A Biologically Informed Hylomorphism

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Abstract

Although contemporary metaphysics has recently undergone a neo-Aristotelian revival wherein dispositions, or capacities are now commonplace in empirically grounded ontologies, being routinely utilised in theories of causality and modality, a central Aristotelian concept has yet to be given serious attention – the doctrine of *hylomorphism*. The reason for this is clear: while the Aristotelian ontological distinction between *actuality* and *potentiality* has proven to be a fruitful conceptual framework with which to model the operation of the natural world, the distinction between *form* and *matter* has yet to similarly earn its keep. In this chapter, I offer a first step toward showing that the hylomorphic framework is up to that task. To do so, I return to the birthplace of that doctrine - the biological realm. Utilising recent advances in developmental biology, I argue that the hylomorphic framework is an empirically adequate and conceptually rich explanatory schema with which to model the nature of organisms.

There's no denying that contemporary metaphysics is experiencing an Aristotelian revival of sorts wherein dispositions, or 'causal powers' are no longer regarded as scholastic superfluities, ideally to be explained away, but are instead being put to work in everything from theories of colour to theories of modality. But while the Aristotelian doctrine of 'potentiality' is now widely understood as being fairly innocuous and even theoretically advantageous, there has been a recent notable rise in the defenders of a much more contentious Peripatetic postulate – the doctrine of *hylomorphism*. According to the ontological principle of hylomorphism, the *natures* of entities are in some sense metaphysically, or conceptually bipartite: they have both a *material* and a *formal* aspect. Thus, fully "grasping the nature" of an entity requires understanding it as the conceptual union of *both* aspects.

The minor surge of the defence of this doctrine notwithstanding, it's certainly safe to say that hylomorphism isn't currently *en vogue*, even amongst the most ardent defenders of a neo-Aristotelian metaphysic. To my mind, there's a simple reason for this: while the contemporary defenders of this doctrine have done quite a lot of work in precisely explicating what the *conceptual* notion of 'form' amounts to, comparatively little has been done toward showing that this is a concept with *empirical* content. If we believe, as I do, that an effectual impetus to join a particular philosophical church must consist in more than simply being given a conceptual dissection of its characteristic complex metaphysical doctrine, the paucity of practitioners in the hylomorphic pews should come as little surprise.

With this in mind, this paper is a kind of altar call – its aim is to show that the hylomorphist's claim that fully grasping the nature of entities is a "two concept job" can be given firm empirical footing. To do so, I bring the conceptual focus back to its Aristotelian origin – the biological realm. My claim is that recent advances in developmental systems biology afford us an empirically tractable picture of the hylomorphic nature of biological entities by way of elucidating what the *formal* aspect of that nature consists in. The hope is that, having been enriched by an empirically informed conception of form, hylomorphism might once again be seen as good news for metaphysics.

Hylomorphism: A Matter of Definition

Taken generally, hylomorphism is the doctrine that fully capturing the metaphysical 'nature' of an entity requires an appeal to two distinct (though ultimately intimately interrelated) concepts – *matter*, and *form*. Or, to put it another way, according to hylomorphism, any adequate metaphysical definition of an entity must be two-fold – it must encompass the nature of the entity *qua* matter and *qua* form. But what does

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this bipartite distinction amount to? Let us say that to define the nature of an entity *qua* matter is to define it as an organised, connected collection of discrete parts; here, 'organisation' and 'connectivity' are to be understood, at the very least, both spatially and causally (and perhaps temporally), and 'discrete' denotes their being ontologically, or existentially independent from one another. To define the nature of an entity *qua* form, on the other hand, is to define it as a holistic, dynamically directed structure; more on this momentarily.

