Evo-Devo and Niche Construction

Daniel B. Schwab and Armin P. Moczek

Abstract

Much thinking in evo-devo is dominated by a mindset that views traits and trait variants as emergent properties of genes and genomes, and environments as strictly external to and separable from the organisms that develop within them. Growing evidence accumulating across diverse fields is increasingly questioning the continued usefulness of this framework, resulting in calls for a more explicit recognition and integration of the interdependencies between development, environment, and phenotypic evolution. In the first section of this chapter, we review the ubiquitous and diverse roles that environmental conditions play in instructing developmental outcomes, as well as how failure to provide proper environmental signals can disrupt development or lead to the expression of novel phenotypic variants. In the second section, we discuss how the environmental conditions that organisms experience are often modified by the organisms themselves, how these interactions can reciprocally shape development, and how their study is best advanced within the context of niche construction theory. In the final section, we address how the integration of niche construction theory with five research programs central to evo-devo (i.e., evolutionary innovation and diversification, developmental bias, developmental plasticity, genetic accommodation, and inclusive inheritance) can lead to a more holistic and complete understanding of development and developmental evolution.

Keywords

Ecological development • Developmental plasticity • Developmental bias • Genetic accommodation • Non-genetic inheritance

D.B. Schwab (✉) • A.P. Moczek
Department of Biology, Indiana University, Bloomington, IN, USA
e-mail: schwabd@umail.iu.edu; armin@indiana.edu

L. Nuño de la Rosa, G.B. Müller (eds.), *Evolutionary Developmental Biology*,
https://doi.org/10.1007/978-3-319-33038-9_46-1

Contents

Introduction

Evolutionary biologists seek to understand how and why biological evolution unfolds the way it does, including the origins of adaptations and the mechanisms that shape short- and long-term patterns of diversification. Historically, such questions have been approached through the framework of the Modern Synthesis, which integrated Darwinian natural selection, population-level thinking, and Mendelian inheritance in the mid-twentieth century. Application of this framework enabled the rigorous, quantitative examination of important evolutionary processes and, through its successes over many decades, deeply ingrained dichotomies that now characterize the way we conceptualize organismal evolution. For example, phenotypes are generally viewed as rooted in genes and genomes, and environments – though increasingly recognized as an important source of developmental information – nevertheless remain conceived as passive, external to, and separable from the organisms responding to them and the selective pressures that they impose. Without question, this conceptual framework has enabled countless advances in our understanding of the nature of biological evolution; however, a subset of foundational objectives of evolutionary biology have stubbornly resisted productive investigation through conventional approaches. For example, the processes that enable, shape, or bias the origin of novel, complex traits and the corresponding major transitions in evolution that they facilitated are of fundamental interest to the discipline. But because of their entrenchment in deep time, and the lack of phenotypic variation accessible to quantitative and population genetic approaches, contemporary evolutionary biology has thus not been able to provide satisfactory resolution to these challenges. However, here as well as in other contexts, the increasing integration of evolutionary developmental biology (evo-devo) with conventional approaches has begun to significantly enhance the explanatory reach of evolutionary biology.

Traditional evolutionary biology treats developmental processes as proximal, that is, development translates genotype into phenotype, but by itself does not influence or direct evolutionary outcomes beyond simply excluding those that are developmentally inaccessible. Consequently, understanding how development works is generally not considered necessary for understanding the evolutionary process. However, a large body of evidence has now accumulated that thoroughly challenges this assumption. Evo-devo has shown that evolution frequently proceeds through changes in the genetic and physiological regulation of developmental processes, taking advantage of the highly modular organization of organismal function at all levels of biological organization, from gene regulation to organ systems. As such, innovation and diversification in evolution are enabled through – and channeled or biased by – the differential reuse and recombination of otherwise conserved developmental building blocks. This focus on how phenotypes are constructed in development and re-assembled in evolution has illuminated many issues traditional evolutionary biology had to leave unresolved, such as the origin of phenotypic novelty, the maintenance of homology, or the frequent, independent re-use of the "same" developmental pathways to build fully or partly convergent traits in unrelated organisms. More generally, thanks to these efforts we now understand that the nature of development may itself be a source of evolutionary innovation, encouraging change in certain directions over others. Understanding the nature of development has thus emerged as critical to understand why evolutionary change unfolds the way it does.

