History, Philosophy and Theory of the Life Sciences

Gillian Barker
Eric Desjardins
Trevor Pearce *Editors*

# Entangled Life

## Organism and Environment in the Biological and Social Sciences

Springer

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# Contents

# Introduction: Perspectives on Entangled Life

**Gillian Barker, Eric Desjardins, and Trevor Pearce**

**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

[1] It 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 way 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 engineering—have 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 evo-devo, 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 organism-environment thinking and its paths in different periods and contexts, from Romantic science to Darwin's own thought; from the American Pragmatists to twentieth-century 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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# Part I
# Historical Perspectives

# The Origins and Development of the Idea of Organism-Environment Interaction

**Trevor Pearce**

**Abstract** The idea of organism-environment interaction, at least in its modern form, dates only to the mid-nineteenth century. After sketching the origins of the organism-environment dichotomy in the work of Auguste Comte and Herbert Spencer, I will chart its metaphysical and methodological influence on later scientists and philosophers such as Conwy Lloyd Morgan and John Dewey. In biology and psychology, the environment was seen as a causal agent, highlighting questions of organismic variation and plasticity. In philosophy, organism-environment interaction provided a new foundation for ethics, politics, and scientific inquiry. Thinking about organism-environment interaction became indispensable, for it had restructured our view of the biological and social world.

## 1 Introduction

That creatures are shaped by the world around them is not news. Several centuries before the Common Era, the Hippocratic author of "Airs, Waters, Places" argued that our forms and habits are affected by the climate, the air we breathe, and the water we drink. For example, the inhabitants of Phasis reportedly had the deepest voices known because they breathed "air which is moist and damp and not clean" (Lloyd 1978, 162). As I will show, however, this concrete notion of various external conditions affecting the health and features of living beings was gradually replaced in the second half of the nineteenth century by the abstract idea of an organism's environment. The new dichotomy of organism and environment proved both useful and portable. By the 1890s, it was already operating as an essential framing device in scientific and philosophical arguments. In biology and psychology, the

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environment was seen as a causal agent, highlighting questions of organismic variation and plasticity. In philosophy, organism-environment interaction provided a new foundation for ethics, politics, and scientific inquiry. Thinking about organism-environment interaction became indispensable, for it had restructured our view of the biological and social world.

In the first part of the chapter, I will describe the origins of the idea of organism-environment interaction in the work of Auguste Comte and Herbert Spencer. I will then demonstrate how the idea played a central role in late-nineteenth-century debates over the causal factors of evolution—specifically the controversy over August Weismann's account of heredity and the discovery of the so-called "Baldwin Effect." In the third section, I will follow the idea of organism-environment interaction into philosophy: the pragmatist philosopher John Dewey made the relationship between organism and environment the foundation of his new theories of ethics, education, and scientific inquiry. This chapter and those that follow illustrate how an apparently simple idea—that organisms interact with environments—came to have complicated and lasting consequences, from debates in philosophy and the social sciences to theories of niche construction and human evolution.

## 2 Origins of an Idea[1]

The English word 'environment' was coined in the late 1820s by the Scottish essayist Thomas Carlyle and popularized in the second half of the century by the philosopher Herbert Spencer. But what is so important about a word? It is not as if earlier thinkers had any trouble discussing the influence of external factors on organisms. For example, Buffon wrote the following in his multi-volume *Natural History*: "The temperature of the climate, the quality of food, and the evils of slavery [i.e., domestication]—these are the three causes of change, alteration, and degeneration in animals" (Buffon 1766, 317). Soon after, French naturalists began to employ umbrella terms for these and other factors, the most influential of which were Jean-Baptiste Lamarck's 'circumstances' and Georges Cuvier's 'conditions of existence.' Lamarck used 'circumstances' to refer to climate, temperature, environing media (water, air), habits, movements, actions, etc. (Lamarck 1801, 13, cf. Lamarck 1809, 1:238). Cuvier's *conditions of existence* was a more formal notion based on the fact that "nothing can exist that does not bring together the conditions that make its existence possible" (Cuvier 1817, 1:6). If terms like 'conditions' and 'circumstances' already existed, why use the word 'environment' in the first place? In this section, I will show that the organism-environment dichotomy emerged from philosophical reflection on the nature of life. Its originator, at least in the English-speaking world, was Spencer.

