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Promises and limits of an agency perspective in evolutionary developmental biology

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Abstract

An agent-based perspective in the study of complex systems is well established in diverse disciplines, yet is only beginning to be applied to evolutionary developmental biology. In this essay, we begin by defining agency and associated terminology formally. We then explore the assumptions and predictions of an agency perspective, apply these to select processes and key concept areas relevant to practitioners of evolutionary developmental biology, and consider the potential epistemic roles that an agency perspective might play in evo devo. Throughout, we discuss evidence supportive of agential dynamics in biological systems relevant to evo devo and explore where agency thinking may enrich the explanatory reach of research efforts in evolutionary developmental biology.

KEYWORDS

affordance landscape, evolvability, niche construction, symbiosis

1 | INTRODUCTION

1.1 | The theoretical foundations of agency

An agent-based perspective in the study of complex systems is well established in diverse disciplines such as the cognitive sciences, behavioral psychology, artificial intelligence, and adaptive complex systems theory, yet is only beginning to be applied to evolutionary developmental biology (Andrews, 2020; Dooley, 1997; Kelso, 2016; Sultan et al., 2022). Part of the challenge of doing so lies in the terminology associated with this framework; *agent*, *goal-* or *end-oriented behavior*, *purpose* or *purposiveness*, *affordances*, etc., range from unfamiliar to completely occupied by colloquial connotations that seem to leave little room for their usage in evo devo. However, new terminology is incorporated into biological disciplines all the time, including terms with strongly divergent colloquial connotations or definitions in other fields: *fitness* has a precise meaning in (evolutionary) biology which outside of it is lost in most contexts, and the same applies to

everything from *plasticity* to *life history* and *tool kit*. This does not generally pose a problem because we train ourselves to disregard all but the precise, discipline-specific definitions of a term. What matters in this process most of all, however, is whether new frameworks and terms inspire new research able to advance questions a field has thus far struggled with, or opens questions that previously did not present themselves, or both.

In this essay, we aim to introduce, define, and begin to assess the utility of such a new framework—a perspective focused on *biological agency*—in evolutionary developmental biology. Our specific goals are to define agency and associated terminology formally, explore the assumptions and predictions of an agency perspective, and then apply this to select processes and key concept areas relevant to practitioners of evolutionary developmental biology. We conclude by considering the potential epistemic roles that an agency perspective could play in evo devo. Throughout, we discuss evidence supportive of agential dynamics in biological systems relevant to evo devo and explore where agency thinking may enrich the explanatory reach of existing research efforts, but also

highlight where we sense the limits of the explanatory utility of an agency perspective in our field.

1.1.1 | Agents and agency

The concept of *agency* is used widely in the cognitive sciences, psychology, and allied fields in which agents are defined primarily as goal-directed entities able to monitor their environment, select and perform specific actions available to them in a given situation with the objective to achieve a specific, intended goal (Beer, 1995; Franklin & Graesser, 1997; Levin, 2019, 2022; Wooldridge & Jennings, 1995). With their reliance on cognitive constructs such as intentionality, goal-directedness, and ultimately mindedness, definitions such as these are difficult to apply to fields such as evolutionary developmental biology. However, recent efforts have molded agency definitions into a much more workable form: for example, Walsh (2018) defines agency as “an organizationally closed system's capacity to build and maintain itself through the exchange of matter and energy, to differentiate itself from its environment through this capacity, and to exploit its environment in ways that promote its own continued persistence.” Building on this, Sultan et al. (2022) define agency as “the capacity of living systems to participate in their own development, maintenance, and function by regulating their own structures and activities in response to the conditions they encounter.” Crucially, these latter definitions do not require agents to have a mind and be conscious. Instead, agency is seen when component parts assemble into larger wholes, which in the process acquire biological degrees of freedom

not available to component parts alone, yet available to the larger whole to promote its continued persistence and resilience. Agents are thus more than the sum of their parts; they feature higher-order organization and a degree of individuation which empowers them to act on their own behalf (Kelso, 2016; Levin, 2019).

The agency concept is often introduced at the level of the entire organism (Fulda, 2017; Kelso, 2016; Walsh, 2015), although many trace the origin of agential dynamics to lower levels of biological organization such as single cells, tissues, and organs (Baluška & Reber, 2019; Barandiaran et al., 2009; Kauffman & Clayton, 2006; Levin, 2019; Pezzulo & Levin, 2016). If so, then agents may be viewed as nested within one another, with important implications for how we contextualize the regulatory interactions between organisms, their component parts, and their immediate environments. For example, Levin (2019) views any complex biological systems including organisms as consisting of multiple nested selves or agents, each maintaining its own locus of agency only to the extent that it restricts information flow from its neighbors and establishes local states different from those of the collective (scale-free cognition *sensu* Levin, 2019; see also Pezzulo & Levin, 2016). As this is an open area of debate in the philosophy of biology, for the purposes of this manuscript we suggest that it is worth trying an agency perspective on for size across the foci of evo devo and seeing where this shift in perspective is useful for furthering our investigations and deepening our understanding; further steps can then be taken to assess the evidence for the legitimacy of agential dynamics across levels of organization (Table 1).

TABLE 1 Glossary

Agency: The capacity of living systems to participate in their own development, maintenance, and function by regulating their own structures and activities in response to the conditions they encounter (after Sultan et al., 2022). Agency as it is discussed here is *not* a specific reference to consciousness or complex cognitive abilities that would allow for activity guided by mental representations of possible outcomes.

Affordances: Properties of the organism-environment system, jointly determined by the external conditions and the capacities of the organism itself, that bias the organism's regulation of its behavioral and physiological capabilities in pursuit of self-maintenance and function.

Repertoire: The range of behaviors and physiological processes that an organism has the capability to employ and regulate during the pursuit of its goals in a biased (appropriate) manner in response to what its current conditions afford.

End-oriented (Purposive): A property of agential dynamics that explains why an organism biases its behavioral and physiological repertoire in ways that conduce to the attainment of self-maintenance and function in response to its affordances. End-orientation is *not* a claim that living systems must have cognitive representations and desires that guide their activity.

Open-endedness versus Closed-endedness: Closed-endedness is a property of a system with a finite number of affordances and a correspondingly finite repertoire, and thus, limited adaptive capacity. If all components of a closed-ended system are known, all behaviors of the system can be predicted. In contrast, open-endedness is ascribed to systems that do not have a fully deterministic set of affordances—in other words, these systems have an adaptive capacity to respond to novel circumstances by biasing their repertoire accordingly via mechanisms that cannot be fully predicted a priori. This is a heuristic tool that explains the stochastic adaptive capacity of living systems.

1.1.2 | Affordances and repertoires

Typical descriptions of organismal dynamics treat organisms and their component parts as objects—organisms are the passive vessels of internal biochemistry at a nexus with the external thermodynamics of the environment, being separate from and passive to the conditions under which they develop and evolve. An agency framework casts this traditional construal of the organism-environment dichotomy in a new light with the concept of an *affordance* (Walsh, 2015). When living things are described as agents, systems that build and maintain themselves by exploiting their external and internal conditions in ways that promote the systems' persistence, then these conditions are more usefully conceived of as affordances. However, affordances are more than a set of conditions, instead they constitute relational, emergent properties; what certain conditions “afford” or “provide” for an organism is determined jointly by the external properties of the organism's setting as well as the capacities of the organism itself (Fulda, 2017; Gibson, 1979; Walsh, 2015). A living system's *repertoire* of behaviors and capacities is reciprocally constituted by its present set of affordances; the situations it can respond to (to its benefit or detriment) are determined by its behavioral and physiological capacities at present, just as these capacities are only meaningfully described as capacities to do something *in light of a present situation*, or an affordance (Chemero, 2003; Fulda, 2017). For example, to a fish, a body of water affords three-dimensional living quarters and a source of oxygen for cellular respiration. To a dragonfly, the same body of water offers a place where her nonamniotic eggs will be safe from desiccation and her offspring can begin their aquatic juvenile life. To a water strider, it offers a horizontal hunting ground to feed on prey that fall onto the water's surface. These various living systems do not merely succumb to an unyielding external selective environment, but rather they actively register the presence of conditions that they are able to respond to and exploit with their behavioral and physiological repertoires in ways that promote their continued functioning and existence. Alternatively, to a songbird that cannot swim, this body of water affords something negative—the risk of death, because the bird's repertoire does not include functionally coordinated swimming, no matter how much it would benefit the bird to stay afloat. Furthermore, an agency perspective makes room for agents to play an active role in *changing* their affordances during ontogeny as well as during evolution. As external conditions change, so do the affordances offered to an agent and the repertoire it possesses; likewise, as a living system's component parts develop its repertoire also

changes, as do the sets of conditions to which it can respond.