The claim of hylomorphism is that both of these concepts must be put to use in successfully "capturing the nature" of an entity – but what is involved in this task? Clearly, "capturing the nature" of an entity is to be understood as getting a grip on *what that entity is* in some metaphysically fundamental sense. In line with the now-popular Lockean understanding advocated in contemporary metaphysics, let us say that "capturing the nature" of an entity amounts to understanding *why* and *how* that entity possesses its characteristic set of properties: getting a grip on the *nature* of a clump of Gold, for instance, plausibly involves understanding *why* it has such-and-such surface-level properties (reflective surfaces, malleability, conductivity, etc.), which involves understanding *how* it comes to have them (through its molecular structure, or electron count, or etc.) – thus Kripke's (1980) appeal to its "periodic" nature.[1] On this line of thinking, citing the *nature* of an entity affords one rich explanatory power with respect to its possession of a set of typical features – *why* those features are there (or why they *could* be there), and *how* they got there (or how they *would* have gotten there), etc.[2]

Defining the nature of an entity *qua* matter then is to cite an entity's organised, connected collection of discrete parts as explanatory with respect to its possession of a characteristic set of features.[3] I take it that this sort of definitional methodology won't be unfamiliar to the reader – it is, after all, representative of the prominent philosophical project of reductionism – and so it's probably unnecessary to spend too much time on it here. What's more important for present purposes is to flesh-out precisely what it means to define the nature of an entity *qua* form. My approach here will be to trace the Peripatetic thread as it has weaved through contemporary hylomorphic accounts by distilling a set of shared criteria for a *formal* definition present in the literature.[4] Though I've already briefly mentioned a putative description of such a definition, it's instructive to consider it in more detail. To do so, I'll distinguish three aspects of a 'formal definition'; though, as we will see, these three are in some way intertwined.

Firstly, to define the nature of an entity *qua* form is to offer an explanatory basis for its characteristic features in something "over and above" its mereological constituents. Formal definitions are often understood as demarcating *higher-order* facts *about* an entity's constituents – typically they either pick-out some privileged *relation* of those constituents (Fine 1999; Johnston 2006), or else some sort of *process* of (Koons 2014), or *metaphysical operation* on (Marmadoro 2013) those constituents. Importantly, in virtue of referring to something appropriately higher-order, formal definitions are taken not to refer to any *extra* mereological part of those entities (Johnston 2006; Rea 2011; Marmadoro 2013), nor are they understood as being *reducible to* any competing material definitions which might concern those parts (Robinson 2014; Jaworski 2016).[5]

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[1] *cf.* Putnam (1975)

[2] In his *Essay Concerning Human Understanding*, Locke (1690/1995) referred to this as the dependence of an entity's 'nominal' essence upon its 'real' essence. For an instance of this in the context of contemporary hylomorphism, see Oderberg (2011)

[3] This contemporary notion of 'matter' is closest to what commentators have called 'functional matter' in Aristotle – see Lewis (1994). Notably, this contemporary formulation doesn't place any particular emphasis, as Aristotle did, on matter's definition as *pure potentiality* and its subsequent role in underlying accidental property-change.

[4] Note that this won't involve any careful exegesis of Aristotle – the reader is free to think of these aspects of a formal definition as *neo-Aristotelian*.

[5] The exception to this rule is Koslicki (2008), who views formal definitions as picking-out some further "non-material", though mereological, part of an entity. However, as this isn't widely held, and as Aristotle himself

Secondly, a formal definition of an entity's nature picks-out some irreducibly higher-order fact about that entity and its constituents precisely because to define that nature *qua* form is to represent the entity as an ontological *unity* – as *metaphysically one*. In contrast to a material definition, wherein appeal is made to a collection of various discrete mereological parts and pieces, a *formal* definition's explanatory prowess is grounded in a *holistic* conception of an entity (Johnston 2006; Oderberg 2007; Rea 2011; Marmadoro 2013). The *unity* that formal definitions are meant to appeal to is understood as being importantly distinct from the "mere togetherness" that characterises the content of a material definition: to be sure, the latter cites an organised, *connected* collection of parts, but the former cites that collection *as one*.

