
Introduction

A flood of new research insights has revealed as never before the intimate causal relationship in which organisms and their environments are bound together. Development is modulated—in astonishingly complex ways—by induced epigenetic modifications, parental nutrient and stress levels, chemical and physical conditions at the cellular level, and a host of other environmental factors and feedbacks. Just as the environment participates in shaping the organism, the organism's presence, activities, products, and byproducts modify its environment. By virtue of these environmental modifications, organisms influence their own functional and selective circumstances and, through effects on shared habitats, those of cohabiting neighbors. At this point, these phenomena are solidly established. The challenge is to expand our understanding to encompass these complex causal interactions and feedbacks.

This book is a close re-examination of the organism–environment relationship. It draws on a rich and diverse biological literature to explore how environments influence individual phenotypes and how these realized phenotypes in turn influence their environments. The book goes on to investigate the broader ecological and selective consequences of these reciprocal effects. Examples and case studies from across the biodiversity spectrum are discussed. Throughout the book, salient research questions and potential approaches are highlighted to make clear how this integrative perspective can generate testable hypotheses; an overall research agenda and some practical applications are laid out in an epilogue.

In focusing on the organism–environment relationship, the book builds on, and synthesizes, two recently emerged disciplines. First, recognition of

the environment's role in shaping gene expression, and, hence, individual phenotypes, has led to the emergence of *ecological developmental biology* (S. Gilbert 2001; Sultan 2007; S. Gilbert and Epel 2009). In an “eco-devo” approach, developmental mechanisms and outcomes are explicitly studied in the context of environmental conditions. Flexible individual responses to the environment, or *plasticity*, are included within this broad, unified approach to environmentally mediated development.

The second newly emerged discipline focuses on the other side of the organism–environment relationship—that is, the effects of organisms on the environment. Individually and collectively, subtly or dramatically, organisms inevitably alter their abiotic and biotic circumstances. These organismic impacts, and the resulting changes in selection pressures, are known as *niche construction* (Lewontin 1983, 2000; Odling-Smee et al. 2003; Scott-Phillips et al. 2013; or, alternatively, *eco-evolutionary feedbacks*, Pelletier et al. 2009; Travis et al. 2014). Each of these exciting new areas of study focuses on only one of the causal arrows that constitute the organism–environment relationship. To more fully understand this dynamic, reciprocal relationship, the influences of organisms and environments on each other must *both* be taken into account. Accordingly, the book further aims to bring together eco-devo insights with those from niche construction, to determine the joint consequences of these processes for ecological interactions and natural selection. The goal is to frame a more integrated understanding in light of current developmental, ecological, and evolutionary knowledge.

The book begins with a chapter on development. This initial chapter examines the regulatory roles of epigenetic and environmental factors to argue

for a unified eco-devo approach based on the *norm of reaction*. With this eco-devo approach as a starting point, the second chapter builds a conceptual framework for understanding the adaptive encounter between the individual organism and its environment. The third chapter describes the precise cues and transduction mechanisms that underlie plastic eco-devo responses. The subsequent two chapters explore in detail how such phenotypic responses modify the environmental conditions that organisms experience, and how diverse organisms modify their external environments across temporal and spatial scales. The sixth chapter discusses the consequences of individual eco-devo responses (*trait-mediated interactions*) and niche-constructing impacts for the structure and function of ecological communities. A substantial final chapter considers natural selection in the light of the organism–environment relationship, including a discussion of transient and inherited environmental effects on phenotypes (such as induced epigenetic changes), and selective feedbacks that result from the effects of organisms on their environments. These mutual influences make clear that adaptation and, consequently, natural selection result from the functional and fitness consequences of the two-way organism–environment relationship.

The book aims to offer a shift in emphasis and focus that may lead to new and different insights, fresh ways to interpret known phenomena,

and research questions that might not otherwise arise—a “way of seeing” (as Richard Dawkins described his influential 1982 book, *The Extended Phenotype*). The reader is invited to think through a diverse array of biological scenarios and to consider in his or her own terms several key issues that are raised as open questions. Throughout, the goal is to discover where this shift in focus might lead.

The opportunity to develop an integrated understanding of the organism–environment relationship comes at a critical time and, indeed, not a moment too soon. The emergent field of ecological developmental biology has directed attention to the mechanisms and outcomes of individual development in the context of real-world environmental conditions. As a result of escalating human activities, natural habitats are being disrupted and transformed at an unprecedented rate. Biological researchers are keenly aware of the interdependence of organisms and their environments. We seek urgently to know how altered climatic, atmospheric, and biotic conditions will affect the development and function of organisms—their phenotypes as expressed in the real world—and how these effects will in turn alter their persistence, ecological communities, and evolutionary trajectories into the future. These questions provide powerful and immediate motivation to work toward an updated conceptual scheme for biological inquiry, in which the complex interactive relation of organisms to their environments occupies the central place.