1.1.3 | End-oriented activity (Purposiveness)

For a living system to be an agent and thus experience its conditions as affordances, it must be capable of responding to them *as affordances*—either by exploiting the opportunities they provide for the attainment of self-maintenance and persistence or by mitigating impediments to those ends. Hence, an agency framework requires us to grapple with the idea of biological normativity and purpose (Walsh, 2021). Purposiveness is not intended to evoke cognition or consciousness (although cognitive and conscious agents like humans possess highly sophisticated levels of purposiveness, to be sure); rather, it offers an alternative means of explanation for biological activities. The types of explanations we are used to in biology (whether they are genetic, ecological, or selective in nature) are mechanistic explanations, ones that identify which biological *causes* produce which biological *effects* (Walsh, 2015), and this mode of explanation has been incredibly fruitful in filling out traditional descriptions of organisms as the *objects* of evolutionary and developmental processes (please note that Mayr's distinction of proximate vs. ultimate causation in biology delineates between processes acting on different biological timescales, but both still refer to *causes that produce their respective effects*, so for the purposes here, both still offer mechanistic types of explanations; Mayr, 1961). Purposive explanations, on the other hand, identify biological means (parts of an agent's repertoire) as *conducting* to biological ends, or in other words, explain an agent's employment of its repertoire by referencing how it conduces to the agent's goals (Ayala, 1970). Thus, when a living system acts agentially by responding to its present affordances, its coordinated actions manifest as conducting to the biological ends or goals of maintenance and survival. Viewed this way, the same biological event can and will have both a mechanistic and a purposive, agential explanation.

Evocations of purpose are already used in a colloquial sense throughout biology, including *evo devo*. Larvae seek out shelter *to pupate safely*, imaginal discs use circulating concentrations of insulin-like peptides *to regulate their growth* relative to nutritional conditions, amoeboid cells use pseudopodia *to colonize a wound side*, and so on. These colloquial references to purpose are normally made with an understanding that one really only means: larvae in past generations that happened to seek out shelter and pupated safely were selected for, as were imaginal discs that happened to regulate their

growth in response to insulin-like peptides, and this past selection can be referenced to explain why these mechanisms persist. It is fair to ask, then, what exactly an explanation based on agential purposiveness could add to an understanding of organisms. For an agential framework, it is crucial that mechanistic explanations do not differ between a chance event or an event that occurred for a purpose. For example, references to past selection can explain why past larvae that successfully sought out shelter survived, but this same explanation cannot explain why *this* larva in *this* present moment is seeking out shelter in a dynamic, responsive way and why it would continue to do so even in conditions that it or its ancestors never encountered before. Mechanistic descriptions tell us *how* an agent regulates its own structures and activities in response to the conditions they encounter, while a purposive description tells us *why*.

Consider bacterial chemotaxis behavior, the capacity of a bacterium to direct its movement toward or away from chemicals in its environment by sampling their concentration. Chemotaxis consists of two types of movement, random tumbling and swimming in a straight line; if a bacterium senses that it is moving towards an attractant like glucose it will move straight for a longer period before tumbling, but if it senses that the concentration gradient of the attractant is decreasing, it will tumble sooner to try a new direction of movement at random (Alon et al., 1999). A mechanistic explanation of what causes chemotaxis would describe how extracellular chemical signals are detected by transmembrane receptors and how these receptors transduce the signal to flagellar motor proteins, which rotate differentially to produce tumbling and straight-line movement (Alon et al., 1999). Crucially, though, this mechanistic explanation of how flagellar motion is generated cannot be distinguished from undirected, chance alternations between tumbling and straight-line motion. However, if we know that this bacterium has the capacity to digest glucose, and that glucose digestion provides nourishment to the bacterium, then another type of explanation surfaces—one that can distinguish whether or not something is a chance event. To explain why chemotactic movement will result in robust directional movement toward glucose regardless of starting position along the gradient, one must refer to the bacterial goal of obtaining nourishment and recognize that glucose affords this to the bacterium (Fulda, 2017). The outcomes of purposive action, of an agent acting on its own behalf, will be robust against a range of alternate initial conditions, while chance occurrences would not.

For an agency framework to expand the construal of organisms as more than objects, as agents that play an

active role in changing their affordances during ontogeny and evolution, agential activity must occur for a *reason*. For glucose to be an affordance that conduces to a bacterium's goal of nourishment, the bacterium must be able to bias its repertoire (regulate chemotaxis) in a way that conduces to the attainment of its goal of getting nourishment. In general terms, to respond to its conditions as affordances, an agent must coordinate some appropriate goal-directed processes to bring about and maintain the stable end-state of continued persistence. This end-state is all that is being referred to as a reason, or a goal. In an agential framework, then, purposiveness or end-oriented behavior is simply the manifestation of a living system in action *as an agent*.

1.2 | Agency in relation to other approaches to the study of complex systems

An agency perspective does not reject the explanatory power of reductionist approaches that dominate contemporary evolutionary developmental biology, but emphasizes the explanatory gap left behind if living systems' ability to influence the action of their component parts is ignored. As such it echoes some positions taken by other theoretical frameworks (see also Table 2). For example, *developmental systems theory* is a theoretical framework that, after its emergence in developmental and behavioral psychology in the 1980s, began to influence philosophers of biology and systems biologists (Oyama, 2000). Developmental systems theory considers causes in development to interact in complex, often nonadditive ways, rejects the partitioning of causal variation into genetic and environmental components and their interactions, views evolution as a change in the composition and distribution of developmental systems, and more generally considers development and evolution as both cause and effect of each other (Oyama et al., 2001). Many of these positions are shared with *complex adaptive systems theory* (Camazine et al., 2020; Holland, 2006). Like developmental systems theory, complex adaptive systems theory is not a single, unified theory and instead encompasses more than one theoretical framework. And like developmental systems theory, it views the causes of why and how complex systems behave the way they do and possess the properties they have as distributed within the system and as emerging through self-organization. In the process complex systems—including but not necessarily restricted to biological or even ontogenetic systems—are provided with a high degree of resilience in the face of perturbations (Bechtel & Richardson, 1993; Wagner, 1999).

TABLE 2 Comparing key tenets of developmental systems theory (DST), complex adaptive systems theory (CAST), and an agency framework

The evolutionary process: Foundationally, DST upholds that evolution ought to be conceptualized as a change in the composition and distribution of developmental systems rather than a change in gene frequencies. An agency framework is fully congruent with this perspective, as it highlights that organisms *as agents* contribute to evolution in diverse ways that are not captured by a gene-centric view of evolution alone: within an agency framework, developmental plasticity, behavior, learning, and ecological engineering may all be genuine evolutionary processes if they shape heritable variation and its transmission across generations.

Contextualism: Both DST and CAST emphasize the notion that life cycles are not the unfolding of predetermined ontogenetic information but are themselves contingent and contextually dependent. An agency framework is consistent with this perspective but extends it further with the explicit articulation of an *affordance*, a property determined jointly by the organism and the environment, that highlights that an organism's abilities are only meaningfully abilities to do something in light of a certain environmental context.

Causal cointeractionism and causal dispersion: Both DST and CAST emphasize the notion that the causes of development are decentralized, distributed diffusely across developmental systems, yet able to interact in complex, often nonadditive ways. An agency perspective is, to a degree, congruent with this perspective in that it recognizes diverse contributions to developmental and evolutionary outcomes. However, an agency perspective diverges from DST and CAST in its explicit recognition of the whole organism as a cohesive, self-regulating unit exhibiting a unique level of causal control over its own development and interaction with the environment.

