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Evo-Devo: A Science of Dispositions

Christopher J. Austin

Abstract

Evolutionary developmental biology (evo-devo) represents a paradigm shift in the understanding of the ontogenesis and evolutionary progression of the denizens of the natural world. Given the empirical successes of the evo-devo framework, and its now widespread acceptance, a timely and important task for the philosophy of biology is to critically discern the ontological commitments of that framework and assess whether and to what extent our current metaphysical models are able to accommodate them. In this paper, I argue that one particular model is a natural fit: an ontology of *dispositional properties* coherently and adequately captures the crucial casual-*cum*-explanatory role that the fundamental elements of evo-devo play within that framework.

The recent advent of evolutionary developmental biology (evo-devo) has ushered in a novel conception of the organism and its place in the biological world, one which has substantially built upon the theoretical framework of the Modern Synthesis by offering new perspectives on the nature of both *ontogenesis* and *evolution*. In contrast to the crude reductionism of genocentrism, evo-devo places emergent, epigenetic, environmentally-sensitive causal factors at the explanatory centre of morphogenesis. And although population-level, allele frequency-based explanations are no doubt explanatory with respect to the evolutionary process of natural selection, evo-devo's unique focus on the developmental mechanisms which intrinsically constrain and shape morphology paints a colourful and powerful new picture of that process. Given the potential *gestalt*-shift inherent in the framework of evo-devo, it is instructive now to reflect on whether and to what extent our current philosophical concepts are able to coherently and adequately model that framework and its accompanying empirical and experimental data – a question that has yet to be given serious philosophical attention.[1] What I want to suggest is that capturing the *ontology* of evo-devo is a task that ought to be performed by putting to service the contemporary philosophical framework of *dispositional properties*. My claim is that the integrated causal-*cum*-explanatory role that the elements central to the framework of evo-devo play with respect to ontogenesis and evolutionary progression is one that is adequately and sufficiently captured by the theoretical nature of dispositional properties. Evo-devo is, or so I will argue, a science of dispositions.

1. A Contemporary Conception of Dispositional Properties

In order to substantiate that claim, we'll need to first have a firm grip on the *nature* of dispositional properties. Of course, given the size of the contemporary literature on dispositions, there is quite a lot of variation in the particulars here – but rather than comparing and contrasting the merits of various specific accounts, what I want to do below is to draw out a few of what I consider the most important and defining features of these properties, ones which I think, for all practical purposes, function as the "lowest common denominator" features of a wide-variety of more specialised accounts.[2] Getting clear on

[1] Though there has been some interesting recent work on applying a broadly Aristotelian metaphysics of the sort on offer here to the realm of biology – see Walsh (2006) and Boulter (2012).
[2] Of course, this is only a general overview, or summation which itself takes in to account a vast amount of recent literature – readers are encouraged to consult the accompanying footnotes for further details and discussion.

these core features is a necessary first step, for these features, as I will go on to argue, are precisely the ones which we find in the properties which comprise the core ontology of evo-devo.

Dispositional properties are commonly understood as intrinsically *causal* properties, responsible for the production of particular states of affairs ('manifestation states') upon the occurrence of another precursive state of affairs ('stimulus conditions'). For dispositional realists, the *causal* nature of these properties is often characterised in contrast with 'categorical' properties: while the latter are taken to be intrinsically *inert*, being supposedly imbued with their causal *oomph* in virtue of participating in higher-order natural laws (as exhibited in Armstrong 1997), or else in virtue of their relation to sets of (abstract or concrete) possible worlds (as exhibited in Lewis 1986), dispositional realists have traditionally understood those properties to be the real sources of *power* in the world in virtue of their being *intrinsically* causal.[3] They are so in virtue of their acting as ontological "switches" of sorts, causally mediating the influence of the latter states to bring about the former ones. In the philosophy of physics for instance, the property 'negative charge' is commonly taken to be a dispositional property – when its bearers meet a like-charged particle (its stimulus condition), they repel with a certain momentum (its manifestation state). This is a causal role, according to dispositional realists, which is *intrinsic*, or "of the nature" of 'negative charge'. Importantly, while dispositional properties in "fundamental" ontologies may be realised by solitary material elements, most of these properties are realised by an entire system, comprised of a complex network of interacting elements: whenever, upon the occurrence of a particular set of conditions, such a network initiates a series of step-wise internodal causal connectives which lead to its production of a particular end state, that network realises a dispositional property.[4]

In this way, dispositional properties are *functionally defined* with respect to their specific stimulus/manifestation pairs: whatever performs the function of causally mediating the occurrence of a particular manifestation state upon the occurrence of a particular stimulus conditions *is* an instance of the dispositional property defined by that specific pair.[5] It's important to note that when we designate a structure as an instance of a functionally defined property, we are operating at a certain level of abstraction, eschewing the more precise details of the causal pathway by which that function is carried out and focusing instead on the general end states between which that pathway runs.[6] Thus, when a system realises a particular dispositional property, the pathway from 'stimulus' to 'manifestation' often "reaches over" a multi-stage causal gap – and we are afforded evidence of the existence of such properties when these gaps are reliably and repeatedly bridged upon the occurrence of a set of appropriate conditions.