The last aspect of this type of definition makes clear what this distinction really amounts to, as defining an entity's nature *qua* form involves an appeal to an entity as a *causally unified system*. This is typically cashed-out by the claim that a formal definition picks-out a higher-order causal activity *of the entity as a whole* (Jaworski 2012), or else one that is in some sense an emergent, irreducibly *cooperative activity* of an entity's constituents (Rea 2011). The causal unity implicit in a formal definition doesn't consist simply in the fact that a particular entity performs a particular higher-order activity which involves each of its parts operating in causal unison, but also that this structure orients these parts, as a whole, toward a particular causally privileged end, or ends. As one might expect of an Aristotelian account, to define the nature of entity *qua* form is to cite as explanatory (in the relevant sense) its holistic causal "directedness" toward some end-state(s) (Oderberg 2007; Rea 2011; Jaworksi 2012; Marmadoro 2013). In some sense then, a formal definition represents the entity's constituents as non-autonomous participants in a singularly directed, dynamically continuous structure.[6] Thus we see again, now more clearly, the *higher-order unity* that a formal definition is meant to capture – namely, a holistic, goal-directed activity, ontologically attributable to an entity only as a singular causal system (Jaworski 2016).

As I understand it then, to define the nature of an entity *qua* form is to demarcate its holistically higher-order, dynamically directed causal structure as uniquely explanatory with respect to its possession of a set of typical features. Now that we've a better grip on what a *formal* definition amounts to, the pertinent question is, given this conception, what's required in order to give a plausible defence of hylomorphism? For our purposes, as the more contested aspect of the doctrine, let us ask: what's required in order to give a plausible defence of the applicability of a *formal* definition of an entity's nature? To answer that question requires getting clearer about the nature of the defence I want to offer. As I've said, my aim is to display and defend an empirical incarnation of the conceptual framework of hylomorphism. Thus, in explicating that framework, I have focused on the doctrine's core definitional claims, rather than any of its purported ontological commitments. As it happens, precisely *what* those commitments are is widely disputed, even among its adherents. If an entity's nature admits of a formal definition does this entail, for instance, that we must reformulate our account of mereological composition (Fine 1999; Johnston 2006; Koslicki 2008), or that we must countenance a novel ontological category whose members are imbued with unique, "downwardly directed" causal powers (Oderberg 2007; Rea 2011; Jaworksi 2012)? Or does such an admission merely require helping ourselves to a non-ontological free lunch, delivered simply *via* a process of abstraction (Marmadoro 2013)?

Rather than taking a particular stance on this issue, my aim is to focus on the widely-accepted *definitional* project: after all, every defender of hylomorphism presumably agrees that the doctrine is committed to the claim that fully capturing the nature an entity requires an appeal the dichotomous descriptive machinery of *matter* and *form*, irrespective of whatever the ontological underpinnings or

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[6] expressly argued against this type of position (see *Metaphysics VII*, 17 and *VII*, 3-6), I haven't considered her view in any detail here.

[6] Marmadoro (2013) refers to this phenomenon as the "re-identification" of an entity's constituents with respect to the function of its 'substantial form'.

consequences of those descriptions are taken to be. With the account laid out above then, the project of this paper is to show one way in which this definitional project may be vindicated; such vindication might be taken to entail particular ontological consequences for the doctrine, and although I won't be defending them in detail here, I will briefly address them in the final section. As already mentioned, to do so, the paper will focus on the clearly more contested aspect of the doctrine – *formal* definition. For my defence to have succeeded, it will have to have shown that the concepts invoked in this type of definition have a plausible empirical instance. Importantly, with the above discussion in mind, the success of this defence requires (a) showing that form is *conceptually independent* of matter, and (b) showing that form plays a *unique explanatory role* with respect to matter: (a) is satisfied if a *formal* definition of an entity, as explicated above, can be made without explicit appeal to its *material* definition, while (b) is satisfied if such a definition is able to play an explanatory role with respect to the possession of a characteristic set of an entity's features which is uncapturable by appealing to its *material* definition.[7]

My claim is that if we focus on the biological realm, itself once the fount of Aristotelian inspiration, a contemporary defence of the principles of hylomorphism is available: recent advances in developmental systems biology have shown, or so I will argue, that fully capturing the nature of biological entities is a job which requires both matter *and* form.