[1]In parts of this section I have drawn on material from Pearce (2010a).

Naturalists in the first third of the nineteenth century, following the work of Carl Linnaeus, Buffon, and Lamarck among others, became more and more interested in the influence of external conditions on organisms. This interest was most pronounced in the proto-ecological writings of Alexander von Humboldt, Augustin de Candolle, and Charles Lyell (see Pearce 2010b, 501–506). The geographical method of Humboldt and Candolle was an attempt to connect specific plants to particular local circumstances. For example, in his "Physical Table of the Equatorial Regions," Humboldt showed how flora vary with altitude, geology, air temperature, the snow line, and the composition and pressure of the atmosphere (Humboldt and Bonpland 1805, 41–42). Candolle, following Humboldt, discussed "the influence of external elements or agents on plants," specifically "the influence of temperature, of light, of water, of the soil, and of the atmosphere" (Candolle 1820, 362). He linked such external influences to Cuvier's notion of conditions of existence: "Specific plants, given their organization, require specific conditions of existence: one cannot live where it does not find a specific quantity of salt water; another where it does not have, at some time of year, some quantity of water or intensity of sunlight, etc." (Ibid., 384). Lyell extended Candolle's work, pointing out that other organisms make up part of the relevant external conditions:

> The stations of different plants and animals depend on a great complication of circumstances,—on an immense variety of relations in the state of the animate and inanimate worlds. Every plant requires a certain climate, soil, and other conditions, and often the aid of many animals, in order to maintain its ground. (Lyell 1832, 140)

Thus naturalists in the early nineteenth century were investigating the influence of external factors—physical and biological—on plants and animals, and employing terms such as 'conditions' and 'circumstances' to refer collectively to such factors.

But though Humboldt and Candolle emphasized the importance of external circumstances, the move to singular terms like '*milieu*' or 'environment'—and to a more explicit organism-environment dyad—was made by philosophers. Spencer's use of the word 'environment' and his emphasis on the organism-environment relationship derived from his reading of the French philosopher Auguste Comte. In the French tradition, the term '*milieu*' (medium) as the counterpart of '*organisme*' was an innovation of the 1830s, although Lamarck had earlier employed the plural '*milieux*' to refer to environing media such as water or air (Canguilhem 1952). In several texts of 1833, for example, the zoologist Étienne Geoffroy Saint-Hilaire linked changes in an organism to changes in its *milieu ambiant*.[2] He claimed that there are two sorts of facts relevant to developing organisms: those belonging to the essence of a type and those involving the intervention of the ambient world. It is

[2]Geoffroy (1833a, 88–89n) quotes Blaise Pascal making a related point. However, this is not an accurate quotation but a loose reading of the earlier thinker's well known remark, "I am very afraid that this nature might itself only be a first custom, just as custom is a second nature" (Pascal 1669, 199; Pascal 1991, 208).

the latter that explain why pears from the same orchard are sometimes large and sweet, sometimes small and sour (Geoffroy Saint-Hilaire 1833b, 68–69; see also 1833a, 89n).

Comte went further in the third volume of his *Course of Positive Philosophy*, making the relationship between organism and *milieu* the basis of his conception of life. He attacked Xavier Bichat's claim that life is simply the set of functions that resist death:

> The profound irrationality of [Bichat's] conception consists above all in its complete elimination of one of the two inseparable elements whose harmony necessarily constitutes the general idea of *life*. This idea supposes, indeed, not only a being so organized as to possess the vital state, but also, no less indispensable, some set of external influences that make possible the achievement of that state. Such harmony between the living being and the corresponding *medium* evidently characterizes the fundamental condition of life. (Comte 1838, 288–289, original emphasis)