In this abstraction, we not only shift the focus away from the *particulars* of the pathway between those end states – that is, the various links comprising the causal chain between those states – but also the various particular ways in which that pathway might be traversed. And given that there is a multitude of distinct instances of a particular type of stimulus condition which will lead to a multitude of distinct instances of a particular type of manifestation state, it is generally accepted that a dispositional property

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[3] For some good representations of this ideological contrast, see Ellis (2001), Bird (2007), Chakravartty (2007), Mumford & Anjum (2011), Vetter (2015).

[4] Note that the philosopher's paragon of dispositionality – the property of 'fragility' – is realised (in most cases) by a complex microstructure, and 'breaking' is in fact a complex, multi-stage process featuring the aligning of various micro-events that represent decreasing degrees of structural integrity.

[5] Understanding dispositions to be 'functionally individuated' arose from their initial attempted reduction to subjunctive conditionals (especially counterfactuals), prominent in Quine (1974) and later, in Lewis' (1997) 'simple conditional analysis'. However, even for the contemporary dispositional realist who decisively eschews this reductionist project, those properties are nevertheless understood as being essentially characterised functionally, roughly in terms of their 'antecedents' and 'consequents'.

[6] Oftentimes in the process of scientific discovery, operating at that level of abstraction is obligatory, as we have yet to uncover the underlying mechanistic configurations which causally connect pairs of end-states. Arguably, our ability to identify causal structures at this level is a prerequisite for the success of that process, given that scientific progress often consists in the discovery of such mechanisms.

must be defined by two states which are *determinables*, not *determinates*: for a system realising a disposition is capable of producing an extensive, gradient-like range of quantitatively distinct manifestation states – each being a particular instance of its manifestation *type* – in response to its receiving a variety of specific stimulus inputs. In this way, the *activity* of dispositional properties is best described functionally, as their existence establishes a functional relation between a set of input values, or particular determinate instances of determinable stimulus conditions, and a set of output values, or particular determinate instances of determinable manifestation states.[7] To put it in another, perhaps more careful way: dispositional properties are responsible for establishing a causal link of *functional co-variance of state-values* between two determinable end states.[8]

Because they are responsible for the reliable and repeatable production of particular end states, dispositions are commonly understood as *teleological*, *goal-directed* properties – ones which are causally "directed toward", or *for* those ends. Although the "directedness" of these properties has at times been seen as an unwanted appropriation of an unviable form of physical intentionality, or as requiring those properties to bear proper relations to non-existent states of affairs, for the dispositional realist, nothing so mysterious is happening here.[9] As these are properties *defined* by what they *do*, a dispositional property's having a particular 'goal' of bringing about a specific event is simply tantamount to it being the property primarily (causally) responsible for bringing that event about (under certain circumstances); thus the reader may substitute Mayr's (1992) 'teleonomic' for 'teleological' here, if one understands dispositions as intrinsically "programmed" *via* their functional role. For a certain class of dispositional properties however, their teleological character is exhibited in a stronger sense, in that the systems which realise these properties are oftentimes capable of exhibiting the phenomenon of *persistence*, maintaining the production of a particular end state "as a result of changes occurring in the system that compensate for any disturbances taking place (provided these are not too great) either within or [external] to the system, disturbances which, were there no compensating changes elsewhere, would prevent the realisation of the [end state]".[10] This process of "course correcting" towards a particular end state is characteristic of the causal process initiated and mediated by dispositional properties present in biological systems, and it is one which occurs in a systematic and non-accidental fashion, over a wide range of perturbations.[11]

On account of both the *functional* nature of these properties – with respect both to their individuation and their activity – and their goal-directedness, dispositions are often categorised as *multiply realisable* properties, being importantly "disassociated" from the particularities of the underlying causal systems which comprise them.[12] Because they are functionally individuated, *whichever* such system reliably and repeatedly traverses their particular pathway from stimulus to manifestation constitutes the 'realisation' of those properties – thus, many distinct underlying systems may realise one and the same dispositional property. Furthermore, due to their functional activity (captured by their establishing a relation of causal co-variance of state-values), no *particular* causal pathway through any one of those

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[7] This fact is what has come to be known as dispositions being "multi-track". See Martin (2008), Manley and Wasserman (2008), and Vetter (2013) for fuller discussions.
[8] This is the relation that Lewis (2000: 190) called 'causal influence', which is the foundation of Woodward's (2003; 2010) influential 'manipulation' theory of causation.
[9] That dispositional properties do exhibit a type of 'physical intentionality' was originally defended by Place (1996), and more recently by Molnar (2003) and Mumford & Anjum (2011). For a prominent critique, see Armstrong (1997).
[10] Nagel (1977: 272)
[11] See Walsh (2012), and Mayr (1992)
[12] The multiple realisability of dispositions is often expressed by defining them as properties which have their 'causal roles' *essentially*, thus distinguishing them from their 'categorical bases' – see Ellis (2001), Cross (2005), and Bird (2007). This conception has often been utilised in arguments against their genuine causal efficacy - though see McKitrick (2005) for a detailed reply to these sorts of criticisms.