Objectivity versus agency: An agency framework distinguishes itself from DST and CAST most fundamentally in that the latter two retain a model of living systems as the *objects* of various causal influences in development and evolution. Viewed this way, an externally determined parameter space configures the degrees of freedom available to ontogenies or populations, respectively, and diverse influences then determine the exact outcomes of development and evolution. During the process, the organism itself remains a passive participant. In stark contrast, an agency perspective views organisms as causal *agents* able to shape the configuration space within which they themselves develop and evolve. Put another way, agents and the configuration space within which they function are both cause and effect of each other.^a

^aTenets of DST drawn from Griffiths and Gray (1994), Robert et al. (2001). Tenets of CAST drawn from Camazine et al. (2020), Holland (2006).

None of these positions directly conflict with an agency perspective on living systems; however, viewing living systems *as agents* articulates unique *additional* positions with the potential to yield testable predictions absent from developmental or complex adaptive systems theory (Table 2). First, both developmental and complex adaptive systems theory prioritize *self-organization* as the main cause underlying the *emergence* of adaptive behaviors and resilience to perturbation (e.g., von Dassow et al., 2000; Wagner, 1999). Complex systems function the way they do because of causes distributed diffusely *within* the system and in the absence of an ordering influence from the system as a whole, or in the words of Kelso (2016): “self-organization means that the system organizes itself, not that there is a *self doing the organizing*” (Kelso, 2016, emphasis added). In contrast, an agency perspective explicitly recognizes this self in a biological system as the entity referred to as the agent and highlights the ordering influence it can have on its component parts. Second, developmental and complex adaptive systems theories view the parameter (or configuration) space within which complex systems function as outside of the control of the system itself. Configuration spaces simply exist, and complex (developmental) systems self-organize, adapt, and exhibit resilience within these preconfigured spaces (Wagner, 1999).

In contrast, an agency perspective highlights the agent's ability to structure and alter the configuration space within which it is positioned, thereby shaping its own affordances (Walsh, 2015). Intriguingly, this latter point is not unique to an agency perspective, but has interesting antecedents in diverse fields relevant to evolutionary developmental biology: for instance, the concept of the *stem cell niche* captures a phenomenon that exists solely on the level of cells and tissues *arranging themselves* in ways that create a larger whole that then reinforces its own persistence while creating microenvironmental conditions conducive to the coordinated maintenance of stem cells and their proper differentiation (Scadden, 2006). The broader concept of *niche construction* likewise emphasizes whole organisms' abilities to nonrandomly modify and structure environmental conditions in a way that alters their selective environment or that of their offspring, often in an adaptive manner (Odling-Smee, 2010; Schwab et al., 2017). Here it is the individual, taking action, *acting on its own behalf* by systematically modifying the environment around it. Similarly, the *holobiont* concept emphasizes that the joining of and interactions between multiple symbiotic taxa creates both *larger wholes* that are more than the sum of their component taxa and their respective affordances, and *larger selves* able to now

direct the action of their component parts (Gilbert et al., 2015; Margulis & Fester, 1991; Rosenberg & Zilber-Rosenberg, 2016). These conceptual affinities suggest that an agency perspective on living systems is already rather implicit in various biological fields. Therefore, the focus of the next section is how a more *explicit* formulation and application of a theory of agency may benefit research in evolutionary developmental biology.

2 | APPLYING AN AGENCY PERSPECTIVE TO KEY PROCESSES IN EVO DEVO

In this section, we apply an agency perspective to key processes targeted by research in evolutionary developmental biology. Our goal here and in subsequent sections of this manuscript is to assess the degree to which agential properties and dynamics are detectable for a given process, and whether an agency perspective changes or nuances how research objectives and hypotheses may be articulated.

2.1 | Embryogenesis

During *embryogenesis*, gametes fuse to form a totipotent zygote. Subsequent rounds of cell division, cellular differentiation, and rearrangements then transform a single cell into a three-dimensional embryo composed of tissues with specific identities, competencies, and spatiotemporal relationships relative to each other. Here, *embryonic induction* refers to the process whereby un- (or less) differentiated cells transform into progressively differentiated cell types (>200 in many adult vertebrates including humans), tissues, and organs. Embryonic induction is traditionally defined as the process through which one set of cells produces substances, or more generally *creates conditions*, that change the behavior, morphology, proliferative status, and cytogenetic differentiation of recipient cells and tissues (Barresi & Gilbert, 2020). Put another way, throughout embryogenesis cells and tissues actively engage in (often reciprocal) intercellular crosstalk to initiate and direct the outcomes of subsequent rounds of phenotype construction. Because all cells within an individual (with only rare exceptions) possess the exact same genomic content, it is understood that such “cellular differentiation *must result from* regulation of the expression of specific subsets of the total genomic set of genes” (Sawyer & Knapp, 2003, p. 103; emphasis added). Much of contemporary developmental biology and evo devo focuses precisely on this

relationship—how differential gene expression directs cellular differentiation in particular and embryogenesis broadly, and how changes in gene regulation bring about the diversification of (embryonic) form and function in development and evolution. However, careful examination of the definition of embryonic induction stated above reveals its reliance on intercellular and tissue-level interactions. An agency perspective on embryogenesis would thus emphasize that the causal underpinnings of embryogenesis reside not just in the differential expression of genes and their products, but also in the cellular structures, their spatiotemporal relationships to other tissues, and their reciprocal interactions, *that put these gene products to use* (Pezzulo & Levin, 2016). In insect embryos, for example, homeotic selector proteins function as segment-specific regional identifiers once embryos have formed segments able to establish and reciprocally reinforce segment boundaries and identities. During echinoderm gastrulation, it is the advancing archenteron that induces the formation of a mouth in the opposing (animal) pole of the gastrula, with which it will eventually fuse, forming a feeding tube. As such, an agency perspective emphasizes that it is the embryo—with its parts and as a whole—that is influencing its own differentiation, creating conditions that facilitate the ordered progression of subsequent rounds of phenotype construction.

2.2 | Organogenesis

Similar dynamics appear evident during *organogenesis*, in which tissue-level interactions often play prominent roles in reciprocally constructing important components of the developmental environment within which organs form, and in guiding the way component parts integrate functionally with each other (Gerhart & Kirschner, 2007; Salazar-Ciudad et al., 2003). For example, mammalian tooth development is initiated by the reciprocal interactions between epithelial and mesenchymal cells (Kassai et al., 2005), which guide growth and folding of the epithelial–mesenchymal interface, eventually resulting in the initiation and elaboration of future tooth cusp sizes and shapes. During later stages, this same interface generates both dentin and enamel layers, which upon tooth maturation, arrest in place in whatever configuration cusps have reached by this developmental time point. As a result, tooth shape is specified well before teeth erupt and begin to function (Jernvall, 2000). This sequence of events underpins the extraordinary morphological (and functional) diversity of all mammalian teeth in existence both within and among taxa (Hunter &

Jernvall, 1995; Wilson et al., 2012). Yet when we ask what determines or controls this diversity in tooth size and shape, much of it appears to reside on the level of interacting tissues.

When we scale up to the formation of entire organ systems and the interactions among them, similar dynamics emerge once more. For example, during early vertebrate development muscle precursors migrate at random throughout the embryo but stabilize in positions relative to where bones are forming at the same time (Herring, 2011), thereby ensuring their coordinated and integrated development. Similarly, motor neurons proliferate abundantly during early development yet are maintained only if they find themselves close to developing muscle tissue (Kovach et al., 2011). The vascular system also expands randomly during embryogenesis, but subsequently biases its differentiation through its attraction to hypoxic conditions, such as those where muscular-skeletal growth is occurring (Marti, 2005). In each instance, complex and discrete developmental processes integrate with each other through reciprocal interactions, in the process forming higher order levels of organization, which in some cases acquire a certain degree of autonomy, able to then direct the further differentiation and action of their component parts. For example, any perturbation, e.g., via injury, changes in nutrition, or newly introduced mutational variation, is sensed via the muscular-skeletal system in place by then and accommodated by it through subsequent rounds of phenotype construction via remodeling of existing skeletal elements, adjusting the attachments of ligaments and muscles, (re)training of motor neurons, and the balancing of mechanical load across the entire body (Herring, 2011; Uller et al., 2018). These adaptive and functionally integrated modifications did not necessitate the evolution of novel genes or regulatory settings, instead they are products of the self-constructing and self-adjusting nature of muscular-skeletal growth. Applying an agency perspective to the study of organogenesis and morphogenesis may thus appropriately emphasize the roles played by tissue-level interactions in directing organ (system) formation within individual organisms, especially those through which the developing system affords itself flexibility to ensure that tissue-level interactions couple naturally even in stochastic conditions, and, via heritable changes in these interactions, on an evolutionary scale.