Comte's notion of life followed that of the naturalist Henri-Marie Ducrotay de Blainville, whose definition of "organized body" (i.e., organism) included "acting on environing external bodies and being affected by these bodies" (Blainville 1822, xxii; see Comte 1838, 295).[3] Comte, however, labeled the two parts of the dichotomy: he insisted that "the idea of life constantly supposes the necessary correlation of two indispensable elements, an appropriate organism and a suitable medium" (Comte 1838, 301). Attaching a footnote to 'medium,' Comte called it a new expression designating "the total ensemble of external circumstances, of any kind, necessary to the existence of each particular organism" (Ibid., 301n). Hence '*milieu*' was introduced as an abstract singular term to replace plural terms such as 'circumstances' or 'conditions of existence' in the context of a new philosophical account of life.[4]

English followers of Comte appropriated his new dichotomy. The author and critic George Henry Lewes, for example, emphasized in a debate over progress in the fossil record that organisms were "the resultant of two factors—Life and

[3]For more on the connections between Comte, Blainville, and Lamarck, see Petit (1997) and Braunstein (1997).

[4]Related German concepts and terminology would require a history of their own. Thomas Carlyle seems to have originally coined the word 'environment' to translate the German word '*Umgebung*' (Pearce 2010a, 248). Phrases like "*der Organismus und seine Aussenwelt*" were used in medical writings beginning in the early 1800s: e.g., "the reciprocal determination of the organism and its external world" (Kilian 1802, 150). Philosophically inclined physicians such as Johann Christian Reil and Moritz Naumann also employed this *Organismus-Aussenwelt* dichotomy (Reil 1816, 63; Naumann 1821, 349, 1823, 162). Later in the century German translations used both '*Aussenwelt*' and '*Umgebung*' for Spencer's 'environment' (Spencer 1880, 1:294, 365, 1882, 308, 380). The *Organismus-Umgebung* dyad is apparently absent from German texts prior to the reception of Comte and Spencer. The following is one early usage, before Spencer but after Comte: "form and activity, part and whole, organism and environment are in perfect harmony" (Köstlin 1851, 1:352). Peter Sloterdijk (2005) claims that Jakob von Uexküll (1909) invented the concept of environment, ignoring this rich nineteenth century background.

Circumstance" (Lewes 1851, 996).[5] Lewes's serial summary "Comte's Positive Philosophy" likewise claimed that "*organism* and *medium* are the two correlative ideas of life" (Lewes 1852, 666, original emphasis; cf. Lewes 1853, 167). The word 'environment' was first used in a biological context by the social thinker Harriet Martineau as her preferred translation of Comte's '*milieu*.' Phrases like "the reciprocal action of the organism and its environment" thus appear for the first time in Martineau's translation of Comte's course (Comte 1853, 1:401).

Nevertheless, before Spencer got a hold of it, the word 'environment' was still very rare; he made it a central concept in his popular philosophical accounts of biology and psychology, and by the end of the century it was a common term. Having recently befriended Lewes, Spencer read both Lewes's summary and Martineau's translation of Comte in 1852–1853. Spencer shared Comte's interest in demarcating the living and the non-living, and had previously defined 'life' as "*the co-ordination of actions*" (Spencer 1852, 252, original emphasis). In his later *Principles of Psychology*, however, he adopted Comte's position and Martineau's vocabulary: "the changes or processes displayed by a living body, are specially related to the changes or processes in its environment" (Spencer 1855, 368). This special relation, according to Spencer, is one of correspondence and continuous adjustment:

> The life of the organism will be short or long, low or high, according to the extent to which changes in the environment, are met by corresponding changes in the organism. Allowing a margin for perturbations, the life will continue only while the correspondence continues; the completeness of life will be proportionate to the completeness of the correspondence; and the life will be perfect only when the correspondence is perfect. (Ibid., 376)

This progressive language indicates that Spencer's account of the correspondence between organism and environment was also related to the idea of evolution, for life evolves by improving organism-environment correspondence: as life progresses, said Spencer, this correspondence extends in space and time (i.e., organisms can adapt to external causes less frequently encountered) and increases in speciality, generality, and complexity (Ibid., 394–465). Finally, Spencer declared mind and intelligence merely advanced forms of life; thus he argued that "the manifestations of intelligence are universally found to consist in the establishment of correspondences between relations in the organism and relations in the environment" (Ibid., 483). Spencer's organism-environment dichotomy was thus relevant not only to physiology and zoology but also to psychology, sociology, and ethics, as he attempted to show in later works.