Back to Biology: Building an Organism

Aristotle's argument that the principles of his hylomorphic metaphysic were truly *in rei* was primarily grounded in the physical principles he believed to be *in natura* – that is, in the biological realm. If you're after a robust understanding of that metaphysic then, you'd be better off examining starfish, rather than statues.[8] Accordingly, most philosophers who've since taken up the hylomorphic mantle have placed biological entities as paradigms of that metaphysic – and rightly so. However, although few deny that the doctrine naturally dwells in the "land of the living", even fewer have taken on the project of providing a detailed account of *how*, and *in what way*, that realm is to be characterised by its metaphysical principles. Typically, at best, these philosophers merely suggestively cite practicing biologists' rather vague delineations of characteristic *phenomena of life* – homeostasis, emergence, etc. – as empirical undergirding for the doctrine's metaphysics (as in Jaworski 2012). More commonly however is the simple, though unexamined posit of biological entities as hylomorphic exemplars – one often finds 'humanity' atop the candidates for form, for instance (as in Rea 2011).[9] In what follows, I want to offer a more empirically specific focus, by examining in detail the particularities of an important class of biological entities.

Rather than taking on the "big picture" task of providing a hylomorphic account of the nature of biological entities *tout court*, I want to take up the more minute, and more manageable task of providing a hylomorphic account of the nature of the biological individuals which make-up biological entities. Why? One reason is practical: on my view, providing an empirically robust hylomorphic account of the nature of a biological entity – a starfish, for instance – is a complex and complicated affair requiring a perhaps unappreciated amount of philosophical subtlety. Better then, for the purposes of this paper, to make an attempt at the more practical task of providing such an account for the individuals which compose biological entities; ideally, the account I offer will be generalisable, "upwards" as it were, though I won't

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[7] The requirement that *form* provides novel *explanatory* power with respect to an entity's constituents, rather than a *causal* power *over them*, is explicitly defended by Rea (2011) and Jaworski (2012).

[8] The choice of creature here was no accident – Aristotle was quite interested in sea-creatures (in *History of Animals*), and sea urchin mouths are now known as 'Aristotle's Lanterns'

[9] None of this is meant to suggest that these philosophers haven't dressed the doctrine with interesting and elucidating metaphysical flourishes – they certainly have. The point is simply that their doing so is often largely independent of any examination of the finer biological details. A notable exemption is Walsh (2006), and to a lesser extent, Boulter (2012).

be arguing for that here.[10] Another reason is principled: the focus of my examination may not be best conceptualised as full-fledged entities in their own right, but they are most certainly biological *individuals*; more on this in a moment. And being biological individuals, it's reasonable to expect that a hylomorphic account ought to apply to them just as equally as it does to the larger individuals they compose.

That said, the individuals I want to focus on are called *developmental modules*, currently on the centre stage of research in the field of developmental systems biology. Developmental modules are discrete biological systems causally responsible for the development of particular morphological features. A foundational fact upon which the edifice of systems biology is built is that the morphological development of organisms is a rather piecemeal affair. More specifically, that an organism's development is controlled *discretely*, by individualised organismal sub-systems which initiate and direct the formation of its various body parts – eyes, legs, and the like. These sub-systems – or, developmental modules – are treated as individuals in part due to their relative causal autonomy during the process of development: they are characterised equally by an extremely high causal connectivity among their constituents and an extremely low causal connectivity with other parts of the organism (Raff & Sly 2000; Erwin & Davidson 2009). They are, in other words, discernible bundles of tightly-knit causal loops whose activities are responsible for an organism's development of a particular trait. But developmental modules are also individuals in perhaps a stronger sense, as recent advances in evolutionary developmental biology (evo-devo) have made clear: they are able to be generationally inherited, and so are traceable (with modification) throughout evolutionary history (Hall 2003; Davidson & Erwin 2006; Wagner 2014), a fact which may even merit them a place at the ground-floor of the elusive, proper "level of selection" (Brigandt 2007; Brakefield 2011; McCune & Schimenti 2012).[11] In a perfectly respectable sense then, developmental modules, the organismal sub-systems causally responsible for the production of particular morphological traits, are biological *individuals* – and ontologically important ones at that, as it is their activities which give shape to the fully-featured biological entities we're more directly acquainted with.