2.3 | Metamorphosis

Developmental dynamics during *metamorphosis* also appear congruent with an agency perspective. Metamorphosis describes the transition from and/or replacement

of juvenile features with the future, sexually mature adult form. Depending on phylum and class, such reorganization may entail radical changes in symmetry, shape, and internal organization, and the loss of larval and gain of adult appendages, organs, and organ systems, alongside their behavioral and physiological functions (Barresi & Gilbert, 2020). Current research programs on the control of metamorphosis often focus on the roles of endocrine cascades and their interplay with tissue and body region-specific target genes and pathways (reviewed in Nijhout, 2013; see also Kamsi et al., 2021). Yet, like embryogenesis discussed above, metamorphosis is first and foremost a biological process that plays out on the level of tissues, their coordination relative to each other, their dependence on spatial organization and other component parts, and the *increased individuation* that tissues and the traits they give rise to are generating as metamorphosis unfolds (Belles, 2020). For example, much of the adult body of *Drosophila* (including the entire head, all appendages, and most adult organ system components) derives from imaginal discs and histoblasts, groupings of cells specified during late embryonic development which then undergo their own distinct ontogenies within the larval body. Imaginal discs proliferate during much of larval development as epidermal invaginations, which develop specific two- and three-dimensional arrangements and positional relationships to other structures that inform series of patterning events, with each round of patterning creating the conditions for subsequent differentiation events (Kojima, 2004). In the process, primordia acquire some degree of autonomy to reinforce their own compartment boundaries, relative sizes, and integration with other traits (Bryant & Levinson, 1985; Klingenberg & Frederik Nijhout, 1998). Less extreme forms of holometabolous metamorphosis seen in the majority of insect taxa nevertheless feature the same principles (Švácha, 1992): adult beetle legs derive from their larval precursors which semiautonomously coordinate their own development in response to the spatiotemporal and nutritional conditions they encounter (Rohner et al., 2021); the head of adult *Onthophagus* dung beetles are built to large extent from larval source tissues which in the process integrate information on sex (to allow formation of sexually dimorphic heads; Linz & Moczek, 2020) and nutrition (to optimize scaling; Casasa et al., 2020). Some of the same dynamics buffer head formation against perturbations, including severe surgical and genetic alterations which are nevertheless channeled toward orderly and functional outcomes by the self-constructing and -correcting nature of head development (Busey et al., 2016; Zattara et al., 2017; this has also been shown in amphibians, Vandenberg et al., 2012). As before, the

dynamics of metamorphosis are largely amenable to, and perhaps even extended by, agential concepts: an agency perspective highlights the end-oriented nature of dynamic developmental processes that generate an increasingly sensitive and flexible repertoire for a developing organism, alongside new dimensions of affordances that emerge as one life stage transitions to another. An agency perspective may extend conventional considerations by drawing attention to the mechanisms and consequences of the potential interplay between agential dynamics driving metamorphosis between the level of individual organs and that of the whole organism (Levin, 2019).

2.4 | Regeneration

The *regenerative abilities* of developmental systems hinted at in the preceding paragraph are perhaps among the best illustration of what proponents of an agency perspective consider examples of agency in action, utilizing *affordances* as determined by a developmental system's abilities in relation to its current environment, toward the achievement of a particular developmental end state, or *goal*. Posttraumatic regeneration of body parts lost to injury is phylogenetically widespread and ranges from the replacement of lost tissue from neighboring epithelia to the regeneration of internal organs, appendages, and in extreme cases entire bodies from fragments (reviewed in Bely & Nyberg, 2010; Zattara, 2020). In each case it represents a phenomenon operating on multiple levels and organized to varying degrees by cells, tissues, and *the increasingly reconstructed part itself*. For example, many regenerative events involve the formation of a blastema (often referred to as *epimorphic* regeneration), a mass of undifferentiated cells at the wound site derived either from pluripotent stem cells, cells that have not yet fully differentiated into a terminal cell type, or—as is commonly the case—*dedifferentiating* cells (Tiozzo & Copley, 2015). Blastema cells proliferate, and in the process cover the wound site, limit loss of fluids and the possibility of infection, and then through reciprocal signaling with the remaining limb or organ stump organize exactly what regions need to be regenerated: loss of an entire arthropod leg results in the formation of an entire replacement limb, yet if the leg is severed at the tibia only those distal components will regenerate (Zattara, 2020). Other regenerative events rely less on blastema formation and cell proliferation and more on the remodeling and rearrangement of existing tissue, referred to as regeneration via *morphallaxis*; like epimorphosis, regeneration via morphallaxis necessitates extensive cell–cell and tissue–tissue communication, cell

migration, and tissue folding (Bely & Nyberg, 2010). While such regenerative capacities are not limitless, these processes illustrate the ability of cells to cooperate toward an invariant endstate, the healthy target morphology, from diverse initial conditions *and crucially*, cease activity when the goal has been achieved (Levin, 2022). Importantly, regeneration is *not* merely a recapitulation of embryogenesis discussed earlier: while embryogenesis follows a highly stereotypic sequence of developmental events along a trajectory of continuously increased differentiation and specialization of cell types, most regenerative events are as unique as the injuries initiating them, *and* in the case of epimorphosis require significant cellular *dedifferentiation* (Zattara, 2020). However, like embryogenesis and especially organogenesis, epimorphosis and morphallaxis require the coordinated and precisely context-dependent actions and interactions of cells, tissues, as well as remaining and newly created body parts toward a particular developmental outcome or *goal*: the complete reconstruction of part of an organism lost to injury, and its functional integration within the larger whole to replace the loss in affordances generated by the physical loss.

2.5 | Niche construction

Niche construction is operationally defined as occurring when an organism modifies environmental conditions in ways that alter selection pressures experienced either by itself, another member of its population, a descendant, or other taxa (Matthews et al., 2014). Niche construction is ubiquitous, including during development, for instance, when organisms alter ontogenetic environments via chemical excretions or the constructions of physical structures such as pupal cases, dams, burrows, galls, nests, etc. (Odling-Smee et al., 2003). Niche construction is not the only conceptual framework that recognizes the environment-modifying capacity of organisms (e.g., social and coevolutionary theory, sexual selection, eco-evolutionary feedback theory, extended phenotype concept, etc.); yet where niche construction theory diverges is in its more explicit recognition of organism-mediated modifications of the environment as shaping phenotypic variation within populations, as an alternate route toward adaptive fits between organisms and their environments, and as a possible route of nongenetic inheritance in cases in which niche constructing activities occurring in one generation affect the selective conditions experienced by subsequent generations (Laland et al., 2015; Schwab et al., 2017). Lastly, in cases in which niche constructing activities also affect the

selective conditions experienced by other taxa, it can give way to *ecosystem engineering*, as in the soil conditioning executed by earthworms, the construction of wetland by beavers, the transformation of savannahs by hippopotami, or coral reef formation (Erwin, 2008).

Niche construction theory originated from within evolutionary ecology and has not been a traditional focus of evo devo thinking (Schwab et al., 2017; but see Laland et al., 2008). However, research in evo devo is increasingly recognizing the interplay between development and ecological context as a significant determinant of ontogenetic outcomes, and as a source of bias in the structuring of selectable variation in natural populations, perspectives shared with niche construction theory. What niche construction adds and most of evo devo still lacks is the reciprocal perspective, namely that environmental and ecological conditions may at least in part be actively created by organisms themselves, that is, that ontogenetic environments can be both cause and effect of organismal development (Schwab & Moczek, 2021).