The 1855 edition of Spencer's *Principles of Psychology* was not widely read. But with the publication of the first three parts of his System of Synthetic Philosophy—*First Principles* and *Principles of Biology* in the 1860s and the second edition of the *Psychology* in the early 1870s—his ideas became more and more popular, especially

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[5]For evidence that Lewes—and not Spencer—wrote this particular article, see Pearce (2010a, 256n17).

in the United States. In 1871, the philosopher-historian John Fiske gave a series of lectures at Harvard on Spencer's evolutionary philosophy that were simultaneously published in *The World*, a New York newspaper (Berman 1961, 79; Nelson 1977; cf. Fiske 1874). The next year, Edward Livingston Youmans founded the magazine *Popular Science Monthly*, which consistently promoted Spencer's views (Spencer 1872; Youmans 1872). By the late 1870s, William James was assigning Spencer's books to his psychology and philosophy classes at Harvard and the young John Dewey was borrowing these same books from his college library in Vermont (James 1988; Feuer 1958). As Spencer's ideas spread, so did his abstract dichotomy of organism and environment. In the next two sections, we will see how the idea of organism-environment interaction framed a series of conceptual discussions in the 1890s—first in biology and then in philosophy.

## 3 Environment, Plasticity, and Variation

Spencer's *Principles of Psychology* introduced the idea of organism-environment interaction to the English-speaking world. 'Interaction' suggests a mutual influence: the environment affects the organism just as the organism affects the environment. But Spencer talked mostly about just one causal direction: environments modifying organisms. In the fourth section of the chapter, I will show how some philosophers rejected Spencer's account in favor of a more truly interactive view of the organism-environment relationship. But as will become clear in this section, late-nineteenth-century biologists and psychologists focused primarily—as had Spencer—on the environment as an agent of organismal change.

In the late 1880s, Herbert Spencer published a short book entitled *Factors of Organic Evolution*. Spencer emphasized the importance of its topic in the preface, declaring that the question of which casual factors are operative in evolution "demands, beyond all other questions whatever, the attention of scientific men" (Spencer 1887, iv). A few years later, Spencer got his wish: in the 1890s the "factors of evolution" question attracted the attention of a whole variety of scientists and philosophers, becoming the focus of numerous debates, books, and articles. The idea of organism-environment interaction played a key role in these debates, for one of the main points of contention was whether the role of the environment is primarily that of producing or that of preserving variation.

One of the central problems of the factors of evolution debates of the 1890s was the nature and origin of variation. Charles Darwin's first use of the term 'environment'—which appeared only in his last works—shows that the environment was given a kind of causal agency in such discussions:

> In many cases it is most difficult to distinguish between the definite result of changed conditions, and the accumulation through natural selection of indefinite variations which have prove[d] serviceable. If it profited a plant to inhabit a humid instead of an arid station, a fitting change in its constitution might possibly result from the direct action of the environment. (Darwin 1875, 2:281)

This mention of the possible importance of "direct action of the environment" contrasts with Darwin's earlier inclination "to lay very little weight on the direct action of the conditions of life" (Darwin 1859, 134). It is notable that Darwin first speaks of the environment as an important agent in his book *Variation of Animals and Plants under Domestication*: the *Origin of Species* had for the most part placed variation in a black box, whereas *Variation* made it the central theme.

The main player in the debates over the factors of evolution was the German naturalist August Weismann. Darwin, shortly before he died, wrote a prefatory note to a collection of Weismann's early essays. Darwin's words show that the origin of variation was seen as the next big problem in biology:

> Several distinguished naturalists maintain with much confidence that organic beings tend to vary and to rise in the scale, independently of the conditions to which they and their progenitors have been exposed; whilst others maintain that all variation is due to such exposure, though the manner in which the environment acts is as yet quite unknown. At the present time there is hardly any question in biology of more importance than this of the nature and causes of variability. (Weismann 1882, vi)

Variation was an important problem because although most naturalists—even American holdouts—now admitted the fact of evolution, there was much disagreement as to its causes or factors (LeConte 1878, 786–787).[6] For example, the American paleontologist Edward Drinker Cope argued that natural selection is a restrictive but not an originative factor: that is, it rejects variations but does not produce them (Cope 1887, 350–351). Cope was following the Duke of Argyll (among others), who argued that natural selection "gives an explanation, not of the processes by which new Forms first appear, but only of the processes by which, when they have appeared, they become established in the world" (Argyll 1867, 229). Explaining the origin of variation, for Spencer (1887) and Cope (1887), involved determining how the environment could act as a producer of variation and not merely its preserver.