distinct systems *defines* a particular dispositional property – thus, *many* distinct underlying causal graphs of the same system will realise one and the same dispositional property. The same point applies with respect to their goal-directedness and the accompanying phenomenon of persistence, due to the underlying causal architecture which realises a particular dispositional property being capable of various "course-correcting" alterations. Dispositions are therefore in this sense *explanatorily emergent* – although they may be ontologically "nothing over and above" the various causal networks (and variations thereof) which realise them, they cannot be strictly *identified* with any particular such network.[13]

2. The Central Ontology of Evo-Devo: Developmental Modules

Now that we've got a grip on the core features of dispositional properties – their functional individuation and activity, their goal-directedness, and their multiple realisability – it's time to examine the precise place at which I'd like to put them to work in a biological context. My claim is that these properties are present in what I consider the central ontological elements of evo-devo – 'developmental modules'. In order to show that this is indeed the case, let us look at what developmental modules are, and what role they play within evo-devo.

The foundation of the evo-devo framework consists in the theoretical integration of the principles of ontogenesis with the process of natural selection: in this framework, understanding the causal structure of organismal *development* is central to understanding the mechanism of *evolution*. Because the course of evolution is charted *via* the phylogenetic tracing of the appearance of novel morphological structures among populations, the discipline of evo-devo is concerned with specifying what the causal ground of particular morphological structures is, as well as the mechanisms by which novelty among such structures arises. Although the specific answers to these questions will be different in different cases, the general picture that evo-devo paints is that the ontogenesis of organisms is ontologically divided in to discrete sets of systems – developmental modules - each responsible for the development of a particular (structural) morphological feature (e.g. eyes, fins, wings, etc.) - and that it is these systems' intrinsic generative capacities which are causally responsible for providing the morphological novelty which subsequently shapes the evolutionary (read: selective) landscape.

Developmental modules are often epistemically identified with respect to particular *genetic regulatory networks* (GRNs) which consist of a hierarchical set of genes, their transcriptional products, their cross-regulatory interactions, and their interactions with epigenetic factors, whose "intrinsic behaviours and functional interactions yield a mechanistic explanation of an identifiable developmental process or transformation".[14] The GRNs which are taken to comprise developmental modules contain multiple interacting sub-circuits, each of which play distinct roles within the overall network with respect to the production of its associated morphological structure – minimally, each module consists of a sub-circuit whose products exert (spatial and temporal) regulatory control over the expression of a downstream target gene battery whose products specify cell-type fate, and are thus responsible for the actual "building" of a particular morphological structure.[15] These sub-systems function in a unified fashion with respect to the production of discrete morphological features in virtue of their particularly high degree of internal integration *via* the inter-module functional cooperation of their parts – that is, *via* the tightly-knit regulatory domain established by their elements' transcription factors, corresponding *cis*-regulatory sites and their resultant signalling cascade (Erwin & Davidson 2009), as evidenced by the analysis of their expression patterns (Raff & Sly 2000).

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[13] For a good discussion of 'explanatory' vs. 'ontological' emergence, see Walsh (2013).
[14] Von Dassow & Munro (1999: 313)
[15] The former sub-circuit has been recently referred to as a network 'kernel' (Davidson & Erwin 2006), 'core regulatory network' (Graf & Enver 2009), or 'character identity network' (Wagner 2007; 2014)

On account of these networks' being highly internally integrated, they are also highly *robust*, such that intra-species mutational variations among their component elements, and epigenetic variations on their regulatory structure generally have little to no effect on their generative competence with respect to their resultant morphological structure (Davidson 2001; Carroll 2008; Wagner & Lynch 2010). Typically, these networks are robust not merely in virtue of simply possessing a number of 'redundant' elements (gained perhaps through various duplication events), but on account of their ability to maintain their generative integrity (with respect to their associated morphological structure) by "re-wiring" their regulatory architecture such that certain non-isomorphic elements (elements that have distinct structural compositions) are able to become isofunctional (playing the same function within the system) – this is the phenomenon of *degeneracy*, now thought to be ubiquitous in the biological realm (Greenspan 2001; Mason 2010), and a *sine quo non* of developmental systems' ability to evolve (Edelman & Gally 2001; Whitacre & Bender 2010).[16]