At the same time, several key perspectives in evo-devo have remained remarkably traditional. Specifically, much research in evo-devo continues to view developmental evolution as ultimately rooted in genes and genomes, a mindset that has critically shaped concepts and terminology in the field, such as the postulate of a genetic toolkit or the notion of selector genes. Secondly, while practitioners of evo-devo increasingly recognize the environment as an important source of information needed to instruct normal development, it remains viewed as an agent that is separable from the organism, whose role in development is passive and whose role in evolution is restricted to shaping selective conditions.

In this chapter, we discuss the value of both perspectives in the light of accumulating evidence. We first review the pervasive role environmental conditions play in enabling and instructing developmental processes, and in shaping developmental outcomes. Secondly, we explore the notion that rather than viewing environments solely as external and passive, they may better be understood as at least in part shaped by organisms themselves. We then present how integrating the field of niche construction, a conceptual framework that has emerged independently in evolutionary ecology, provides promising opportunity to incorporate these revised perspectives, thereby expanding the explanatory power of evo-devo in particular, and evolutionary biology in general. Throughout, we highlight examples of evo-devo case studies that, by integrating a revised evaluation of the role of the environment into their research programs, have the potential to advance long-standing and critical questions in the biological sciences.

Organism, Environment, and the Promise of Niche Construction Theory

To Develop is to Interact with the Environment

Recent decades have seen a growing appreciation for the environmentally responsive nature of developmental processes and their outcomes (e.g., see the chapter on "▶ Eco-Evo-Devo"). This increased focus is due in part to an understanding that environmental signals, acting across multiple levels of biological organization, are often necessary for the completion of normal development. For instance, the neuroendocrine systems of many developing organisms are primed to receive environmental signals that relate information on nutritional conditions, temperature, and season (Gilbert and Epel 2015). The reception of these signals is subsequently integrated to generate changes in gene expression, physiology, morphogenesis, and behavior, in extreme cases specifying discrete, alternative phenotypes such as the nutritionally responsive horned and hornless morphs of *Onthophagus* dung beetles, the temperature-dependent sex determination of some amphibian and reptile species, and the summer to winter changes in coat color and texture that are characteristic of arctic foxes. However, these obligate environmental signals are not comprised solely of external, abiotic factors, but are increasingly recognized as encompassing other developing and evolving organisms that reside internally within responsive individuals. This includes contributions from microbial symbionts, which are often responsible for providing crucial signals for normal host development. For instance, microbiota contribute to pre-embryonic development by mediating cytoplasmic incompatibility across most major arthropod taxa, establish the anterior-posterior axis in embryonic nematodes, influence tissue and organ development in a wide array of invertebrate and vertebrate taxa, and induce settlement and metamorphosis in marine invertebrate larvae (reviewed in Gilbert et al. 2012; Landmann et al. 2014; Shikuma et al. 2014). Environmental conditions, however generated, therefore play an instructive role in normal development in a wide range of taxa and in diverse circumstances.

Just as the significance of environmental conditions in instructing the developmental trajectory of organisms is now broadly recognized, ecologists and evolutionary biologists have also begun to appreciate that these interactions need not point unidirectionally from environment to developmental system. Rather, organism-environment interactions may more commonly be reciprocal, with developmental systems constructing environmental conditions that then allow the next phase of environment-responsive development to take place. For instance, the growth and differentiation of a given cell is influenced by the prevailing cellular and physiological environment in which it finds itself, characterized by the presence or absence of nutrients, morphogens, and paracrine or endocrine factors. In response to this internal environment, cells specify patterns of gene expression that affect not only the growth and differentiation of future cells, but also their own developmental context at later points in development. At higher levels of organization, diet for instance has long been known to shape pharyngeal jaw morphology in cichlids (Greenwood 1965), as well as gut formation and differentiation from invertebrates to vertebrates (e.g., Agrawal et al. 2002; Ledon-Rettig et al. 2008), in each case affecting future foraging and dietary environments experienced throughout the remainder of development. In sum, organisms execute their development in tight interdependence with the environment, with significant aspects of the ontogenetic environment being both cause and effect of organismal development.

