DOI: 10.1111/ede.12325

EDITORIAL

WILEY

Biases in the study of developmental bias

In November 2018 the Santa Fe Institute hosted a two-day workshop titled *Developmental Bias and Evolution*, funded by a grant from the John Templeton Foundation. Involving 34 participants and 22 talks, the workshop covered a wide range of approaches toward the study of bias exerted by developmental systems in the production of phenotypic variation, the impact such bias might have on evolutionary dynamics, and the methods that exist to assess the nature and consequences of this impact. Talks included historical retrospectives, philosophical examinations, and a great diversity of empirical treatments of the subject. Significant discussion and debate followed each presentation, and creative tensions emerged around key issues that characterize the diversity of perceptions of what, exactly, constitutes bias in developmental systems, when or how such bias may be evolutionarily relevant, and at the most basic level, whether the concept of developmental bias is itself useful in fueling a productive research program. This special issue is meant to capture this diversity of viewpoints, and to provide a collection of perspectives that will inform and motivate the next round of research, and the next generation of researchers.

WHAT IS DEVELOPMENTAL BIAS?

Developmental processes transduce diverse genetic and environmental inputs during phenotype production, causing some phenotypes to arise more frequently than others (Uller, Moczek, Watson, Brakefield, & Laland, 2018). The resulting phenotypic variation is thus not isotropic, but biased in certain directions. At the extreme end of this scenario stands the complete inability of development to produce a conceivable variant, and it is at this point that the bias inherent in organismal development becomes synonymous with the narrower notion of "developmental constraint." But if bias is an inherent feature of all of development, if very nature of development is to channel phenotypes towards preferred outcomes, is a term such as developmental bias needed? Or to paraphrase the title of Salazar-Ciudad's talk at the workshop, *why should we call it developmental bias, when all we mean is development*?

Brigandt (2019) responds to this challenge by positing that even if we cannot agree on exactly what we mean by developmental bias, including its distinctness from development per se, the term, and its study are worthwhile and timely because they are able to motivate a valuable research program. He argues that concepts such as novelty or evolvability likewise carry with them some ambiguity, such that they mean different things at different levels of biological organization, and to different practitioners. What makes them valuable, however, is, according to Brigandt, that they establish a shared intellectual identity across disciplinary boundaries that motivates investigation, exchange, and a collective advancing of an explanatory framework. The same can be said for developmental bias, whose many manifestations may be differentially nuanced by different researchers and disciplines, yet coalesce around a shared understanding that developmental bias shapes, and is shaped by evolution in ways that have the potential to greatly impact our understanding of why and how developmental evolution unfolds as it does.

Hordijk and Altenberg (2019) in turn emphasize that the idea that phenotypic variation could ever be unbiased is simply a historical artifact, resulting from a mindset that treats genetic and its associated phenotypic variation akin to "a gas that can fill any selective phenotypic bottle." But everything we know about the nature of development teaches us that the processes that produce organisms and their traits will also structure the phenotypic variation that emerges as a result of variation in genetic and environmental inputs. To Hordijk and Altenberg *unbiased* phenotypic variation is thus as sensible as the idea of *unstructured* development. Instead, they posit that the questions that need to be asked should not stop at if development biases phenotypic variation, but rather, *how* development *structures* variation, with what consequences for evolutionary processes, and how the structuring imposed by developmental bias may itself evolve. Using a cellular automata model of ontogeny their contribution then seeks to address precisely these and related questions.

DEVELOPMENTAL PLASTICITY, DEVELOPMENTAL BIAS, AND DEEP TIME

Developmental plasticity is the ability of an individual to adjust patterns of phenotype expression in response to environmental changes (Pfennig et al., 2010). Developmental plasticity, and related phenomena such as phenotypic accommodation (the mutual adjustment of multiple traits in response to perturbations) and genetic accommodation (heritable changes in the regulation of an environmentally induced trait) are increasingly considered relevant in the initiation and structuring of phenotypic variation, including the origin of phenotypic novelties (Moczek, 2012). The resulting possibility of plasticity-led evolution is the subject of five contributions to this issue. Uller, Feiner, Radersma, Jackson, and Rago (2019) explore how assumptions meant to simplify the starting point for a conceptual framework set the stage for what counts, and what does not, as an evolutionary explanation, and why prevailing idealizations prevent an integration of the role of development in general, and plasticity in particular, in evolutionary theory. Parsons, McWhinnie, Pilakouta, and Walker (2019) then explore how developmental plasticity may contribute to developmental bias, and how the resulting biased variation may echo past adaptations that reflect the evolutionary history of a lineage, or alternatively, serve to initiate evolution when environments change. The contribution by Levis and Pfennig (2019), in turn, focuses on the gaps in our knowledge of the mechanisms and consequence of plasticity-led evolution regarding the developmental mechanisms, traits, or taxa most affected by it, and provide suggestions for future research approaches to address these shortcomings. Draghi (2019) then examines the evolution of, and through, plasticity by using a modeling approach that incorporates developmental noise to explore the competitive and evolutionary relationships of specialist and generalist genotypes inhabiting a heterogeneous landscape. These models show not only how plasticity may arise in the context of specialization, but also how developmental noise may help a mutant with imperfect plasticity compete successfully against its ancestor, thereby providing an evolutionary path through which subsequent mutations can refine plasticity toward an optimum (Draghi, 2019). Finally, Jackson (2019) extends our conceptualization of plasticity-led evolution into deep time and explores where and how to examine its manifestations in the fossil record.