Working in concert, these integrated and robust sub-systems compose the regulatory architecture of individual developmental modules which are causally responsible for the specified production of individual morphological structures within the ontogenesis of a particular taxon, evidence for which is gathered from ectopic expression experiments[17], or else by the principled decomposition of genotype-phenotype mappings.[18] They are able to do so because, being highly internally integrated and generatively robust, these modules are likewise 'generatively entrenched' at very crucial points within the developmental "program" (Raff 1996; Schank & Wimsatt 2000), functioning as informational intermediaries situated between a set of embryonically internal intra- and inter-cellular upstream signals and the downstream expression of a multitude of proteins that determine cellular differentiation and morphogenetic competence within a particular 'morphogenetic field'. In this way, developmental modules form the bottleneck of the 'developmental hourglass' where the sands of a wide variety of input signals are sifted through their narrow gates in a specialised fall among a diverse set of target genes (Galis & Metz 2001; Kalinka *et al.* 2010). As mediators of the flow of regulatory information, developmental modules operate to effectively translate "…the 'abstract' positional information of early development into specific developmental individuality by controlling character-specific gene expression".[19] It is because they function as crucial causal fulcrums in the process of the ontogenesis of particular morphogenetic structures that developmental modules are central to the discipline of evo-devo: they are the naturally dissectible, discrete units which direct the development of organisms.

This central developmental position which these modules occupy not only grants them a certain *stability*, captured by their generative robustness as described above, but also a corresponding and complementary degree of *flexibility* – for the nature of their constitutive regulatory architecture, and their occupation of the developmental bottleneck of ontogenesis allows them to function as an important ground of *variation* with respect to their associated phenotypic traits. Indeed, one of the fundamental posits of the evo-devo framework is the existence of stable developmental resources whose *inherent plasticity* is the causal ground of such variation.[20] In a notable shift from the neo-Darwinian perspective,

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[16] This phenomenon is the ground of Dynamic Systems Theory's conceptualisation of the morphological structures associated with such modules as 'attractor states' which carve-out a wide, 'meta-network' basin in the topology of an organism's epigenetic landscape. See §4.
[17] This technique was especially prominent in Halder *et al.* (1995); For a general contemporary review in a particular case, see Ashery-Padan & Gruss (2001).
[18] See Wagner & Altenberg (1996)
[19] Wagner (2014: 98)
[20] The extreme conservation of HOX-genes (and their associated networks) within the animal kingdom is perhaps the most prominent, and extreme instance of this general phenomenon. See Carroll, Grenier, and Weatherbee (2001), and Wilkins (2002) for excellent summaries.

evo-devo favours a 'structuralist' approach[21], wherein intra-kind phenotypic diversity is understood to be underwritten by a common set of developmental resources which themselves constrain and specify the variability of their associated morphological structures according to their own "generative rules".[22]

For we now know that the morphological structure produced by a single developmental module, being underwritten by a particular genetic regulatory network, is capable of a wide variety of intra- and inter-cellular environmentally induced phenotypic variation - this is the phenomenon of *phenotypic plasticity*, attested to by the reality (read: quantifiability) of *reaction norms* (Pigliucci 2001; West-Eberhard 2003). As we have seen, on account of the unique developmental position of these modules, they function as causal mediators of sorts, interpreting cascades of upstream "inputs" into downstream "outputs" *via* their production of transcription factors which enact regulatory control at the *cis*-regulatory sites of downstream target genes (Gurdon & Bourillot 2001; Tabata 2001; Mann & Carroll 2002). As a result, heterochronical and heteropical alterations in upstream signalling results in downstream qualitative alterations (shape, size, pigmentation, etc.) of the phenotypic character of the structure generated by that module (Schlichting & Smith 2002; Aubin-Horth & Renn 2009).

Thus, the morphological structure generatively specified by a single developmental module consists of a definite range of variations on that structure – specifying a demarcated *morphospace* of these permutations – and so must in a certain sense be "defined by its variational tendencies"[23], or its set of "developmental trajectories, [correlated with] the particular set of environmental conditions to which [it] is exposed"[24], in such a way that it represents, as Love (2009: 57) puts it, "an idealised type…constructed from ample and acknowledged variation".[25] The discovery that the intra-species *stability* of developmental modules undergirds the ability for phenotypic *flexibility* puts those modules at the centre of the evo-devo project – for if developmental *constraints* are best thought of as limiting cases of developmental *possibilities*, these modules and their properties may be the ontological basis for *evolvability*, as the raw material upon which the various processes of natural selection operate (Kirschner & Gerhart 2006; Brigandt 2007; Brakefield 2011; McCune & Schimenti 2012).

3. Development, Dispositionally

As I have shown, according to the theoretical framework of evo-devo, developmental modules occupy an importantly privileged position in virtue of their playing an integrated causal-*cum*-explanatory role with respect to the ontogenesis of organisms *and* the process of evolution. The claim of this paper, and what I shall now show, is that this is a role adequately and sufficiently captured by the theoretical nature of dispositional properties – namely, their functional individuation and activity, their multiple realisability, and their goal-directedness.