Weismann's essays on heredity, beginning with "On Heredity" in 1883, explicitly attacked the relevance of environment-induced variations to evolution and thus directly contradicted the work of authors such as Spencer, Cope, and Argyll. This new theory of heredity argued that the germ cells that give rise to offspring should "be regarded as something standing opposed to and separate from the entirety of cells composing the body"; a corollary of this claim was that so-called "acquired characters," those caused by the action of the environment during an organism's lifetime, could not be inherited (Weismann 1883, 1885; Moseley 1885, 155). Weismann's theory provoked a storm of criticism, most of which was focused on the problem of variation. George John Romanes for example, following Spencer, argued that mutual co-adaptation of parts within an organism could not be explained

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[6]For more on this period in the history of biology, see Bowler (1983), (1988), and Richards (1987, 331–503).

by merely "fortuitous variation" and natural selection; it had to rely on a tendency of those parts to vary together, i.e., on "the inherited effects of use and disuse" (Romanes 1887, 406; cf. Spencer 1887, 12–17).[7]

Romanes (1888) coined the term 'Neo-Darwinian' to describe naturalists such as Weismann who "aim at establishing for natural selection a sole and universal sovereignty which was never claimed for it by Darwin himself." There were certainly people whose views approached this sovereignty claim. Alfred Russell Wallace, for example, wrote the following in his book *Darwinism*: "Whatever other causes have been at work, Natural Selection is supreme . . . . The more we study it the more we are convinced of its overpowering importance" (Wallace 1889, 444). Cope (1889) replied by repeating that selection could not be the whole story: "selection cannot explain the *origin* of anything, although it can and does explain survival of something already originated; and evolution consists in the origin of characters, as well as their survival." Argyll (1889) accused the neo-Darwinians of rejecting "any conception which tends to break down the empire of mere fortuity in the phenomena of variation." Nevertheless, Weismann gained many followers, most notably Edward Bagnall Poulton and other Oxford naturalists. As Grant Allen put it a few years later,

> for a year or two after the appearance of Weismann's memoirs, nothing else was heard of in *Nature* and in the scientific societies. Weismannism became the fashionable creed of the day . . . . Young England, as a biologist, swore by the continuity of the germ-plasm, and laughed to scorn the inheritance of the acquired faculty. (Allen 1890, 538)

Naturalists were divided into warring camps: Poulton, in a letter to a friend, actually made a two-column list of individuals arrayed for and against Weismann's view.[8]

The debates over Weismann's theory are usually remembered simply as debates over the inheritance of acquired characters; the problem is that the latter phrase now evokes an easily dismissed Lamarckism, concealing a number of interesting issues. Looking more closely at the relevant texts reveals that the factors debates concerned the importance of organism-environment interaction during ontogeny and its role in evolution, and thus the origin and nature of variation—problems which remain relevant today (Barker 1993; West-Eberhard 2003; Jablonka and Lamb 2005; Laubichler 2010; Schwander and Leimar 2011).

That the relation between organism and environment framed late-nineteenth-century discussions of the factors of evolution is most clearly seen in the work of the three scientists who in 1896 co-discovered what we now refer to as the "Baldwin Effect": Henry Fairfield Osborn, Conwy Lloyd Morgan, and James Mark Baldwin. The Baldwin Effect occurs when environment-induced (and presumably adaptive) ontogenetic variations give groups of organisms time to develop corresponding

[7]In their later debate, Weismann capitulated to Spencer on this point, formulating his theory of germinal selection—or selection on elements of the heritable material—as a means of "directing variation" at the organismic level (Weismann 1895, 432). For more on Weismann's germinal selection theory, see Winther (2001).