At the same time, a growing literature demonstrates that the environment-constructing nature of organismal function need not be limited to developmental processes per se or take place only within the boundaries of the organism. Instead, even external environments may be shaped in profound ways by organisms, including the same organisms whose development, physiology, and behavior is then subsequently affected by these same, constructed environments. Understanding the causes, nature, and consequences of these interactions are the central objectives of niche construction theory, as introduced next.

Organism and Environment as Cause and Effect of Each Other

First acknowledged by Richard Lewontin (1983) and subsequently refined into a theoretical framework by others (reviewed in, e.g., Odling-Smee et al. 2003), niche construction theory states that organisms, via their physiology and behaviors, modify their own and each other's niches in nonrandom and often systematic ways. A substantial literature now exists that documents the nature and scope of these modifications, which can range from the construction of physical structures such as nests, dams, and burrows to alterations of chemical states in the surrounding environment (i.e., perturbational niche construction), to the selection of alternative habitats and social environments (i.e., relocational niche construction; reviewed in Odling-Smee et al. 2003). The nature and scope of these modifications can range from being active and nonrandom changes to the local environment to byproducts of organismal physiology and behavior. For instance, the digging and tunneling behaviors of earthworms modify the surrounding soil in ways that increase its ability to capture and retain rain water, reduce its clay fraction, facilitate gas exchange, and increase its nutrient content due in part to the concentration of nitrogen and phosphorus found in worm excrement (discussed in Odling-Smee et al. 2003). At the same time that these modifications aid individual worms in maintaining osmotic balance, they also alter the soil ecosystem in ways that benefit other worms, soil macroinvertebrates, and plants. Therefore, the developmental, ecological, and evolutionary consequences of these niche constructing traits need not be limited to the niche constructor itself, but can generate important byproducts that scale-up to shape the ecology of other species and even influence ecosystem-level processes (Erwin 2008). Additional well-studied examples that illustrate the same features include the niche constructing activities of beavers (leading to wetlands), hippopotami (transforming savannahs), or corals (enabling reef formation).

By actively constructing and modifying their biotic and abiotic environments, niche constructing organisms have the potential to alter the developmental and selective environments acting upon them in directional ways that can (but do not necessarily have to) increase organism-environment fit. These effects may most commonly manifest in nature when niche construction buffers the developmental and evolutionary responses of populations against stressful environmental conditions. For instance, larvae of the goldenrod gallfly, *Eurosta solidaginis*, secrete factors that induce galls to form on goldenrod plants, providing the gallfly with a constant source of nutrition as well as protection from parasitoids and avian predators (Abrahamson et al. 1989). In this case, niche construction imposes stabilizing selection and decreases the range of environmental conditions experienced by the organism. Ecological and population-genetic models provide further evidence that niche construction can significantly alter the rate and direction of evolution, generate eco-evolutionary feedbacks, and influence whether genetic variants are maintained or lost (Laland et al. 1999; Silver and Di Paolo 2006; Kylafis and Loreau 2008). Therefore, niche construction may contribute in diverse ways to the complementarity between organisms and their environments, i.e., to adaptation. Furthermore, by systematically biasing selection pressures, niche construction may rightly be considered an evolutionary process (alongside natural selection, drift, etc.), one that allows organisms to be both the object and creator of the conditions under which natural selection occurs.

Because most organisms are thought to engage in some form of niche construction during ontogeny (Laland et al. 2008), environmental modifications may be fundamental to the normal development of the organisms that generate and experience them. At the same time, clear parallels exist between the constructive and reciprocal nature of developmental processes that are increasingly the focus of evo-devo studies and those organism-environment interactions that are characteristic of niche construction. Yet although such linkages have been acknowledged previously (e.g., Laland et al. 2008), the field of niche construction remains as of yet poorly assimilated with contemporary evo-devo. Below, we highlight several objectives and conceptual foci of contemporary evo-devo that we believe to be especially well aligned with niche construction theory.