Examples of niche construction are all inevitably examples of agency in action: larval antlions construct pitfall traps to aid in prey capture (Büsse et al., 2021), tent caterpillars collectively create developmental environments that protect against predators and thermal perturbations (Fitzgerald, 1995), and adult dung beetle mothers bequeath upon their offspring a nursery complete with food and the microbial community necessary to digest it, which larvae then further (re)construct into an external rumen (Schwab et al., 2016, 2017). Moreover, constructing niches is itself a context-dependent process that may be learned from conspecifics (as in nest building in birds; e.g., Guillelte et al., 2016), spatiotemporally flexible to enable regeneration (as in web-repair in orb-weaving spiders; e.g., Tew et al., 2015) and responsive to natural variation in resource quality (as in the flexible adjustment of dung quantity to dung quality in the larval provisioning by dung beetle mothers; Moczek, 1998). In all these cases, it is individual organisms pursuing a particular goal in a manner that is adaptively responsive to circumstances, with the organism being both object and agent of the conditions under which natural selection then operates. Applying an agency perspective to the study of *ecological* niche construction thus highlights organisms' causal influence in determining aspects of their physical environment, whereas applying an agency perspective to the study of *developmental* niche construction emphasizes organisms' causal influence in determining robust, context-sensitive phenotypic outcomes. And while this influence requires the genetic, cellular, and organ-system level processes that underpin organismal function, knowledge of lower-level mechanisms by themselves appears insufficient to

understand the agency of the larger whole and self. Intriguingly, this perspective parallels in many ways what we aimed to articulate in earlier sections: agential dynamics appear to manifest on multiple levels, and at each level the agent *matters* in determining ontogenetic outcomes, be it the establishment of a feeding tube during gastrulation, the functional integration of muscular, skeletal and vascular systems during organogenesis, or the construction of a nursery. This continuum extends even to interactions among unrelated organisms, as discussed next.

2.6 | Symbiosis

Like niche construction, symbioses have not been a traditional focus of evo devo. Yet also like niche construction, symbioses broadly and host-microbiome interactions, in particular, are increasingly understood as integral components of many developmental and life history processes: for instance, host-associated microbes help induce metamorphosis (Shikuma et al., 2014; Sneed et al., 2014; Whalan & Webster, 2014) and shape survival-reproduction trade-offs in invertebrates (Emelianoff et al., 2008), regulate reproductive timing in plants (Leonardo & Mondor, 2006), affect learning outcomes (Chu et al., 2019; Vuong et al., 2017), and provide critical nutritional supplementation (Douglas, 2009) in a variety of taxa. In these instances, interactions with microbiota may be conceptualized as a means by which hosts supplement cues and resources to inform critical developmental decisions of their own, that is, in agency terms the individual (host) organism complements its inherent physiological repertoire with cues and resources afforded by its microbiome. However, host-microbiome interactions also instruct organogenesis, such as germline development in nematodes (Foray et al., 2018) and gut differentiation in mice (Hooper & Gordon, 2001; Sommer & Bäckhed, 2013), *including* the formation of organs dedicated to housing microbial partners, as in the induction and differentiation of the light producing organ of bobtail squid (McFall-Ngai, 2014). These symbiotic relationships tightly couple the repertoire and affordance landscapes of host and microbe. In these latter examples, host components interact with microbial partners in the construction of organ systems that otherwise would not exist at all (or at least not in a functional configuration) and which in the process acquire a certain degree of autonomy, able to reinforce and direct their own subsequent development, allowing the microbiota's affordances and those of the host to change in tandem (Gilbert et al., 2015; Margulis & Fester, 1991; Sultan, 2015). More generally, the potential value

for evo devo research on host–microbiome interactions from an agency perspective is similar to the arguments made for niche construction above: host–microbiome interactions have the potential to causally influence development, create alternate routes of inheritance in those cases in which microbial partners are vertically transmitted, contribute to (context-dependent) heritable variation in populations, and provide opportunities for differentiation and diversification among populations and species. Already, a growing number of case studies support such contributions in diverse taxa (insects: Feldhaar, 2011; Lemoine et al., 2020; dung beetles: Parker & Moczek, 2020; Parker et al., 2019, 2020, 2021; Schwab et al., 2016; flies: Morimoto et al., 2017; Nguyen et al., 2020; stickleback fish: Smith et al., 2015; see also Corbin et al., 2017; Renoz et al., 2019).

3 | APPLYING AN AGENCY PERSPECTIVE TO KEY CONCEPTS IN EVO DEVO

The preceding sections suggest that agential dynamics manifest during diverse biological processes relevant to contemporary evo devo research. Thus, an agency perspective may be helpful in framing or refocusing research programs aimed at identifying developmental contributions to biasing, hindering, or facilitating developmental evolution. In this next section, we aim to apply the same approach to key concepts in evo devo, with the goal of identifying where and to what extent they are at odds with, congruent with, or possibly enhanced by an agency perspective.

3.1 | Developmental plasticity

Developmental plasticity is commonly defined as the capacity of a single genotype to produce different phenotypes in response to varying environmental conditions (Whitman & Agrawal, 2009). Biologists have long been aware of the capacity of individual organisms to alter their development and physiology in response to environmental conditions, but the evolutionary significance of this capacity has remained controversial. On the one hand, central to the modern synthesis of evolutionary biology is the idea that phenotypic change wrought by the environment does not influence the genes that an individual transmits to its offspring; accordingly, early in the field's history, any phenotypic variability displayed by a genotype was considered to be mere “environmental noise” that ought to be minimized through controlled laboratory experiments. On the other

hand, before long it came to be recognized that quantitative genetic models often lack significant explanatory power without explicit recognition of $G \times E$ interactions (Falconer, 1989; Via & Lande, 1985). Furthermore, recent years have witnessed the accumulation of evidence for a theory of *plasticity-first* evolution, wherein an organism's pre-existing context responsiveness can facilitate the production of novel phenotypes that precede, rather than follow, changes in genotype during the course of evolution (reviewed in Levis & Pfennig, 2019; Moczek et al., 2011; West-Eberhard, 2003; see also the section on *Innovation* below). Central to these latter realizations is an understanding that living systems have evolved to interpret their genetic information in a diversity of adaptive, context-dependent ways.

Implicit in these views, then, is recognition of the active role developmental systems play in adjusting their outputs to suit changing conditions in pursuit of their system-level objectives. Although specific agency terminology has yet to surface in this context, much of agency *thinking* is already embedded in the study of the mechanisms behind and evolutionary consequences of developmental plasticity. Defined another way, developmental plasticity can be seen as the capacity of a living system to bias phenotype construction in response to environmental conditions in ways that generate an affordance landscape for the system that is more amenable for the developmental system's pursuit of its objectives. These adaptive plastic responses allow individual organisms to maintain and even enhance function and fitness across a range of environments, buffering the response to natural selection. Intriguingly, developmental *robustness*, that is, the production of canalized phenotypes in the face of environmental or genetic perturbations, has traditionally been viewed as the extreme opposite of developmental plasticity. Yet viewed from an agency perspective, plasticity and robustness can be seen as complementary phenomena that *collectively* allow living systems to attain and maintain a stable endstate in response to their conditions (Schwab et al., 2019).

For example, studies of plasticity in plants have demonstrated that traits involved in resource acquisition often show functionally appropriate patterns of plasticity, including increased biomass allocation to roots in response to low-nutrient soils and increased leaf area relative to overall plant biomass in response to lower light conditions (Sultan, 1987). Such longer-term developmental plasticity can compensate for some of the inevitable reductions in growth that occur under resource limitation, allowing a given genotype to grow and reproduce successfully in diverse conditions. Plants also display elegant short-term physiological plasticity,

adjusting traits such as leaf angle, stomatal aperture, and photosynthetic rate in response to aspects of the environment that vary more rapidly on a temporal scale, such as light intensity and humidity (Sultan, 1996). Likewise, the Burmese python exhibits dramatic organ remodeling that correlates with the need for intestinal functioning after being fed. The small intestine increases in size three-fold, and the transcriptional profile of the intestine shows a massive upregulation of genes involved in metabolism and intestinal functioning as well as genes involved in cell division and apoptosis as early as six hours postfeeding (Andrew et al., 2015; Starck & Beese, 2001). These dramatic changes return to prefeeding levels within 10 days of a meal, minimizing energy expenditure when digestion is no longer occurring. Modes of plasticity, whether short- or long-term, localized or extensive, can thus all be construed as processes that allow organisms to modify their affordance landscape by orchestrating changes within their component parts (Sultan, 2015).