FROM CONSTRAINT TO FACILITATION: THE EVOLUTIONARY CONSEQUENCES OF DEVELOPMENTAL BIAS

The second half of this special issue is then devoted to diverse case studies on the significance of developmental bias in micro- and especially macroevolution. This includes the second foray into deep time through a contribution by Jablonski (2019), who discusses how the study of present-day species and their development may be leveraged to predict developmental bias in the fossil record, and, conversely, how analyses that begin with the fossil record may be used to predict developmental bias in extant lineages.

The significance of *learning* as a potential source of bias in the production of evolutionarily relevant phenotypic variation is the focus of a contribution by Laland, Toyokawa, and Oudman (2019). Learning does many things for organisms: It may help solve problems and increase adaptive fit, it may solve novel problems and hence introduce novel phenotypes into phenotype space, and if learning occurs via observing other individuals it may fuel the nongenetic inheritance of acquired traits. Laland et al. (2019) explore the different types of biases that may manifest along the way, and when and how they may affect adaptive evolution, evolutionary rates and outcomes, and evolvability. Behavior also features prominently in a contribution by Wilkins (2019), which examines the role of developmental bias in facilitating the domestication of a select subset of mammalian species. Here, the term "domestication syndrome" refers to a suite of behavioral, morphological, and physiological traits that all underwent concerted evolutionary change during domestication events, even though none of them were selected deliberately, thereby providing a particularly compelling example of developmental bias in evolution. Among others, Wilkins (2019) reviews how selection for tameness alone may be sufficient to fuel the domestication syndrome and the significance of the regulation of neural crest cell development and the nature of neuroendocrine systems in that process. Another major evolutionary transition is the subject of a contribution by Gilbert (2019), namely the role of developmental symbioses in the multiple origins of herbivory. Gilbert's contribution echoes key points stressed by other authors as well, such as the significance of plasticity-led evolution, where the facultative acquisition of symbionts precedes the evolution of features that ensure reliable transmission across individuals, and how, like learning, if transmission of symbionts occurs across generations it constitutes a case of nongenetic inheritance of what initially began as an acquired trait.

A different approach, yet one that makes striking connections to several other contributions, is taken by Hu, Linz, Parker, and Schwab et al. (2019). Focusing on a single taxon, the dung beetle genus *Onthophagus*, the authors assess the role of developmental bias in contributing to innovation, adaptation, and resilience. This assessment is repeated across multiple levels of biological organization: Gene regulatory networks, where the authors emphasize the facilitating nature of cooption and repurposing of pre-existing network components in developmental innovation; developmental plasticity and its role in enabling, within generations, integrated and often adaptive phenotypic adjustments in the face of environmental fluctuations, including to novel environments never encountered before, thereby creating the conditions for evolution by genetic accommodation; and developmental symbioses and niche construction, which enable organisms to build teams, actively modify their own selective environments, and create alternate, non-genetic routes to inheritance and adaptation.

The issue then closes with three contributions that examine manifestations of developmental bias, including its facilitating as well as constraining consequences on phenotype evolution across diverse traits. These include the role of relative developmental duration in the evolution of the mammalian retina and cortex (Finlay & Huang, 2019), the significance of developmental integration in the developmental evolution of the skeletal system (Kavanagh, 2019), and the role of developmental constraints in the multiple origins of parthenogenesis (Galis & van Alphen, 2019).