Advancing Evo-Devo Through the Study of Niche Construction

We conclude this chapter by briefly highlighting five interrelated topic areas that feature prominently within contemporary evo-devo research programs and discuss how they are conceptually aligned with, and empirically approachable through, niche construction theory. We then consider how the integration of niche construction into these long-standing research programs may allow evo-devo to overcome important conceptual roadblocks, thereby enhancing its explanatory reach as an integrative discipline.

Evolutionary Innovation and Diversification

One of the most celebrated contributions of evo-devo to evolutionary biology has been the realization that much of the innovation and diversification in evolution is enabled through the modular nature of developmental processes and the re-use and rearrangement of otherwise conserved developmental building blocks (see the chapter on "▶ Modularity in Evo-Devo"). More recent work, often placed in the realm of ecological developmental biology (eco-evo-devo), has added to this the realization that selectable phenotypic variation contributed by development is itself a function of environmental context within which developmental systems operate: for example, environmental conditions influence the presence and degree of genetic and phenotypic correlations and determine whether genetic variation will remain cryptic or manifest in selectable phenotypes (reviewed in Paaby and Rockman 2014). Niche construction theory heavily emphasizes this latter relationship as well: ecological conditions feedback on patterns of phenotype expression, often across generations, and in the case of ecosystem engineering, across many taxa. Indeed, examples of ecosystem engineering ranging from the construction of coral reefs and beaver dams to the oxygenation of soils by bioturbators all possess the property of generating novel ecological niches and opportunities for evolutionary innovation and diversification to occur (Erwin 2008).

What niche construction theory adds, and contemporary evo-devo lacks, is the reciprocal view: the emphasis on environmental conditions as something that is at least in part actively created and shaped by the organism itself. Like other phenotypes, niche constructing abilities themselves are contributed to by developmental (and physiological, behavioral, etc.) systems and, depending on their respective heritable variation in natural populations, may contribute to population divergence, ecological radiations, and niche innovation. The greatest value of better integrating evo-devo, eco-devo, and niche construction perspectives on organism-environment interactions may thus lay in how these extend each other's explanatory power: evo-devo and eco-devo may inform niche construction theory by offering possible developmental, physiological, neurobiological, or microbiological mechanisms that have enabled or constrained the origin and diversification of niche constructing abilities. In return, niche construction theory forces evo-devo and eco-devo to move beyond a mindset that views environments solely as an external agent of selection and to formulate hypotheses that also take into account that environmental conditions may themselves evolve and that this may contribute significant heritable variation biasing the processes of developmental innovation and diversification in natural populations.

Developmental Bias

Among its central aims, research in evo-devo seeks to clarify the causal-mechanistic basis by which phenotypes and phenotypic variants arise during development and how these processes of phenotype construction in turn interact with evolutionary processes. One emerging observation from these efforts is that phenotypic variation is systematically biased by the process of development, with some phenotypes more likely to be generated than others (see the chapter on "▶ Developmental Drive"). This bias emerges on a variety of organizational levels. As highlighted in the introduction, the highly modular nature of development, from cis-regulatory elements, genes, and signal transduction pathways to morphogenetic processes and organ systems, has enabled phenotypic evolution to proceed via rearrangements of its component parts in developmental space, time, and context (see the chapter on "▶ Modularity in Evo-Devo"). Here, bias results from the re-use of the same developmental modules and causes what should be independent evolutionary events to instead unfold as parallelisms, yielding nonhomologous traits made up of deeply homologous components in the process. At the same time, this developmental bias does not just limit or constrain what may be allowed to evolve, but instead also facilitates the emergence of novel and functionally integrated traits through the re-use of pre-existing components already selected to work well together.

A related but also distinct form of bias emerges through the exploratory, demand-based, and self-regulatory nature of many developmental processes. For instance, the formation of muscular-skeletal attachments is highly reliant on the exploratory behavior of muscle precursor cells, which migrate randomly during early development and are only maintained into later stages if they manage to innervate muscles. This combination of exploratory behavior followed by somatic selection, which is seen in many other contexts (see the chapter on "▶ Facilitated Variation"), demonstrates how developmental processes may be inherently biased towards producing functional, well-integrated states, even in the face of environmental or genetic perturbations.