More specifically, the claim I want to make is that *developmental modules are dispositional properties*.[26] As we have seen, the developmental modules of evo-devo are causally responsible for the specified production of their associated morphological structures in developing organisms in virtue of their serving as a functional bridge between intra- and inter-cellular signalling and specific downstream genetic expression patterns which initiate particularised developmental pathways resulting in the formation of

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[21] See Amundson (2005) for an excellent in-depth discussion of the 'structuralist' paradigm and its relation to that of the Modern Synthesis.
[22] Cf. Müller (2008)
[23] Von Dassow & Munro (1999: 316)
[24] Pigliucci *et al.* (1996: 81)
[25] In developmental systems theory, this is modeled by stating that "equivalent [modules] share an equivalent topology of their phase and configuration spaces" (Jaeger & Sharpe 2014: 73). See §4.
[26] It should be noted that while this general claim has been made before – namely, by Wagner (2000) and Eble (2005)– , it has yet to receive a philosophically precise treatment.

those structures. These modules therefore function as ontological "switches", causally mediating the influence of certain activating conditions to produce particular states of affairs: given the appropriate stimulus conditions, developmental modules reliably and repeatable produce particular end states. Thus, these modules' characteristic activity is appropriately "higher-order", after the fashion of dispositional properties – that is, at a certain level of abstraction, away from the various complexities of the aforementioned particularities: operating at a high 'causality horizon' (Salazar-Ciudad & Jernvall 2013), the important activity of these modules can be usefully modelled with respect to their mediating the "reach" over a wide, multi-stage causal gap from a particular set of stimuli toward a particular end state.

Recall that on account of their aforementioned roles as causal mediators between upstream signalling pathways and downstream target genes, the generative competence of developmental modules consists not only in their being responsible for the intra-specific development of a particular morphological structure, but also in their being responsible for various intra-specific (qualitative and quantitative) permutations on that structure. Because the causal pathway between upstream intra- and inter-cellular signals and downstream "trait-building" genes is one which can be traversed in many distinct ways (according to the variability in those upstream signals), a single module must be conceptualised as responsible for the specified production of an entire *reaction norm* consisting of a wide range of environmentally correlated variations on its associated morphological structure, defining a *morphospace* with respect to that structure. Thus, in any particular instance, in "interpreting" specific collections of a generalised class of upstream positional signals into specific forms of a generalised downstream morphogenetic state, these modules are responsible for mediating the causal co-variance of *determinate* state-values between two *determinable* variables. Accordingly, their *functional activity* in this respect ensures that no single developmental module is capable of being *defined* by any *particular* causal pathway through any one of its distinct upstream-downstream mappings.

Indeed, in the contemporary literature, it is the performance of this important higher-order *functional role* which has taken centre stage in the study of developmental modules. Because attempting to define any particular module with a *specific* set of genetic elements has proven an unfruitful endeavour, the focus has largely shifted to conceptualising these modules as centres of *generative*, rather than genetic *specificity* (Rieppel 2005; Love 2009; Brigdandt 2009). For while it's undeniable that tracing the particularities of repeated genetic architectural themes throughout evolutionary time has led to incredibly important insights in establishing molecular-based phylogenetic lineages, the aforementioned phenomenon of *degenerative robustness* ensures the existence of multiple variations in the regulatory architecture responsible for the production of a single, specific morphological structure.[27] In other words, over time, and in successive generations, the specific generative role once played by a particular complex of genetic elements in a particular regulatory configuration becomes *autonomised*, gaining a kind of (at least partial) independence from its original underlying architecture.[28]

As a consequence of this, any particular developmental module must be conceptually "disassociated" from any single, specific underlying networked mechanism and its constitutive processes: though for every particular module (and its associated morphological structure) we may be able to experimentally demarcate a meta-network of such mechanisms, we cannot strictly identify that module with any *single* member of that meta-network. I suggest then that a natural way to philosophically characterise the "hierarchical disconnect" (Ereshefsky 2012) between generative *function* and genetic *structure* that results from the degenerative robustness of developmental systems is *via* the metaphysical distinction between *disposition* and *realiser*. In other words, the fact that many *distinct* underlying regulatory

[27] It's worth mentioning that some interesting and exciting new work suggests that there may be "core" GRNs which function as evolutionarily conserved sub-system bases of developmental modules; see Wagner (2007; 2014), Davidson & Erwin (2006), and Graf & Enver (2009).
[28] See Müller & Newman (1999), Müller (2003), and Hall (2003) for particular examples.

genomic structures lead reliably and repeatedly to the *same* 'epigenetic valley' in intra-specific morphospace, and thus play the *same* functional role with respect to the production of a particular morphological trait-type, suggests that these varied and distinct structures all instantiate a common higher-order, functionally defined property – that is, a single, *multiply realised* dispositional property. Thus, as Rieppel (2005: 25) puts it, it seems that "…the best way to capture 'developmental modules' is as homeostatic property cluster natural kinds with causal properties that are instantiated by individuals" which perform a generative function "…through the tokens that instantiate their causal properties and propensities".[29]