[8]Poulton to Henry Fairfield Osborn, 31 December 1891: Folder 11, Box 77, General Correspondence, Department of Vertebrate Paleontology Archives, American Museum of Natural History.

phylogenetic variations (Kemp 1896; Baldwin 1896). The importance of this purported "new factor," as Baldwin called it, cannot be understood outside of the context of the factors of evolution debates. (In what follows, I will focus on Osborn and Morgan; Christopher Green discusses Baldwin's contributions in the next chapter.)

At a meeting of the American Society of Naturalists in 1891, Osborn lamented that "after studying Evolution for a century we are in a perfect chaos of opinion as to its factors" (Osborn 1891, 193). In Osborn's framing, the debates over these factors were centrally about the power of the environment to produce variations:

> By the [principle of Lamarck] we diminish the powers of Natural Selection, and increase the powers of Environment; at the same time we greatly simplify the problem of Variation, and render far more complex the problem of Inheritance. By the [principle of Weismann] we throw the entire burden of evolution upon Natural Selection, and eliminate the direct action of Environment; we admit definite laws or causes of Variability, but no definite laws governing the variations of single characters; we greatly simplify the problem of Inheritance. In short, the vulnerable point with the Lamarckians is in solving the problem of Heredity, while their opponents are weakest in solving the problem of variation. (Ibid., 197)

Thus, the followers of Lamarck could take the environment as the primary source of variation, but had difficulty explaining how such variation was inherited, whereas the neo-Darwinians had difficulty accounting for the origin of variation, but no problem explaining how existing variation was passed on.

Employing a distinction between ontogenetic and phylogenetic variation, Osborn was also able to argue that variation in a type of organism following a move to a new environment is not necessarily evidence for the direct action of that environment. The following "crucial experiment" is necessary:

> An organism A, with an environment or habit A, is transferred to environment or habit B, and after one or more generations exhibits variations B; this organism is then retransferred to environment or habit A, and if it still exhibits, even for a single generation, or transitorily, any of the variations B, the experiment is a demonstration of the inheritance of ontogenic variations. (Osborn 1895, 97)

The variations in environment B might be induced by that environment during each successive generation; i.e., the B variations could be merely ontogenetic. But if the B variations persist across generations even when the population has been returned to environment A, then they have become phylogenetic. Osborn is here articulating the important point that a variation induced by a reliable environmental cue each generation mimics a congenital variation.

This point about plasticity and reliable cues was made independently by Morgan during a discussion of several experiments by Poulton: "His experiments neither justify a denial nor involve an assertion of the transmissibility of environmental influence . . . . Can we be sure that there is really a summation of results—that each generation is not affected *de novo* in a similar manner?" He continued: "If each plastic embryo is moulded in turn by similar influence, how can we conclusivly [sic] prove hereditary summation?" (Morgan 1891a, 167). Thus, Morgan agreed with Osborn that ontogenetic plasticity could confound tests of the inheritance of acquired characters: "In experiments to test the question of use-inheritance, the difficulty is to exclude the effects (1) of selection and (2) of individual plasticity." The problem was that "extreme plasticity" could indicate that "the influence of the normal environment is prepotent over the effects of use-inheritance *if* such occur" (Morgan 1891b, 271–272). Hence both Morgan and Osborn highlighted the plasticity of organisms and the environment's role as a producer of variation, but pointed out that such variation was not necessarily heritable.

As Morgan stressed in an essay on Weismann's theories, "all effective variation is a joint product of the inherent activities of germinal cells and the conditioning effect of their environment" (Morgan 1893, 30). Osborn agreed, claiming that organic form is the product of "constitution + the environment" (Dyar 1896, 141). These ideas laid the groundwork for the Baldwin Effect. Osborn presented his version in March 1896 before the New York Academy of Sciences:

> During the enormously long period of time in which habits induce ontogenic variations it is possible for natural selection to work very slowly and gradually upon predispositions to useful correlated variations, and thus what are primarily *ontogenic variations* become slowly apparent as *phylogenic variations* or congenital characters of the race. (Ibid., 142)

The idea of "correlated variations" is the key: it seems that Osborn used this phrase to refer to heritable traits that either mirror or support those traits that had previously been environmentally induced. The basic point is that plasticity, or ontogenetic variation in the face of environmental changes, could give organisms time to develop these correlated congenital variations. The Baldwin Effect was thus a compromise position between Lamarck and Weismann: it emphasized the role of environment-induced variation in evolution without depending on the inheritance of acquired characters. As Osborn put it in a letter to Poulton, "Morgan, Baldwin and myself have independently arrived at certain conclusions regarding the Lamarckian factor which will interest you."[9] Osborn argued that this quasi-Lamarckian process was likely to be important in evolution, "since there is no doubt that the changes of environment and the habits which it so brings about far outstrip all changes in constitution" (Dyar 1896, 142).