Similar kinds of developmental biases may also be inherent in the ways in which organisms engage with and alter their external environment through the process of niche construction, resulting in qualitatively similar developmental as well as evolutionary consequences. For instance, on a general level, niche constructors predictably bias environmental states towards those that best suit the traits of the initial niche constructor or its descendants. Like developmental bias, niche construction thus allows organisms to channel development preferentially towards functional phenotypes that adaptively fit their environment, thereby imposing some directionality on evolution. Further, the traits organisms rely upon to construct their environments, from the chemicals they secrete to the nests they build to the gut endosymbionts they harbor, endow lineages with a sort of *niche construction toolbox*, one that can be engaged over and over independently in different taxa and possibly developmental contexts, thereby on one side biasing the way niche constructors may alter their environments, while on the other facilitating diversification through the use, re-use, and recombination of effective nice constructing activities already honed through previous rounds of selection.

Integrating evo-devo and niche construction perspectives on developmental bias promises a more complete and holistic understanding of the interdependencies of organismal development, phenotype function, environmental conditions, and adaptive evolution. In particular, in the numerous cases in which parental niche constructing behaviors affect early developmental environments of offspring, understanding why and how developmental evolution unfolds the way it does in a given lineage will require an understanding of the ontogenetic basis of both niche construction and offspring embryogenesis, as well as their interactions. The already well-established importance of maternal transcripts in early zygotic differentiation or maternal transmission of antibodies and symbionts illustrate the significance of these interactions, which are likely to exist on many other levels of biological organization as well.

Developmental Plasticity

Developmental plasticity refers to the ability of developing organisms to adjust their phenotypes in response to environmental conditions (see the chapter on "▶ Developmental Plasticity and Evolution"). The field of plasticity research emerged with a focus on plasticity as an exceptional case, one that can be parameterized in quantitative genetic models in the form of G × E interactions and best studied through reaction norm approaches. In recent years, it has become clear that plasticity is a normal feature of development, rather than an exception, and that organisms ranging from the earliest embryos to mature adults are primed to integrate and plastically respond to diverse environmental signals. Furthermore, research from the field of evo-devo has provided a causal-mechanistic understanding of developmental plasticity, elucidating the gene regulatory and physiological bases of plasticity, as well as how such environmental sensitivity evolves across populations and species (Schlichting and Pigliucci 1998).

Both conceptual and mechanistic links exist between developmental plasticity and niche construction: on one level, niche construction necessitates environmental responsiveness in those aspects of development, physiology, and behavior that enable niche constructors to sense, evaluate, and respond adaptively to the often complex and heterogeneous environments that they face. Niche construction is therefore facilitated by developmental plasticity, which can be thought of as providing the mechanistic scaffolding for environmental modifications to occur. At the same time, organismal plasticity and niche construction emphasize opposite causations regarding adaptation: whereas the former allows organisms to maintain high fitness by adjusting their traits to their environments, the latter allows organisms to maintain high fitness by adjusting their environments to their traits. As a result, niche construction may simultaneously be seen as a source of robustness by reliably and systematically buffering developing organisms against stressful environmental conditions. This is illustrated, for instance, by the gall formation of goldenrod gallflies (see above), or the widespread construction of nests, mounds, burrows, etc., across diverse animal taxa. Therefore, developmental plasticity and niche construction may be thought of as reciprocal and interdependent processes.

Despite these obvious linkages, both the evo-devo community and the field of developmental plasticity research are poised to benefit from a more rigorous theoretical and empirical assimilation of niche construction. For instance, it will be critical to experimentally evaluate the extent to which developing organisms are plastically responsive to the environments that they, themselves, have generated through niche construction. Such plasticity will not only influence phenotype formation as expressed through modified norms of reaction, but may also alter the heritability and response to selection of plastic traits, including the extent to which genetic variation may be maintained or lost (Saltz and Nuzhdin 2014). In parallel, theoretical and conceptual models will be necessary to fully understand how and under what circumstances these complex feedbacks influence evolutionary trajectories. Throughout these efforts, it will be important to acknowledge the diverse forms through which plasticity (e.g., morphological, behavioral, learning) and niche construction (e.g., perturbational, relocational) are expressed, as each may influence the outcomes of theoretical models and experimental studies in different ways, thereby illustrating the potentially diverse consequences of these phenomena for development and developmental evolution.