If then we understand developmental modules as multiply realised dispositional properties which are *functionally individuated* with respect to their end-states (that is, the set of variationally-related morphological structures comprising its morphospace), we can conceptualise the ability of their underlying genetic networks to "re-wire" their regulatory architecture in the face of perturbation in order to main their generative integrity as a display of the dispositional, teleological phenomenon of *persistence*. Importantly, this is a goal-directedness with respect to a causal end-state, *not* a historical function, and thus represents a phenomenon orthogonal to the teleosemanticism now prevalent in the adapationist paradigm[30]: modelling this phenomenon does not require any theoretical measurement of these networks' storied, selected-effect fitness-contributions, but rather an appeal to the univocal *causal focus* of large genomic 'meta-networks' comprising wide ranges of intra-specific mutational and regulatory variation (Newman *et al.* 2006; Carroll 2008; Wagner & Lynch 2010). Thus, if we conceptualise dispositional modules *as dispositional properties*, we can understand the association of a particular module with a demarcated set of meta-networks as a consequence of the teleological activity of their commonly realised, higher-order dispositional property.[31]

All of this goes to show that the main pillars of the conceptual framework provided by an ontology of dispositional properties – functional individuation and activity, multiple realisability, and goal-directedness – are quite naturally applicable in the contemporary realm of evolutionary developmental biology. Importantly however, the central ontological elements of evo-devo are not merely plausibly amenable to a general dispositional redescription - as I hope is now clear, the integral theoretical role that developmental modules play within evo-devo *just is* a dispositional role. For serving as the functionally individuated, causally robust ground of determinable state co-variance in virtue of occupying a privileged position as the functional intermediaries connecting the wider, top and bottom ends of the developmental bottleneck of ontogenesis, and so being generatively responsible for the downstream production of a demarcated structural morphospace is at the core of developmental modules' ability to effectively provide a platform for both developmental and evolutionary stability *and* variation.

4. A Powerful Payoff: The Prowess of Higher-Order Holism

Thus far I have argued that the metaphysical framework of dispositional properties is an empirically adequate one, inherently capable of accurately capturing the relevant phenomenon at the conceptual core

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[29] Cf. Boyd (1999) and Wilson *et al.* (2007).

[30] Cf. Winther (2005), and Von Dassow & Munro (1999)

[31] The claim that developmental modules *are* dispositional properties is likely to cause some pause, as 'module' naturally functions as an *entity*-term, rather than a *property*-term. While I'm sympathetic to this reticence, consider that the above discussion is meant to motivate the idea that, due to the genetic and regulatory variation in the entities which are causally responsible for the generation of morphological structures over both developmental and evolutionary time-scales, 'modules' must be defined at an ontologically "higher-level" than those entities. With that in mind, conceptualising 'modules' as dispositional *properties* that are variably realized by those variously distinct collections of entities seems, within the current state of the existing literature, the easiest and most economical way to accommodate that idea. That said, if the reader wishes to replace 'dispositional property' with 'dispositional entity', I can't see that anything essential will be lost in translation.

of the theoretical project of evo-devo. Importantly of course, it's one thing for a proposed framework to *save* the phenomenon, and quite another for it to *explain* it. And while the former task is certainly a prerequisite for its plausibility, the extent to which it performs the latter directly apprises its theoretical utility, and thus often, its desirability. With that in mind, what I want to now show is the way in which the conceptual framework of dispositional properties performs that latter task in virtue of its natural capacity to serve as the metaphysical foundation of a few now prominent conceptual tools in our wider understanding of the causal architecture of developmental sub-systems. The explanatory power of that framework, I suggest, consists in the fact that the positing of the presence of its uniquely natured properties within those sub-systems functions as a sufficiently robust explanation for the theoretical viability of a number of now prominent models of those systems' causal structure. This is an explanatory prowess revealed, as it were, *transcendentally*, in that the distinctive features of that framework's ontology effectively function as the metaphysical preconditions for the tenability of those models.

To illustrate this, I want to focus on a central feature of the nature of dispositional properties as explicated above – their *functional individuation*. Recall that dispositions are metaphysically individuated according to a particular 'causal role' in such a way that the existence of any specific disposition *just is* a matter of some element, or complex of elements establishing a specified link of functional co-variance of state-values between two determinable end states. Accordingly, as "higher-order" properties, dispositions are *multiply realisable* in such a way that two systems comprised of distinct sets of elements can realise one and the *same* dispositional property in virtue of their performing the *same* functional role which defines that property. In the previous section, I argued that developmental modules can be understood as dispositional properties, defined *via* their higher-order generative role with respect to a particular morphospace and multiply realised by a meta-network of GRNs connected *via* mutational and regulatory architectural permutations. What I want to claim now is that conceptualising developmental systems in this way allows us to accurately and adequately model the ontological commitments of an increasingly important concept in our understanding of the mechanisms of evo-devo – namely, the phenomenon of *emergence*, and the associated causal and explanatory import of *holistic*, *structural* features of developmental systems.

