthropology, Emily Schultz argues that recent theoretical work by Bruno Latour and others has enriched and extended the traditional anthropological idea that our interaction with environments is invariably culturally mediated. Moreover, this work relates directly to recent discussions in theoretical biology. Schultz suggests that actor-network theory in anthropology and niche construction theory in biology, when combined, form a conceptual framework that can be applied in both fields—especially at the interface of nature and culture.

The second part of the book is focused on contemporary rather than historical questions. The diversity of contemporary issues is reflected in the mix of approaches (and idioms) appearing in this part—two papers engage with formal models in formal terms; two others engage broader conceptual questions about experimental practice and its theoretical connections. In the first half of this part two philosophers analyze the treatment of organism-environment interaction in population genetics models. Bruce Glymour examines the question of whether adaptation should be thought of as adaptation to specific features of the environment or as adaptation to the environment as a whole. He argues that talking about adaptation *to* some environmental feature requires that the feature interactively cause an increase in fitness. Furthermore, such features can be identified only if their causal influence on fitness is measured. Estimates of the strength of selection depend on how these causal processes are modeled.

Marshall Abrams explores different ways of modeling how organisms experience environmental variation. Should we think of organisms in a given region, for example, as sharing a common environment, or as occupying diverse sub-environments? Both representations raise problems for the notion of relative fitness, and the fitness of an organism will come out differently according to the environmental grain we choose. According to Abrams, fitness is a function of probable reproductive success within each sub-environment, weighted according to the probability that the organism is in fact in that sub-environment. He argues that biologists make choices about environmental grain with the intent of capturing the environmental variation that is causally relevant to the population of interest. Given these choices, however, researchers' descriptions of the process of natural selection can be objective. Jessica Bolker looks to organismal biology to analyze a primary tool of the modern life sciences—the model organism. Bolker argues for the importance of attention to both the biological and epistemological context of such organisms. The former often involves a tension between attempts to standardize and simplify the environments of model organisms and the need to preserve key aspects of organisms' natural environments. The latter depends on whether the organism in question is being used as a surrogate for a different species or as an exemplar of a particular group. Attention to these contexts can help biologists locate deficiencies of current models and develop novel alternatives.

The chapter by Desjardins, Barker, and Madrenas examines the case of human immunology and its inability to translate into clinical outcomes the knowledge obtained from research on the laboratory mouse—a failure that has recently become widely recognized by immunologists. They suggest that in order to achieve clinical success, human immunology will have to depart from the very well established Bernardian reductionist tradition in biomedical research—focusing on finding molecular pathways in animal models in controlled laboratory settings—and instead study humans in their actual environments. This requirement, the authors argue, follows essentially from the fact that the human immune system is such that we cannot sufficiently understand immune responses unless we adopt a research strategy that fully integrates the complex history of interactions between organisms and their environment.

The final part of the book looks at a series of theoretical frameworks for understanding the organism-environment relationship: niche construction, the adaptive landscape, and evo-devo. In the first chapter of this part, Gillian Barker and John Odling-Smee explore the problematical relationship between the conceptions of organism and environment that figure in evolutionary biology and those employed in ecology. They argue that long-standing inconsistencies between the simple idealizations upon which evolutionary and ecological models are based have prevented effective integration of these fields of biological study, despite their obvious interconnections. New perspectives on organism-environment interaction emerging from both disciplines-niche construction and ecosystem engineeringhave recently begun to extend these idealizations and bridge the conceptual gap between the two fields. Barker and Odling-Smee argue that further developing these insights to consider the complex effects that organisms have on each other's evolutionary environments as well as their own yields a new theoretical framework-ecological niche construction-that can in turn contribute, along with evolutionary developmental biology, to the emergence of a broad new perspective in biology that takes full account of organism-environment interaction at all levels to integrate evolution, ecology, and development.