Genetic Accommodation

Over the last few decades, evolutionary ecologists have generated a robust body of empirical and theoretical work investigating the ecological conditions under which selection favors (or disfavors) the evolution of plasticity (Schlichting and Pigliucci 1998). More recent work has begun to emphasize that plasticity may not just be a product of phenotypic evolution, but may itself also be a factor in shaping subsequent evolutionary trajectories: for instance, plasticity has the potential to facilitate the colonization of and persistence in novel environments (reviewed in Pfennig et al. 2010). Further, a growing number of studies have raised the possibility that plastic changes may precede genetic changes during the process of adaptation (reviewed in Pfennig et al. 2010). If correct, developmental systems may readily be able to integrate novel environmental inputs through the coordinated and functional adjustment of their morphology and physiology. This phenomenon, known as phenotypic accommodation, has the potential to enhance fitness by closely aligning organismal phenotypes with their prevailing selective environments (West-Eberhard 2005). For instance, when reared within a terrestrial environment, basal ray-finned fishes in the genus *Polypterus* plastically develop skeletal features and locomotive behaviors consistent with those of stem tetrapods, suggesting that phenotypic accommodation may have acted as a first step in the evolutionary transition of limbed vertebrates from water to land (Standen et al. 2014). Such responses may act as a precursor to phenotypic evolution through the process of genetic accommodation, in which environmentally induced phenotypes become refined and stabilized over many generations via selection on standing genetic variation, formerly cryptic genetic variation, or *de novo* mutation. Evolution by genetic accommodation received its strongest empirical support initially through laboratory experiments, but is now increasingly validated by field studies on diverse taxa such as water fleas (Scoville and Pfrender 2010), sticklebacks (Wund et al. 2008), blind cave fish (Rohner et al. 2013), and house finches (Badyaev 2009).

Although genetic accommodation remains controversial among many evolutionary biologists (e.g., Laland et al. 2014), studies of this phenomenon have historically considered environments through the lens of conventional evolutionary thought: as being an inducer of phenotypes that is both separable from and external to the organism. By contrast, niche construction theory focuses explicitly on the environment-generating capacity of organisms and promotes the argument that environments and organisms are both cause and effect of each other. Yet genetic accommodation and niche construction are at least partially congruent: both focus on the organism, through its development, physiology, and behavior, to act as a sieve through which environmental variation is transduced into phenotypic variation. In so doing, both concepts highlight the largely contingent nature of development and developmental evolution. Similarly, the nature and extent of genetic accommodation has the potential to be modified by the niche constructing activities of organisms in novel environments. For instance, because niche construction can buffer organisms, diminishing the range of environments that they experience, the nature and magnitude of morphological and physiological accommodation that must occur in a novel environment may be lessened or may be directed down some routes and not others. At the same time, because niche construction can generate strong covariance between niche constructing organisms and their environment, constructed selective environments can increase in frequency alongside the traits that construct them, thereby potentially accelerating the rate of genetic accommodation. Empirical and theoretical work is now needed to evaluate the extent to which niche construction can initiate and promote genetic accommodation in natural populations.