As these examples illustrate, an agency perspective appears implicit in diverse contemporary research programs that aim to understand the context-responsive nature of developmental processes on varying timescales. Living systems regulate the developmental plasticity and robustness of their component parts when this conduces to their survival and other objectives. Emphasis on the self-regulating and self-adjusting nature of development as the norm rather than the exception to the rule may be strengthened by a more explicit recognition of developmental systems as integrated wholes that reciprocally make use of their physiological repertoire and influence the structure and function of their component parts in pursuit of their system-level objectives or goals. From an agential perspective, plasticity during development is a paradigmatic example of agents' capacity to adjust their affordance landscape not by affecting their external surroundings but by regulating their own structure and functions to generate a more positive set of affordances.

3.2 | Adaptation

The modern synthesis perspective views adaptive evolution as emerging through the differential retention of rare, beneficial mutations driven by an external, selective environment. This traditional approach accords explanatory primacy to the adaptation-promoting influences of the external environment, without necessitating reference to the internal processes of development and inheritance that are considered adaptation-neutral except perhaps when they act as constraints on what selection can accomplish (Uller et al., 2020). For a trait to qualify

as an adaptation, it must have evolved in response to selection pressure exerted by aspects of the external environment (Dobzhansky, 1942). This traditional commitment to an explanatory "externalism" necessitates a conceptual decoupling of the organism—and the internal processes of development and inheritance—from the environment and the selective pressures that introduce or *cause* adaptive bias in evolution (explanatory externalism *sensu* Brown, 2022). Organismal form and the niche to which it adapts thus are separable and *unequally* dependent on one another: organismal form depends on niches, but niches do not depend upon organismal form. As Lewontin has pointed out: "to make the metaphor of an adaptation work, environments or ecological niches must exist before the organisms that fill them," otherwise environments could not *cause* organisms to fill those niches (Lewontin, 2001).

However, this conceptual commitment to a decoupling of environment from organism obscures the intimate interrelation between an organism's form and function and the conditions in which it finds itself. Adaptations are not differential responses to an environment *per se*, but responses to an *experienced* environment (Walsh, 2015, 2022). An agency perspective underscores that what more cohesively explains adaptation is not the autonomous features of the environment, but something that fundamentally involves the organism itself. The *experienced* environment is neither separable nor autonomous from the organism. Rather, the organism is reciprocally involved in constituting its affordances, the aspects of its surrounding environment that are meaningful for its survival. As referenced prior, the same body of water emerges as a different affordance for the various living systems in its vicinity (fish, birds, water striders, etc.). A living system's biological repertoire and its affordances reciprocally constitute one another; therefore, any change in one begets a change in the other. Thus, an agency perspective suggests that there are no autonomous environments, no pre-existing niches that pose "set" problems to living systems. Instead, idiosyncratic living systems relationally determine the affordance landscapes that a set of conditions provide, given their current form and repertoire. It may be easy to see how a nest, burrow, or social group is an aspect of the environment shaped by the organism that will fundamentally influence the conditions experienced by the organism, and therefore what is adaptive and what is not. Clearly, environmental components differ in the degree to which organisms can causally shape or modify them (Lewontin, 2001). By the same logic, though, the layer of body hair on a mammal generates a meaningful influence on the *experienced* temperature, even if the average thermal energy in the air surrounding that

mammal has not been affected. The presence of a fourth cone cell that can detect ultraviolet light does not affect the density or distribution of pollen-rich flowers, nor the spectra of light cast within an environment, but it does afford insects the opportunity to detect floral UV patterns more easily. An external, autonomous environment of the sort that would “cause” organisms to adapt to its niches cannot exist if organisms themselves fundamentally shape their experience of the conditions around them (Laland et al., 2019).

Furthermore, traditional accounts of adaptation aim to explain how individuals and populations come to have enhanced evolutionary fitness in their environment over time. Thus, despite explanatory power centering on gene sequences and fortuitous mutations contributing to fitness, a crucial outcome to be explained is that of phenotypic *function* increasing in suitability to promote fitness over time. Yet understanding phenotypic functions and their adaptive value for a currently living organism requires an analysis of *the entire organism embedded in its environment*, not simply a reference to past evolutionary success of its lineage: the vertebrate heart evolved to efficiently pump blood, not to make a sound while it is doing so. The animal brain evolved to receive and process incoming nerve signals, not to consume more energy than most other tissues; however, if the activity of the heart or the brain are described solely in terms of physical, biochemical, genetic, and developmental processes, it remains unclear which components of these complex phenotypes might be meaningfully, currently adaptive for a living system attempting to survive and which may simply be “spandrels” necessitated by the workings of the component parts (Kauffman & Clayton, 2006). However, as biologists, we do not perceive this as a problem, because our accounts of function already implicitly hint at the concepts of affordances and repertoire hidden within the typical references to past natural selection.

The agential conceptions of co-constituting affordances and repertoires require a recasting of adaptations as dynamic relations of an agent's repertoire and surroundings that change as affordances change, whether due to genetic mutations or perturbations to the conditions an agent is experiencing. Adaptive evolution does not unfold as populations migrate along fixed adaptive landscapes; rather, organisms play a role in carving their affordance landscapes for themselves. This recasting has profound implications for an understanding of adaptive evolution. Under an agency framework, adaptive evolution is the process of biological form constantly cocreating and responding to a dynamic set of affordances. Organismal form then takes a seat as a key player in adaptive evolution, and perhaps the field

may be on the path to answering Gould and Lewontin's call to “put organisms with all their recalcitrant yet intelligible complexity back into evolutionary theory” (Gould & Lewontin, 1979).

3.3 | Innovation and the origins of evolutionary novelties

Understanding the origins of complex novel traits in development and evolution is one of the cardinal objectives of evo devo, motivated in part because neither parent discipline has so far come close to providing satisfactory answers (Moczek, 2008; Wagner & Lynch, 2010). On one side, developmental biology has provided us with an ever more detailed understanding of the mechanistic underpinnings of trait formation. This approach is immensely helpful because it catalogs everything that must come together, and in what order and circumstance, to enable the formation of complex traits. Yet for the most part this work has informed our understanding of all that can go wrong during the formation of trait form and function but leaves largely unanswered how such exquisite choreography may emerge in the first place. Evolutionary theory in turn looks at the origin of novel complex traits through the lens of changes in the allelic composition of a population over time, and prioritizes selection, migration, drift, and mutation as the only relevant evolutionary processes able to bring about such changes. Yet of those, selection, drift, and migration can only eliminate or reshuffle existing possibilities, not create novel variation. This task is instead left primarily to mutation, but our attempts to successfully explain the origin of the first eye, placenta, or light producing organ, or the transitions from water onto land and into the skies one mutation at a time has yet to materialize (Wagner, 2014).

Instead, most progress toward understanding the genesis of novel complex traits and the nature of innovation in developmental evolution have emerged outside evo devo's parent disciplines. Evo devo was born in part through the realization that the enormous phenotypic diversity surrounding us is facilitated through the context-dependent reuse and reassembly of an otherwise remarkably limited pool of genes, developmental pathways, cell types, and morphogenetic processes. This discovery forever changed our perspective, away from viewing members of different phyla or classes as having come into being independent of each other, toward instead recognizing them as uniquely *assembled*, thereby retaining close affinity toward each other through the use of the same, homologous, ancestral pool of building blocks (Carroll et al., 2004). Paradigmatic evolutionary novelties—butterfly eye spots, beetle horns, the turtle shell, the firefly

lantern—similarly emerged as novel assemblies via the select reuse and repurposing of old genes, pathways, cell types, etc. (Hu et al., 2020; Moczek, 2008). The resulting shift toward understanding the rules that may govern the assembly of novel traits and organisms has since unearthed diverse phenomena congruent with an agency perspective. First, development has emerged as a highly constructive process whereby a given aspect of phenotype formation builds—and critically depends upon—a pre-existing phenotype created during earlier stages of development. As such, development emerged as inherently *responsive to context*: a developing system is continually sensitive to changing affordance landscapes, in part created by its own continued development. Second, development revealed itself as inherently *integrative*: during ontogeny diverse discrete processes integrate with each other through reciprocal interactions, thereby forming higher order levels of organization, which may in turn acquire the ability to feed back to direct the actions of their component parts and their own environment. For example, the formation of imaginal discs during insect appendage initiation, the interactions between the vertebrate forebrain and head ectoderm during eye development, and perhaps most impressively the implantation and subsequent differentiation of the mammalian embryo (Nuño de la Rosa et al., 2021) are among the many examples in which context-responsive integration of diverse processes gives rise to entities which over time acquire an increasing degree of autonomy, able to influence their own subsequent development and immediate environment. Finally, context-responsiveness and integration facilitate *robustness*, that is, developmental systems are able to respond to changes in context by adjusting subsequent rounds of phenotype construction, often in a functionally adaptive manner (Schwab et al., 2019; Uller et al., 2018). What all three of these attributes—self-construction, integration, robustness—share is that they manifest at the level of, and through the actions taken by, cells, tissues, organ systems and the entire individual, *on behalf of* their own construction, adaptation to current conditions, and resilience in the face of perturbations, thereby fulfilling all the requirements for agency.