Although the reductionist rule of the mechanistic magisterium has now long been established in the biological sciences and has provided us with innumerable invaluable insights into both the process of development and of evolution, there is a burgeoning trend in the field of evo-devo which heralds a substantial refocus on the *holistic* features of developmental systems as both causally central and explanatorily indispensable with respect to those processes.[32] Indeed, a holistic conception of organisms and their developmental sub-systems, itself once much maligned as being irrevocably wedded to the failed project of *vitalism*, is now a prominent feature of many evo-devo frameworks.[33] Within these frameworks, the *higher-order functions* of developmental systems are understood as novel, *emergent* features "arising" from the elemental collections which compose those systems (Wimsatt 2000; Callebaut *et al.* 2007; Mitchell 2012; Walsh 2013; Brigandt 2015), and are accredited with playing a causal-*cum*-explanatory role within the process of development which is irreducibly unique, insofar as its dynamic features are attributable to these systems only *qua* holistic structures (Boogerd *et al.* 2005; Huneman 2010; Nathan 2012; Salazar-Ciudad & Jernvall 2013).

A particularly striking and notable instance of the operation of this framework in a contemporary context is found in *dynamic systems theory* (DST), a project begun in spirit by Waddington's (1957) posit of

[32] Interestingly, in contemporary philosophy of physics, metaphysical frameworks for interpreting key phenomena in quantum mechanics – esp. non-locality and entanglement – have also taken the "*holistic turn*". See Morganti (2009) and Ney (2015) for some prominent recent expressions.
[33] For a comprehensive review of the holistic principles of the vitalism movement and their clash with the 'new philosophy of mechanism', see Allen (2005) and Nicholson (2012).

an 'epigenetic landscape', and subsequently fleshed-out with insights from Kaufmann's (1969) Boolean modelling of GRNs (Wang *et al.* 2011; Huang 2012). DST, as a novel modelling technique of developmental systems, has afforded researchers a set of unique conceptual resources with which to understand the process of development, and is now rather widely applied in analyses of everything from sub-organismal cell-fate (Bhattacharya *et al.* 2011; Verd *et al.* 2014) to the evolvability of organism populations (Striedter 1998; Jaeger & Monk 2014).[34] The defining feature of DST is its geometric modelling of the activity of developmental systems as a kinetic traversal across the topological curvatures of an epigenetic landscape (Wang *et al.* 2011; Huang 2012; Davila-Velderrain *et al.* 2015). On DST, the state of a developmental system is conceptualised as a frictionless orb, and the temporal succession of various distinct states of that system throughout the performance of its causal function are understood as the dynamic trajectory of that orb through a pathway geometrically constrained by the topological ridges and valleys of the system's Boolean regulatory configuration.

In this framework, a developmental system's morphological end-state is conceptualised as an *attractor* whose wide *basin of attraction* dynamically constrains the system's various causal trajectories to follow a pathway within the sloping walls of its surrounding topology. Thus it is the *higher-order*, formal properties of a developmental system – that is, the character of the topology defined by its Boolean network connectives – which are explanatory with respect to *why* that system reaches a particular end-state: the dynamics of attractor states (and their metric-bending basins) possess the relevant causal-*cum*-explanatory power. In contrast, the system's *non-formal* properties – that is, the other characteristics of whatever underlying mechanistic elements to which those Boolean values belong – are explanatorily irrelevant, as one and the same structural topology, defined by a "pattern of activity" or a dynamic tendency toward a particular end-state *via* a specific landscape, can be instantiated by any number of distinct sets of underlying constituents composing distinct GRNs (Gilbert & Bolker 2001; Dupré 2013; Jaeger & Monk 2015).

On a more general and wide-reaching scale, the theoretical focus on the emergent, higher-order activity of developmental systems has also been central to the recently prominent rise of *process ontology*. According to this revisionary framework, as Dupré (2013: 30) puts it, "[w]hat are stable and robust in biology are not things, but processes".[35] For the advocates of process ontology, while well-defined sets of mechanisms play an important explanatory role in ontogenesis, it is the higher-order processes instantiated by developmental systems, defined by their *directive activity* with respect to the developmental generation, and homeostatic maintenance of, a particular morphological trait which are to be metaphysically privileged.[36] This is because although a single morphological feature cannot be strictly identified as being generatively specified by any *single* GRN (due to the aforementioned phenomenon of degenerative robustness), the entire collection of networks which are causally responsible for that feature do share something important in common – namely, their instantiation of a higher-order, productive (and preservative) activity with respect to that trait (Brigandt 2007; Rosa & Exteberria 2011; Dupré 2013; Jaeger & Monk 2015). Thus, from the perspective of process ontology, it is the emergent, dynamically directive activities of developmental systems which are the explanatorily central and ontologically stable entities in the biological realm.