Inclusive Inheritance

Because evolutionary biology has long treated biological information as being rooted largely in genes and genomes, it is not surprising that many evolutionary biologists and even evo-devo advocates treat transmission genetics as the only general (and evolutionarily relevant) inheritance system. Yet there is growing recognition that heredity is not simply a genetic construct, but that the construction of developmental environments may be inclusive of multiple interacting mechanisms of nongenetic inheritance that span multiple levels of biological organization. These mechanisms are commonly thought to include (i) *epigenetic transmission*, such as the posttranslational methylation or acetylation of histone proteins, the methylation of cytosines in DNA, and the inheritance of microRNAs, (ii) *parental effects*, ranging from the behavioral interactions between parents and offspring (i.e., parental care), to the germline and environmental transmission of key nutrients and microbiota, and (iii) *cultural inheritance*, such as the transmission of acquired group behaviors via learning (Danchin et al. 2011). In each case, a growing literature has begun to document the causal role of these mechanisms in modifying development to enable the maintenance of parent-offspring similarity (i.e., heritability) and in the adaptive fitting of organisms to prevailing environmental conditions (Gilbert and Epel 2015). As a result, these additional inheritance systems have the potential to bias both the rate and direction of evolution, though this effect may be attenuated by their stability and effect size across generations (Danchin et al. 2011).

Importantly, niche construction provides an additional route for nongenetic inheritance. While the niche constructing activities of individuals may modify ecological conditions and the selective pressures that they generate, the developmental and fitness consequences incurred by these activities need not be limited to a single generation or constructor, but can additionally span multiple generations in the form of *ecological inheritance*. Ecological inheritance occurs when organisms bequeath their modified selective environments to descendant offspring, exemplified by the dams of beavers, the mounds of termites, or the modification of soil nutrients by earthworms and plants, all of which can substantially outlast the lifetime of an individual niche constructor. The nature of ecological inheritance is unique from other sources of nongenetic inheritance, in that the products of niche construction may not only be consequential for an individual's offspring, but can scale-up to affect the structure and functioning of whole populations, communities, and ecosystems. Consequently, ecological inheritance has the potential to influence not only parent-offspring similarity, but can also strongly affect long-term ecological and evolutionary dynamics (e.g., see Laland et al. 1999).

The incorporation of niche construction and ecological inheritance into standard views of inheritance offers significant novel explanatory power to evo-devo practitioners who seek to understand the developmental origins of organismal phenotypes. Much of this promise is already being realized in closely related fields. For instance, it is now clear that gut development is often incomplete without signals from maternal microbiota, that the function of the immune system is informed by maternally acquired antibodies, and that social environments substantially influence cognitive and behavioral development in diverse organisms. Therefore, failure to evaluate the degree to which the ecological inheritance of organisms contributes to parent-offspring similarity and phenotypic variation risks ignoring valuable sources of heritable variation.

Conclusions

In this chapter, we have argued that diverse aspects of normal development necessitate close interactions with the environment, that traditional views regarding the nature and separability of environments and organisms are challenged and extended by niche construction, and that features of contemporary evo-devo are highly complementary to, and may benefit from, a more pronounced integration with niche construction theory. Indeed, we posit that the further synthesis of these two presently disjointed fields promises a deeper and biologically more realistic understanding of the nature of organism-environment interactions and their consequences for phenotypic evolution. Already, advances from both fields have independently led to and reinforced two emergent, unifying themes of organismal development. First, organismal development is a highly *constructive* process: organisms shape their developmental trajectory by constantly responding to internal and external states via diverse developmental processes (as illustrated by evo-devo) or through modifications to ecological niches (as illustrated through niche construction). Second, organismal development is *reciprocally causal*: organisms shape, and are in turn shaped by, their selective and developmental environments. What remains now is to assess in diverse taxa the extent to which an understanding of these interdependencies facilitates a more full accounting of the origins of phenotypic variation, and how they shape, bias, enable, or constrain the evolution of development.

Cross-References

► Developmental Drive
► Developmental Plasticity and Evolution
► Eco-Evo-Devo
► Facilitated Variation
► Modularity in Evo-Devo

References

Abrahamson WG, Sattler JF, McCrea KD, Weis AE (1989) Variation in selection pressures on the goldenrod gall fly and the competitive interactions of its natural enemies. Oecologia 79:15–22

Agrawal AA, Vala F, Sabelis MW (2002) Induction of preference and performance after acclimation to novel hosts in a phytophagous spider mite: adaptive plasticity? Am Nat 159:553–565

Badyaev AV (2009) Evolutionary significance of phenotypic accommodation in novel environments: an empirical test of the Baldwin effect. Philos Trans R Soc Lond B 364:1125–1141

