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EDITORIAL

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Agency in living systems

In June 2022, the Konrad Lorenz Institute (KLI) for Evolution and Cognition Research near Vienna, Austria hosted a 3-day workshop titled *Agency in Living Systems: Conceptual frameworks and research approaches*, funded by a grant from the John Templeton Foundation. In a packed program of empirical, theoretical, and philosophy of science talks and intensive formal and informal discussion, 25 participants from eight countries, along with members of the institute, explored three central questions across disciplines and research systems: the concept of biological agency; how a theory of agency might be built and positioned among established frameworks within evolutionary developmental biology and allied fields; and how agential perspectives may be applied productively to address experimental and theoretical challenges in contemporary biology. Creative tensions emerged around these questions that reveal diverse understandings of what, exactly, constitutes agency as a general property of organisms (as distinct from intentionality, free will, and other specifically human modes of agency), how agency might contribute to the unfolding of development and evolution, and how considerations of agency may complement and enrich existing research programs. This special issue captures this diversity of viewpoints, providing a collection of perspectives that will inform and motivate the next round of research, and the next generation of researchers.

1 | BRINGING AGENCY TO BIOLOGY

Objects respond to influences within a preconfigured parameter space, following rules they themselves cannot change. Biological sciences broadly—and evolutionary and developmental biology in particular—view organisms as objects built by genes and their products, which in turn are shaped by evolutionary processes. As a result, the organism itself remains a rather passive participant in both development and evolution. This way of thinking has been immensely productive in many ways, but has also constrained our understanding of trait determination, inheritance, and the origin of evolutionary novelties (Sultan et al., 2022 and references therein). The KLI workshop on *Agency in Living Systems* probed the merits of an alternative but complementary view—that of biological agency. This perspective posits that organisms can also act as *agents* that participate in shaping their own development and the environment that surrounds them, thereby actively modifying the configuration space within which they grow, respond to perturbations, and evolve (Walsh, 2015).

How such a perspective relates to, complements, but also fundamentally diverges from a Modern Synthesis view of developmental evolution is the subject of the paper contributed by Walsh and Rupik (2023). Employing an innovative "countermapping" approach to contrast the respective ontologies of Modern Synthesis and agential perspectives, and borrowing an effective range of examples from other scientific fields to illuminate their arguments, the authors conclude that the contemporary Modern Synthesis perspective achieves an impressively comprehensive view of the dynamical properties of populations, but at the considerable cost of radically distorting the nature of the biological processes that contribute to evolution. Conversely, Walsh and Rupik (2023) posit that an agency perspective offers the prospect of representing the biological processes of evolution with much greater fidelity, yet at the expense of generality. They emphasize that trade-offs of this kind are integral to science and ultimately inevitable. Yet recognizing such explanatory trade-offs for what they are helps us to distinguish what is solely a feature of a scientific perspective from the actual features of the real world we strive to understand. In his contribution, Fermin Fulda (2023) then addresses one particular concept critical to all accounts of development and evolution, whether conventional or agential—that of the *individual*. We generally take individual organisms to be entities capable of self-organizing and self-regulating in pursuit of their own functional objectives (Walsh, 2015), yet where such individuality is situated has been a subject of much debate: is it the swarm, the colony, the holobiont, or uniquely at the level of the individual organism? Fulda discusses how biological individuals can be meaningfully defined as those that also poses *agential autonomy*, and then applies this criterion to both clear-cut and problematic cases of individuality, and to the explanatory structure of evolutionary developmental biology more broadly.

2 | INTEGRATING AGENTIAL PERSPECTIVES WITH EVOLUTIONARY DEVELOPMENTAL BIOLOGY

Several contributions explicitly explore conceptual affinities between agency theory and common research foci in evolutionary developmental biology. In their paper, Nadolski and Moczek (2023) begin by exploring the terminology, assumptions, and predictions of an agency perspective, and then systematically apply these across levels of biological organization, processes, and key concept areas relevant to practitioners of evolutionary developmental biology, from organ formation, embryogenesis, and metamorphosis to regeneration, symbiosis, plasticity, and niche construction. Building on these insights, the authors then explore where agency thinking may expand the explanatory reach of research efforts aimed at advancing our understanding of the nature of, for example, adaptation, innovation, and evolvability, and how an agency perspective complements, as well as reaches beyond, positions previously articulated by other frameworks such as *complex systems theory*.

Likewise, Snell-Rood and Ehlman (2023) use their paper to review basic features of development that are able to fill with life the metaphorical map linking genotype to phenotype, and how those features may be incorporated into the Mendelian model of evolutionary processes. Working their way across levels of biological organization and complexity, the authors explore the evolutionary significance of basic developmental features such as developmental time and space, regulatory complexity such as signal-response systems and interaction networks, and higher order agential phenomena such as plasticity and developmental niche construction. In the process, the manuscripts by both Nadolski and Moczek (2023) and Snell-Rood and Ehlman (2023) highlight important links between the developing phenotype and the internal and external environment within which it is embedded, to which it responds, and which it shapes through its own actions. Recognizing these links in turn permits a fuller inclusion of ecology in evolutionary models, yields a broader recognition of *causes* in evolution, and highlights areas in evolutionary biology that would benefit from more theoretical attention. This effort is then complemented by a contribution by Jernvall et al. (2023), which focuses on one particular developmental property—*robustness*. Even though ubiquitous across taxa and levels of biological organization, most research on developmental robustness has employed select model systems and organs, limiting the extent of meaningful cross-species and cross-organ comparisons. Jernvall et al. (2023) discuss diverse means, including the lens of agency, with which to develop a more uniform framework to experimentally assess and contrast degree and nature of robustness across contexts.