To return now to the bigger picture, the point I want to make with respect to both the general and specific application of the holistic framework – represented here by process ontology and DST

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[34] There are now several journals devoted to 'dynamic approaches' to biological modelling – for instance *Molecular Systems Biology* and *BMC Systems Biology*.
[35] Cf. Woese's (2004) clarion call for a process perspective in his "A New Biology for a New Century".
[36] Process ontology is closely related to *organicism*, another once disregard theory which is now gaining some traction among systems biologists which embraces a framework of *holism*. See Gilbert & Sarkar (2000) for a comprehensive introductory overview.

respectively – is that the plausibility, and subsequent *viability* of returning anew to this understanding of developmental systems by granting that the higher-order features of those systems play an important explanatory role with respect to the process of development ultimately depends, philosophically, upon one's metaphysics' ability to countenance those features with ontological sincerity. What I want to suggest then is that the theoretical advantageousness and empirically predictive success of these frameworks are phenomena best explained by positing the existence of higher-order, functionally-individuated, multiply realisable *dispositional properties*. In other words: the unique explanatory prowess of the higher-order, structural models that these frameworks utilise only makes sense if, and is most plausible under the supposition that, those structures have a proper metaphysical underpinning - and an ontological inventory of dispositional properties provides just that.

Consider, for instance, what the world must be like – *metaphysically* – if the higher-order 'epigenetic landscapes' of developmental systems are to be properly explanatory with respect to the process of ontogenesis, as posited by DST. An epigenetic landscape, defined by a functionally-specified topology whose emergent hills and valleys are "carved out" by the dynamic potential of various temporal transitions among a system's state-values, reflects a system's developmental constraints as causal correlations which hold between its initial and final state. Granting these topologies explanatory weight then suggests that we are required to conceptualise the GRNs of developmental systems as instantiating a single, though initial-value sensitive higher-order relation of causal correlations which determine their developmental state transitions – that is, as *realising* a single, "multi-track" dispositional property, defined by its functional relation of causal influence which holds among particular stimuli and variations on its manifestation type. The claim here is simple: if the 'creods' which define the curvatures of the topology of an epigenetic landscape of a developmental system are to represent genuinely explanatory generative constraints, those causally entrenched pathways had better be robustly captured by our ontology. And because this particular form of causal privileging is inherent in the very nature of dispositions, I suggest that taking the explanatory project of DST metaphysically seriously requires positing the existence of such properties.

Consider next what the world must be like – *metaphysically* – if developmental systems are best understood as stabilised instances of higher-order, holistic dynamic structures, as advocated by the defenders of process ontology. Because developmental systems are capable of undergoing various alterations in a wide range of their underlying architectural GRN configurations and yet retaining an unchanging dynamic orientation toward the production and maintenance of their associated morphological features, advocates of a process ontology grant these dynamic structures metaphysical prominence in functioning as the defining features of those systems. If we are to reconceptualise developmental systems as higher-order dynamic structures which are capable of being underpinned by a variety of distinct mechanistic configurations, we are seemingly required to posit the existence of repeatable, functionally individuated causal profiles which have a certain amount of autonomy over and above the particularities of the varied networks which satisfy them. Indeed, if these holistic dynamic structures are to properly carve the biological world "at the joints", our ontology had better be capable of granting them the metaphysical weight that job requires. I suggest that this is a requirement easily met by positing that various distinct mechanistic configurations are capable of instantiating a single, higher-order, *multiply realisable* dispositional property, defined by its dynamic "directedness" toward, and accompanying homeostatic regulation of, a particular morphological end-state.

In short then, if we conceptualise developmental systems as not being merely amenable to a dispositional redescription, but as *genuinely realising* dispositional properties, we are afforded the requisite ontological materials for the metaphysical foundation which the aforementioned models are built upon. We are afforded, in other words, an ontology capable of properly grounding the *emergent* and *holistic* phenomena that are central to these increasingly important models of the causal structure of developmental systems. This transcendental benefit is then, I suggest, a powerful advantage of adopting the metaphysical framework provided by an ontology of dispositions.

Summing Up

In the wake of the recent theoretical integration of the processes of organismal development with the principles of evolution ushered in by the empirical advances of evo-devo research, an important aim for the metaphysics of science must be to examine whether and to what extent various ontological frameworks are up to the task of modelling the data central to that research. With the rejection of the utility of the deductive-nomological model in the biological realm being now nearly ubiquitous, and with the subsequent advent of function-focused, mechanism-based models of causality, a *dispositional* ontology is a natural place to start. Indeed, as far as I'm concerned, it is also a fine place to finish – for, as I have shown, the conceptual framework of that ontology *is* up to the aforementioned task.[37] Evo-devo, it may be said, is a science of dispositions.

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[37] Note that I haven't argued that the main competitors to a dispositional ontology – namely, 'categorical' properties – *aren't* up to the task. However, insofar as one can get a conceptual grip on what 'quiddities' amount to, I think that *can* be shown – but I leave it for another time.

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