While agency terminology has been mostly absent in this context, agency *thinking* has already been quite implicit in subsequent efforts to investigate the origins of novel traits in evo devo. For example, an extensive body of work has begun to examine the role of *developmental bias* in evolution, recognizing that developmental systems channel both mutational and environmental inputs toward some outcomes more readily than others and that this process may even be biased toward adaptive phenotypic variation. As such, it became clear that the traditional view of development as a constraint on evolution is incomplete and that the concept of developmental bias more adequately captures development's role

as a facilitator of adaptation and innovation *made possible through the actions of developmental systems* (Uller et al., 2018). Likewise, the framework of *plasticity-first* or *plasticity-led* evolution is predicated on the hypothesis that pre-existing context responsiveness can facilitate the production of phenotypic variation in the face of novel or stressful environments (again often biased toward functional, integrated, and possibly adaptive variants) allowing the production of novel phenotypes to precede, rather than follow, changes in genotype (e.g., feeding morphology in sticklebacks and cichlids: Muschick et al., 2011; Wund et al., 2008; carotenoid-dependent coloration in birds: Badyaev et al., 2017; pigmentation in water fleas: Scoville & Pfreder, 2010; transition from detritus feeding to carnivory in amphibians: Gomez-Mestre & Buchholz, 2006; Kulkarni et al., 2017; Ledon-Rettig et al., 2008; morphological and behavioral traits in dung beetles: Casasa & Moczek, 2018; sexual size dimorphism in the house finch: Badyaev, 2005; water to land transition of vertebrates: Standen et al., 2014). Implicit in this view is once again the recognition of developmental systems' active roles in adjusting their outputs to suit changing conditions, in pursuit of their system-level objectives. As these examples illustrate, an agency perspective already appears implicit in many contemporary research programs aimed at understanding the nature of innovation in *and by* living systems. Expanding on these efforts therefore promises to further advance our understanding of how the genesis of novelty may be scaffolded by the self-constructing, self-regulating, and self-adjusting nature of developing agential systems (Moczek, 2022; Sultan et al., 2022).

3.4 | Evolvability

In the above sections, we emphasized the active role played by developmental systems in the production of traits that are well-integrated, functional, and resilient. We would like to end this section by revisiting the notion that this active role is of course itself a product of evolution, one that was added to over time to generate the developmental repertoires of living systems we observe today (e.g., Abedin & King, 2010; Brunet & King, 2017; Richter & King, 2013). That is, the developmental processes necessary to generate complex traits in extant taxa, from cell division and adhesion to epithelium formation, cellular differentiation and migration, tissue folding, the production, sensing of, and responding to morphogens, the formation of lumens, individuated compartments, etc., all emerged sequentially over hundreds of millions of years (Erwin, 2020; Newman, 2022). Yet once in existence, each of them fed

back in unique ways to influence subsequent evolution by contributing novel degrees of freedom with respect to what development could build, how it could respond to perturbations, and what selectable variation it could produce for evolutionary processes to act upon (Moczek, 2022; Newman, 2022; Watson & Szathmáry, 2016). Put in the language of agency, the evolution of developmental systems can thus be understood as a process that has steadily increased the repertoires of ontogenies, empowering them to pursue an ever-wider range of goals across an ever-expanding range of conditions, thereby creating an increasingly extensive affordance landscape in development and developmental evolution (Moczek, 2022).

Viewing evolvability in evo devo through the lens of agency emphasizes the dynamic nature of developmental evolution of life on earth as a process that *consistently modified its own means*. For instance, early multicellularity in animals was made possible in part through the evolution of the cadherin family of cell adhesion molecules. Cell adhesion enabled cells to stay connected while sliding past each other, allowing organisms to adopt droplet-like architectures as seen today in early embryos and organ primordia (Newman, 2012). Yet, further increases in complexity became possible only following the evolutionary emergence of the *basal lamina*, a firm but flexible extracellular matrix resulting from a mixture of compounds produced and secreted by epithelial cells onto which these cells can then adhere (Fidler et al., 2017). Once in place, the basal lamina expanded affordance landscapes once again, now permitting developmental systems to produce more mechanically stable and persistent architectures such as elongated bodies, appendages, permanent folds, and ridges, which in turn formed critical substrate for subsequent rounds of developmental innovation (Newman, 2016). Thus, while an agency perspective on evolvability clearly acknowledges the significance of key additions to the genetic tool kit of developmental systems during evolution as key expansions of their affordance landscapes, it also directs attention to the roles played by developmental systems themselves in putting such additions *to use* in ways that facilitate further innovation and diversification while also conducing to the ends of survival.

4 | WHERE AN AGENCY PERSPECTIVE IS UNLIKELY TO BE USEFUL

In the above sections, we emphasized the value of an agency perspective in highlighting the role organisms and their component parts can play in their own development, maintenance, and adaptation to novel

conditions, and how acknowledging agential dynamics can stimulate research programs in directions that are currently underdeveloped or unrecognized. Yet other concepts central to evolutionary developmental biology may be less likely to benefit from an agency perspective, even though the terminology commonly used in reference to them may superficially suggest otherwise; the following examples may aid in clarifying what agency is and where it resides by highlighting where it does not.

For example, gene regulatory networks (GRNs) and their evolution are commonly described as driving or enabling phenotype expression and modification, suggesting an active and enabling role in organismal innovation and diversification (Feigin et al., 2022; Verd et al., 2019). Yet, their relevance in developmental evolution notwithstanding, gene regulatory networks are first and foremost *abstractions* of interactions taking place across a variety of levels of biological organization, from regulatory elements residing on chromosomes to the transcription factors binding them, from posttranslational modifications of protein products to protein–protein interactions, etc. Moreover, the boundaries of GRNs are typically entirely operationally defined by the scientists studying them relative to a particular developmental stage, time, trait, and/or level of technology able to detect and resolve them. As such, GRNs do not possess the “distinctive integrated wholeness or global integrity” (Skewes & Hooker, 2009) that a cell does, or a whole organism, or perhaps even an ant colony. While some of the interactions depicted within a GRN may possess the ability to stabilize and reinforce themselves, and make some future interactions more likely than others, that degree of agency does not reside in the GRN *per se*, but in the tissue-level or cellular structures that carry out these regulatory interactions (Walsh, 2015). Thus, GRNs lack the ability to satisfy the agency criteria set out at the beginning of this essay, that is, to *participate in their own development, maintenance, and function by regulating their own structures and activities in response to the conditions they encounter* (Sultan et al., 2022). Rather than being themselves the loci of agency, the regulatory interactions subsumed under a GRN are more akin to parts of the repertoire of the agent(s) that they reside within.

Norms of reaction, likewise, have frequently been given the attribute of driving organismal development and diversification (Murren et al., 2015; Scheiner, 1993; Via et al., 1995). Yet like GRNs discussed above, norms of reaction are statistical abstractions which establish a correspondence between a given phenotype produced by a given genotype or individual in response to a particular environment experienced, but leave undescribed the cellular-, organ system-, and signal-transduction machinery necessary to establish this correspondence. Reaction

norms therefore exist because of the biological agency of organisms and their component parts, not the other way around. By themselves norms of reaction cannot “act on their own behalf,” thus rather than being a locus of agency, reaction norms are a product of it.

Similar considerations will have to apply to other conceptual abstractions of interactions within living systems, such as *metabolic networks*, *allometries*, or *trait variance/covariance matrices*. All share that they depict critically important biological relationships that possess the ability to structure and bias the outcomes of development, the type of phenotypic variation visible to selection, and evolutionary trajectories; thus, they rightfully deserve attention in the study of developmental evolution. Yet the causes underlying these phenomena do not reside within their depictions, and so nuancing the language we use to attribute causation and goal-directed activity in development and evolution may benefit future intellectual exchanges in our field.