LOOKING AHEAD

As is evident from this special issue, developmental bias has captured the interest and imagination of researchers from diverse fields. It is similarly clear that whether or not developmental processes bias phenotypic outcomes is no longer a subject of debate. Instead, what deserves our attention is the role such biasing, or structuring, of phenotypic variation, plays in evolution, the conditions under which it may manifest, and how bias itself may evolve. At the same time, we are witnessing a growing realization that it may be insufficient to view developmental bias merely as a passive process that divides phenotypic outcomes into more or less likely. Instead, developmental bias contains what may be described as creative and generative elements. For example, when developmental responses to novel conditions preferentially bias phenotypic outcomes toward functionally integrated states, or when organisms systematically bias environmental conditions in ways that benefit themselves and their descendants, then developmental bias also contains a degree of *agency*, exerted by organisms and their component parts in directing their own developmental outcomes. While itself an evolved property, such agency has obvious potential to feedback on evolution, influencing direction, speed, and means by which phenotypic change may manifest in a given lineage. While such perspectives undoubtedly make our understanding of what matters in developmental evolution more complicated, they may also empower us to take on persistent challenges in the field, such as the origins of novel complex traits from within the confines of homology, major transitions in evolution, and the evolution of evolvability. The study of the mechanisms and consequences of developmental bias thus promises to continue to make significant contributions to evolutionary biology, and it is hoped that this special issue will help motivate the next round of research efforts able to turn this promise into reality.

Armin P. Moczek

Department of Biology, Indiana University, Bloomington, Indiana

Correspondence

Armin P. Moczek, Department of Biology, Indiana University, Bloomington, IN 47405.

Email: armin@indiana.edu

REFERENCES

Brigandt, I. (2019). Historical and philosophical perspectives on the study of developmental bias. *Evolution & Development*. in press.

Draghi, J. (2019). Developmental noise and ecological opportunity across space can release constraints on the evolution of plasticity. *Evolution & Development*. in press.

Finlay, B. L., & Huang, K. (2019). Relative developmental duration organizes, scales and adapts the mammalian retina and cortex, with a note on dunnarts, mole rats and bats. *Evolution & Development*. in press.

Galis, F., & van Alphen, J. (2019). Parthenogenesis and developmental constraints. *Evolution & Development*. in press.

Gilbert, S. F. (2019). Developmental symbiosis facilitates the multiple origins of herbivory. *Evolution & Development*. in press.

Hordijk, W., & Altenberg, L. (2019). Developmental structuring of phenotypic variation: A case study with a cellular automata model of ontogeny. *Evolution & Development*. in press.

Hu, Y., Linz, D. M., Parker, E. S., Schwab, D. B., Casasa, S., Macagno, A. L. M., & Moczek, A. P. (2019). Developmental bias in horned dung beetles and its contributions to innovation, adaptation, and resilience. *Evolution & Development*. in press.

Jablonski, D. (2019). Developmental bias, macroevolution, and the fossil record. *Evolution & Development*. in press.

Jackson, I. (2019). Developmental bias in the fossil record. *Evolution & Development*. in press.

Kavanagh, K. D. (2019). Developmental plasticity associated with early structural integration and evolutionary patterns: Examples of developmental bias and developmental facilitation in the skeletal system. *Evolution & Development*. in press.

Laland, K. N., Toyokawa, W., & Oudman, T. (2019). Animal learning as a source of developmental bias. *Evolution & Development*. in press.

Levis, N., & Pfennig, D. W. (2019). Plasticity-led evolution: A survey of developmental mechanisms, and empirical tests. *Evolution & Development*. in press.

Moczek, A. P. (2012). The nature of nurture and the future of evodevo: Toward a theory of developmental evolution. *Integrative and Comparative Biology*, *52*, 108–119.

Parsons, K. J., McWhinnie, K., Pilakouta, N., & Walker, L. (2019). Does phenotypic plasticity initiate developmental bias? *Evolution & Development*. in press.

Pfennig, D. W., Wund, M. A., Snell-Rood, E. C., Cruickshank, T., Schlichting, C. D., & Moczek, A. P. (2010). Phenotypic plasticity's impacts on diversification and speciation. *Trends in Ecology & Evolution*, *25*, 459–467.

Uller, T., Feiner, N., Radersma, R., Jackson, I., & Rago, A. (2019). Developmental plasticity and evolutionary explanation. *Evolution & Development*. in press.

Uller, T., Moczek, A. P., Watson, R. A., Brakefield, P. M., & Laland, K. N. (2018). Developmental bias and evolution: A regulatory network perspective. *Genetics*, *209*(4), 949–966.

Wilkins, A., (2019). A Striking Example of Developmental Bias in an Evolutionary Process: The domestication syndrome. *Evolution & Development*, https://doi.org/10.1111/ede.12319