Danchin É, Charmantier A, Champagne FA, Mesoudi A, Pujol B, Blanchet S (2011) Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. Nat Rev Genet 12:475–486

Erwin DH (2008) Macroevolution of ecosystem engineering, niche construction and diversity. Trends Ecol Evol 23:304–310

Gilbert SF, Epel D (2015) Ecological developmental biology: the environmental regulation of development, health, and evolution. Sinauer Associates, Incorporated, Sunderland

Gilbert SF, Sapp J, Tauber AI (2012) A symbiotic view of life: we have never been individuals. Q Rev Biol 87:325–341

Greenwood PH (1965) Environmental effects on the pharyngeal mill of a cichlid fish, *Astatoreochromis alluaudi*, and their taxonomic implications. Proc Linnean Soc Lond 176:1–10

Kylafis G, Loreau M (2008) Ecological and evolutionary consequences of niche construction for its agent. Ecol Lett 11:1072–1081

Laland KN, Odling-Smee FJ, Feldman MW (1999) Evolutionary consequences of niche construction and their implications for ecology. Proc Natl Acad Sci 96:10242–10247

Laland KN, Odling-Smee J, Gilbert SF (2008) EvoDevo and niche construction: building bridges. J Exp Zool B Mol Dev Evol 310:549–566

Laland K, Wray GA, Hoekstra HE (2014) Does evolutionary theory need a rethink? Nature 514:161

Landmann F, Foster JM, Michalski ML, Slatko BE, Sullivan W (2014) Co-evolution between an endosymbiont and its nematode host: *Wolbachia* asymmetric posterior localization and AP polarity establishment. PLoS Negl Trop Dis 8:e3096

Ledon-Rettig CC, Pfennig DW, Nascone-Yoder N (2008) Ancestral variation and the potential for genetic accommodation in larval amphibians: implications for the evolution of novel feeding strategies. Evol Dev 10:316–325

Lewontin RC (1983) The organism as the subject and object of evolution. Scientia 118:63–82
Odling-Smee FJ, Laland KN, Feldman MW (2003) Niche construction: the neglected process in evolution. Princeton University Press, Princeton
Paaby AB, Rockman MV (2014) Cryptic genetic variation: evolution's hidden substrate. Nat Rev Genet 15:247–258
Pfennig D, Wund MA, Snell-Rood EC, Cruickshank T, Schlichting CD, Moczek AP (2010) Phenotypic plasticity's impacts on diversification and speciation. Trends Ecol Evol 25:459–467
Rohner N, Jarosz DF, Kowalko JE, Yoshizawa M, Jeffery WR, Borowsky RL, Lindquist S, Tabin CJ (2013) Cryptic variation in morphological evolution: HSP90 as a capacitor for loss of eyes in cavefish. Science 342:1372–1375
Saltz JB, Nuzhdin SV (2014) Genetic variation in niche construction: implications for development and evolutionary genetics. Trends Ecol Evol 29:8–14
Schlichting CD, Pigliucci M (1998) Phenotypic evolution: a reaction norm perspective. Sinauer Associates Incorporated, Sunderland
Scoville AG, Pfrender ME (2010) Phenotypic plasticity facilitates recurrent rapid adaptation to introduced predators. Proc Natl Acad Sci 107:4260–4263
Shikuma NJ, Pilhofer M, Weiss GL, Hadfield MG, Jensen GJ, Newman DK (2014) Marine tubeworm metamorphosis induced by arrays of bacterial phage tail–like structures. Science 343:529–533
Silver M, Di Paolo E (2006) Spatial effects favour the evolution of niche construction. Theor Popul Biol 70:387–400
Standen EM, TY D, Larsson HC (2014) Developmental plasticity and the origin of tetrapods. Nature 513:54–58
West-Eberhard MJ (2005) Phenotypic accommodation: adaptive innovation due to developmental plasticity. J Exp Zool B Mol Dev Evol 304:610–618
Wund MA, Baker JA, Clancy B, Golub JL, Foster SA (2008) A test of the "flexible stem" model of evolution: ancestral plasticity, genetic accommodation, and morphological divergence in the threespine stickleback radiation. Am Nat 172:449–462