5 | OBJECTCY VERSUS AGENCY IN EVO DEVO—DO WE NEED NEW TERMINOLOGY?

Vitalism is an umbrella term for more or less radical perspectives that all share the premise that “living organisms are fundamentally different from nonliving entities because they contain some nonphysical element or are governed by different principles than are inanimate things” (Bechtel & Williamson, 1998). Put another way, according to vitalists, reductionist explanations based on matter and forces are insufficient to understand organismal development, function, and form. Vitalism gained traction among biologists in the 18th and 19th centuries, such as the embryologist Hans Driesch and the chemist and microbiologist Louis Pasteur (Deichmann, 2022). Yet its appeal to nonmaterial forces and postulation of a *vital spark* or *élan vital* to distinguish living from nonliving entities quickly placed it in a metaphysical realm rapidly at odds with subsequent key discoveries in embryology, biochemistry, and molecular biology. Today these flavors of vitalism are rightfully rejected as pseudoscience.

Vitalism emerged as a countermovement to a view of living systems as *mere machines* whose form and function can be explained as one would explain a regular man-made machine—through detailed knowledge of the identity of and interactions among component parts. Dating back to Descartes' philosophy of the first half of the 17th century, this perspective remains not just alive but in fact dominant in contemporary evolutionary

developmental biology through the application of strict reductionist approaches toward understanding the genesis of biological diversity. This approach has been, without a doubt, immensely productive. Yet it has also encountered persistent challenges, for instance with respect to our understanding of the origins of phenotypic variation, the nature of inheritance, and the origins of novel complex traits and major transitions in evolution (Table 3; reviewed in Sultan et al., 2022; see also Laland et al., 2015). It is here that agency proponents see a valuable opportunity for an agency perspective not to replace, but to complement existing approaches by emphasizing additional sources of causation that are otherwise overlooked by more reductionist approaches (Table 3; Table 2; see also Baedke et al., 2021). Agency is thus not an appeal to immaterialism, instead it is a call to recognize developmental systems at various levels of organization as integrated wholes that influence both the structure and function of their components parts, alongside their external conditions. These influences have a material basis that can be studied empirically and have effects on component parts and conditions that can be quantified and evaluated. More generally, the explanatory value of an agency perspective can be quantitatively assessed by measuring the difference made by hypothesized agential behaviors or dynamics in driving particular biological phenomena, for instance, through the experimental removal of presumed agential behavior, be it the communication between tissues codeveloping to give rise to the same trait (as discussed above for teeth: Hunter & Jernvall, 1995; Wilson et al., 2012), organisms' ability to construct their surrounding niche (as in dung beetle larvae: Schwab et al., 2016, 2017) or the synergistic interactions between hosts and their microbial partners in organogenesis (bobtail squid: McFall-Ngai, 2014).

A growing tradition of work in biological theory and the philosophy of biology has encouraged us to consider that agential concepts, rather than being simply convenient colloquial short-hand, can in fact serve key epistemic functions in our science (Barandiaran et al., 2009; Fulda, 2017; Uller, 2023; Walsh, 2015, 2018). Uller (2023) in particular has argued that the concept of agency can play three distinct epistemic roles: (1) promoting the intelligibility of biological theories, (2) structuring investigations according to specific criteria of explanatory sufficiency, or more radically, (3) offering an additional type of explanation for biological processes including development and evolutionary change, as explicated in Walsh (2015, 2021). We think that the examples in the body of this essay illustrate that in research on key foci of evo devo, agential thinking *already implicitly* colors and informs our understanding of many biological processes, even though it may not formally be recognized by the

TABLE 3 Examples of key concepts and knowledge gaps in evo devo that can be extended through an agency perspective

Key concept or knowledge gap	Perspectives contributed or emphasized by an agency perspective
Phenotype determination	The causal significance of genes and genetic variation in phenotype determination is without doubt, yet by itself has emerged as often insufficient to explain phenotypic outcomes in development. An agency perspective emphasizes an understanding of developmental systems as having evolved to interpret their genetic information in a context-dependent manner, actively adjusting the usage of their component parts (including their genomes) to suit changing conditions in pursuit of their system-level objectives.
Inheritance and heritability	Parents pass on to their offspring not just genes, but also stored transcripts, hormones, nutrients, microbiota, various egg and seed components, territories, knowledge, etc. The roles played by such parental effects in development and evolution is now broadly recognized. Less recognized is the role played by parents in creating external (e.g., through niche construction) and developmental environments (e.g., through transgenerational plasticity) which, bequeathed upon offspring, influence developmental outcomes and (selectable) phenotypic variation. An agency perspective helps emphasize these additional contributions to heritable variation.
Organism-environment fit (adaptation)	Evo devo views developmental mechanisms as providing a proximate understanding of adaptive trait formation, as shaped by an external, selective environment separate from the developmental system itself. In the absence of the developmental system, the environment still exists. An agency perspective instead views developmental systems as active co-constructors of developmental environments, whether they manifest within the boundaries of the organism (e.g., in organogenesis) or outside (e.g., in niche construction, and reciprocal constitution of the <i>experienced</i> environment). Viewed this way, the functional repertoire and environmental conditions of a developmental system continually co-constitute and determine each other both within a life cycle and across generations.
Origins of complex novel traits	The origin of complex novel traits in development and evolution remains poorly understood. An agency perspective highlights (i) the self-constructing, self-maintaining, and self-adjusting nature of developmental systems, (ii) the reciprocal interactions between developmental processes, developmental environments, and developmental outputs, and (iii) the possibility that the development of novel phenotype may precede rather follow changes in genotype. As such an agency perspective complements traditional gene-centric approaches to novelty by highlighting the innovative capacities inherent within developmental systems.
Major transitions in evolution	Many major transitions in evolution involved the creation of novel evolutionary units (e.g., the first eukaryotic cell, multicellularity, eusociality); an agency perspective emphasizes how this process creates higher-order organization and affordances not reflected in earlier stages or in component parts alone.

term “agency” (role 1). Furthermore, many of the explanatory gaps left by traditional evolutionary thinking that have been addressed by evo devo approaches also rely on adjusted criteria of explanatory adequacy, shifting away from traditional dogmas of evolutionary theory and relying on new conceptions of biological interactions (e.g., niche construction; role 2). Perhaps it is no surprise then, if the first two epistemic roles can be seen working “behind the scenes” to various degrees throughout evolutionary developmental biology, that the next step to properly consider as a field is the possible utility of role 3, that is, whether goal-directed activity can be cited as legitimate “difference-maker” in developmental evolution and can be incorporated into our *explanantia* of how living systems function and change over time. Some workers (Levin, 2019, 2022) are already taking seriously

the consideration that if goal-directedness is an inherent feature of how living systems are organized, then this organization may impose a particular order in the world that affects biological processes in ways we can study and use to inform our understanding of the processes and living systems we investigate.

It is also clear, however, that the degree to which an agency perspective may add this explanatory power in evolutionary developmental biology and allied fields very much remains to be fully determined. A primary objective will have to be to critically and empirically examine part-whole dynamics across multiple levels of biological organization within living systems to assess at which level(s) an agency perspective may offer the most explanatory power. Assuming for the moment that an agency perspective indeed does prove useful, does

employing it necessitate the use of agency *terminology*? After all, a lot of agency thinking can be applied—and in fact often appears *implied*—using language we already have available to us in evo devo. Here we believe that being *compatible with* existing language is not necessarily the same as being *part of* that language and the mindset that goes with it, and that *agency*, *agential dynamics*, and *affordances* may indeed prove useful terms to emphasize particular sources of causation. In partial contrast, *goal- or end-orientedness*, let alone *purpose* will require discipline in order to avoid encroachment by colloquial overtones and to use them strictly to describe what an agent in question is acting toward. Yet with its firm emphasis on the self-constructing, self-regulating, and self-adjusting nature of developmental systems we feel that an agency perspective has the potential to contribute substantively to the explanatory portfolio of 21st century evolutionary developmental biology.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no data sets were generated or analysed during the current study.

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