Like Osborn, Morgan understood the Baldwin Effect as bearing directly on "the Lamarckian question," and also framed it in terms of the organism-environment relationship. He outlined the effect in a letter to Poulton dated 12 April 1896, with 'variation' referring to changes "of germinal origin" and 'modification' referring to changes "of environmental origin":

> Let us suppose that a group of organisms belonging to a plastic species is placed under new cond'ns of environment. Those whose innate plasticity is equal to the occasion survive. They are modified. Those whose innate plasticity is not equal to the occasion are eliminated. Such modification takes place generation after generation but *as such* is not inherited. In the meanwhile, however, and concurrently, any congenital variations antagonistic in direction to these modifications will tend to thwart them and to render the organism liable to elimination; while any congenital variations similar in direction to these modifications will

9Osborn to Poulton, 12 June 1896: Folder 11, Box 77, General Correspondence, Department of Vertebrate Paleontology Archives, American Museum of Natural History.

> tend to support them and to favour the individuals in which they occur. (Natural Selection itself will foster variability in given advantageous lines . . . when once initiated.) Thus will arise a congenital *pre-disposition* to the modification in question. The longer the process continues, the more marked will be the predisposition and the greater the tendency for the congenital variations to conform in all respects to the persistent plastic modifications; while the plasticity still continuing in operation, the modifications become yet further adaptive. When relatively perfect adaptation is reached (the conditions remaining uniform) natural selection will slowly yet surely bring the congenital variations up to the level of such adaptation. Thus plastic modification leads, and variation follows: the one paves the way for the other.[10]

In other words, when organisms are plastic, they can adapt to new environmental conditions even without heritable changes; in the longer term, if the conditions persist, more permanent heritable changes that mirror or extend the environment-induced alterations may appear and, via the ordinary action of natural selection, replace the temporary changes.

Morgan's distinction between environment-induced *modification* and congenital *variation* did the same conceptual work as Osborn's division of "ontogenic variation" and "phylogenic variation." These distinctions allowed Morgan and Osborn to tease apart changes caused directly by the environment each generation and inherited changes, and thus to carve out a role for the environment as a producer of variation without endorsing a Lamarckian theory of heredity (although Osborn did later endorse a form of Lamarckism). Traditionally, supporters of Darwin against Spencer had argued that the primary role of the environment in evolution was as "regulator or preserver of . . . variation" (James 1988, 137, cf. James 1880); the work of Morgan and Osborn provided a richer account in which adaptation involved organism-environment interaction both within and across generations. The environment as both producer and preserver of variation was a central part of this new evolutionary story.

## 4 Organism and Environment in Philosophy

Spencer, despite his influence on the factors of evolution debates, was primarily a philosopher. Given his popularity in America, it is not surprising that philosophers such as William James and John Dewey used Spencer's work as a foil for their own ideas. James was amusing but often unkind in his descriptions of Spencer, whom he associated with the idea that the mind was merely a product of its environment (Godfrey-Smith 1996, 66–99). As he joked in a May 1877 letter to the neurologist James Jackson Putnam, "would *I* were part of [Spencer's] environment! I'd see if his

[10]Morgan to Poulton, 12 April 1896: C. Lloyd Morgan letters, Entomological Archives, Hope Entomological Library, Oxford University Museum of Natural History. The quoted points are on a separate sheet enclosed with the letter. Emphasis in original. In the original document, this passage is divided into 11 numbered points (nos. 6–17 of 21 total). I have collapsed them for ease of reading, but have not altered the sentence structure. Cf. Morgan (1896, 316–318).