Denis Walsh tackles the classic evolutionary metaphor of an adaptive landscape. He begins by criticizing several presuppositions of this metaphor, especially the idea that the topology of the landscape is not affected by whether or not certain points on it are occupied. He proposes instead a new metaphor, the affordance landscape, inspired by Gibson's concept of an affordance—what the environment provides or furnishes to an organism. Walsh argues that the idea of an affordance landscape makes clear that biological form and environmental affordances are co-constituting: i.e., they are reciprocally dependent. On this view, changes in form can result in changes in affordances—movement across the landscape—even without changes in the environment.

Next, Rachael Brown asks why biologists studying behavior have made so little use of the new conceptual framework of evolutionary-developmental biology or "evo-devo." Brown notes that behavioral biologists are missing out, suggesting that the developmental processes emphasized in evo-devo are also important in the evolution of behavior. She draws an important parallel between two non-genetic inheritance channels: the first, chromatin-marking of DNA, is a standard topic in evodevo, while the second, social learning, is central to studies of behavior. This parallel indicates that behavior—and not just morphology—involves the interplay between development and evolution, and can be understood via the evo-devo framework.

In the final chapter of the volume, Kim Sterelny traces the causes of a series of increases in cooperative behavior across the evolutionary history of the genus *Homo*. He argues that the richness of human cooperative life is due in large part to positive feedback between the natural environment, human populations, and social structures: that is, new forms of cooperation tend to create or promote circumstances that lead to the evolution of yet further cooperative strategies. Sterelny argues that human niche construction—not only modification of the physical environment, but also organization of informational and learning environments for the next generation—has played a central role in the evolution of cooperation.

No volume on so rich and multifarious a theme can address all the issues that merit attention. We cannot hope here to provide a comprehensive overview of the terrain, but more modestly to draw attention to some of its most interesting features as seen from diverse disciplinary perspectives, to introduce readers to some of the explorations already under way, and to indicate the potential for illuminating further work. Some important topics are only touched on in the papers included here; others do not appear at all. Here we briefly indicate some of the many topics that would have been treated in a sufficiently capacious ideal volume on organism-environment interaction. Readers will no doubt think of others—a further indication of the broad importance of these issues.

A range of historical literatures are beginning to trace the origins of organismenvironment thinking and its paths in different periods and contexts, from Romantic science to Darwin's own thought; from the American Pragmatists to twentiethcentury psychology, psychiatry, and educational theory. The historical papers in this volume give an entree to only some of these discussions. Sterelny and Brown both point toward the need to open up a broader perspective on evolutionary psychology—one that takes full account of organism-environment interaction but there is much more to explore in this area, notably the contributions of feminist evolutionary psychologists. Several related research programs investigate the broad implications of organism-environment interaction for cognition, under the concepts of embodied cognition, enactivism, situated cognition, and situated knowledge. Heft's paper introduces readers to the roots of ecological psychology; both psychology and philosophy have seen a recent resurgence of interest in approaches that draw on the early ideas that his paper delineates. The notion of niche construction is one of the threads tying this volume together, but there are many extensions of this notion into new areas that we have not captured, including ongoing work on its implications for the concept of adaptation. Green sheds a fascinating new light on the origins of the so-called Baldwin Effect; this idea continues to drive conceptual innovation in biology and philosophy. A particularly fast-growing and exciting family of research programs has grown up around organism-environment interactions that involve regulation, from the genomic to the ecological level. Systems biology, evolutionary developmental biology, and epigenetics are among the programs of biological research emerging in this area; each also has inspired a line of philosophical investigation. Another approach combines elements from biology and the social sciences to explore the ramifications of G x E interactions in behavioral genetics and in psychiatry, among other contexts. And quite diverse literatures are looking at the kinds of complexity that organism-environment interaction gives rise to, and its implications for contingency in processes of biological and social change.

These topics are tremendously diverse, yet the researchers engaging each of them share, with each other and with the authors represented in this volume, a focus on the nature of the relationship between organism and environment and a commitment to unraveling the mysteries of entangled life.

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