3 | HIGHER LEVELS OF BIOLOGICAL AGENCY

By focusing on how organisms actively generate adaptive outcomes, an agency perspective can provide fascinating new insights into biological systems above the level of the individual that can complement those gained by existing approaches. Nuño de la Rosa (2023) interrogates evolutionary approaches to reproduction, which have emphasized the sometimes conflicting fitness-maximizing strategies of parent and offspring individuals. Taking eutherian pregnancy as a case study, she instead considers how pregnant females and their embryos interactively modify their physiology, development, and behavior to further the shared goal of successful birth. Accordingly, Nuño de la Rosa (2023) argues that pregnancy has evolved to comprise a "collective reproductive agency from implantation to birth." The origin of pregnancy can be seen as a major evolutionary innovation in part because it provides this new level of collective agency, an insight that points to new approaches to the evolution of alternative reproductive modes, their evolvabilities, and their connections to related behavioral and social innovations. Gordon (2023) in turn examines a very different kind of collective agency: how the behavior of individual ants results in the production of a complex, locally adaptive foraging network for the entire colony (which interestingly is itself a single reproductive individual). Despite the simplicity of the behavior—for example, a momentary, chemically recognized antennal contact between an ant in the nest and a returning forager—these interactions adjust the activity rate of colony members, shape feedback effects, and structure the modularity of the colony's trail system in relation to the stability, energy flow, and resource distribution of the surrounding habitat. By contrasting the behavioral interactions of Harvester ants (which inhabit desiccating but relatively stable desert ecosystems) with those of Turtle ants (which confront rapidly changing resource availabilities in moist tropical forests), Gordon (2023) explores precisely how these activities can be understood as dynamic collective regulatory systems *embedded in* a particular environmental context. This shift from internal determinants of behavior to the dynamic, responsive collective system as causes of functionally adaptive outcomes suggests new research foci for behavioral studies.

4 | MODELING AGENCY

Empirical studies of agency focus on the self-regulating developmental, functional, and behavioral responses of living systems to their environmental circumstances, and how, through these responses, organisms mediate and alter those circumstances. An important challenge in contemporary biology is to develop new modeling approaches that incorporate these organismic activities. Milocco and Uller (2023) approach the responsive organism as an *agent* that, together with its environment, comprises a nonlinear coupled dynamical system. The behavior of this reciprocally interacting system can be examined even without detailed knowledge of the biological pathways involved by building a "black-box" (system identification) model using (a) known environmental inputs and (b) the system's measured outputs across a series of timepoints (see Munch et al., 2022; Sugihara et al., 2012). The authors provide a step-by-step guide for implementing this modeling framework and present an illustrative model that uses in silico data to explore the behavior of an environmentally sensitive two-gene regulatory network with specified temperature-state input patterns, taking gene expression levels over time as the system's outputs. Milocco and Uller (2023) emphasize that the organism and its environment are continually *co-constructing* each other across the life cycle and that this process reflects the key system property of memory —the fact that "past state values affect current state values." The authors argue that modeling these systems of dynamic co-construction as such is fundamental to understanding central biological phenomena such as developmental trajectories, phenotypic plasticity, learning, and niche construction.

Wade and Sultan (2023) incorporate agential features of organisms into a very different type of model to test their impact on adaptive evolution. In a simple two-allele, two-environment population genetics model, the authors assess three well-documented ways organisms respond to environmental stress: seeking out favorable microsites or habitat patches, modifying their environments (for instance, by building burrows or nests), and mediating their experience of a given environment via phenotypic adjustments (adaptive plasticity). Because these adaptive *niche-constructing* activities effectively increase the relative frequency of favorable environments experienced by a population, they increase its mean fitness, thus adding a potentially substantial environmental-change term to the Price equation for adaptive evolution—in addition to the expected term quantifying the fitness increase due to change in allele frequencies. As a result, the further evolution of these niche-constructing traits will be favored. Moreover, since they change the frequency of environments the population experiences, these niche-constructing traits alter selection at *all* genetic loci that have environmentally contingent effects on fitness, in most cases increasing additive genetic variance and hence accelerating the process of adaptive evolution. These insights make clear how including the agential niche-constructing features of organisms can contribute to an expanded understanding of population-genetic dynamics (see also models by Edelaar et al., 2008; Edelaar & Bolnick, 2019; Laland et al., 1999; Odling-Smee et al., 2003; Uller & Helanterä, 2017).

5 | LOOKING AHEAD

As is evident from this special issue, the concept of biological agency has captured the interest and imagination of researchers from diverse fields of inquiry. Indeed, agency thinking is often already implicit in the explanatory reasoning employed not just in evolutionary developmental biology (see discussion in Nadolski & Moczek, 2023), but also in functional and behavioral ecology (Odling-Smee et al., 2003 and references therein), and evolutionary theory (e.g., Edelaar & Bolnick, 2019; Scott-Phillips et al., 2014). The articles presented here make clear the potential benefits of explicitly addressing and incorporating the agential properties of living systems. While agential perspectives may make our investigations more complex, they may also provide exciting new approaches to persistent challenges such as the origins of novel complex traits, major transitions in evolution, the evolution of evolvability, evolutionary dynamics, and the future of adaptive evolution on a rapidly changing planet. Incorporating the mechanisms and consequences of organisms' agential capacities thus promises to make significant contributions across biological fields. It is hoped that this *Special Issue* will help motivate forthcoming research efforts to turn this promise into reality.

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