The pertinent question then is: what is the *nature* of a developmental module? Recall that citing the nature of a thing is meant to provide rich explanatory import with respect to its characteristic feature(s). To answer that question then, we must know which feature(s) the citation of the nature of a module might purport to aid in explaining. The obvious answer seems to be that citing the *nature* of a module should help shed explanatory light upon *the development of its associated morphological trait*: it should, as I earlier put it, importantly aid in explaining the *why* and *how* of that process. Thus, providing an answer as to the *nature* of a developmental module requires some knowledge of what that process amounts to. If we consider that a fully developed morphological feature is nothing more than a particularised spatial configuration of various cell-types, we can get a preliminary grip on the process in question – put simply, it involves putting the correct *things* in the correct *places*. The process of "building" a morphological feature is thus two-fold: it requires the creation of a certain set of cell-types particular to the feature in question, and the arrangement of this set in a particular three-dimensional configuration. More specifically, the operation of that process involves not only that the genomes of a set of cells take on particular expression profiles which determine their individual developmental fates, but also that these specifically expressed cells are spatially coordinated in a particular configuration.

We now know that the process which begins with a collection of cells whose genomes are not in any particular expression state (i.e. pluripotent cells), known as an *imaginal disc*, which over time take on specific expression profiles in a coordinated fashion, requires the activity of an entire *network* of genes (Gurdon & Bourillot 2001; Tabata 2001; Mann & Carroll 2002). It requires a certain set of genes that act

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[10] Aristotle argues (in *Ethics* I, 7) that if the *parts* of a thing (a human eye, for instance) are understood as teleological – that is, having a *form* – so too must the *whole* thing (the human as an entire organism, in this case).
[11] The case is even stronger if one thinks, as Clarke (2013) suggests, that any bits of our biological ontology upon which natural selection operates have the right to be called biological *individuals*.

intra-cellularly to produce the proteins that determine the particular cell-types which "build" the morphological feature in question *and* a set of genes whose protein products (known as *transcription factors*) act *inter-cellularly* to regulate the intra-cellular expression profiles of other genes in neighbouring cells, thereby controlling *which* genes are expressed in *which* cells throughout the disc, as well as *when* and *where* that expression takes place during the development of a morphological feature. Thus we can model the process of the development of an imaginal disc by mapping out a *genetic regulatory network* (GRN) which includes the set of genes whose expression determines particular cell-types, the set of genes which control their expression, and the particularities of the causal, regulatory relationships among them (activation, repression, etc.)

Understood in this way, the development of a particular morphological feature can be seen as the temporal succession of a series of expression profiles of the GRN elements in the cells which compose an imaginal disc. Importantly, this is a process governed by the "regulatory logic" of that GRN, as the expression profile of each cell within the disc evolves over time according to the particularities of its regulatory structure: if G_1 is *highly expressed* at *t* because it is up-regulated by G_2 at *t-1*, then at *t+1*, G_3 and G_4 will be *barely expressed*, due to G1 highly down-regulating both, etc.[12] Over time then, due to the specific regulatory logic of a particular GRN, the cells of an imaginal disc take on a controlled and continuous series of expression profiles *via* a series of patterning processes (Salazar-Ciudad *et al.* 2003) ultimately resulting in the collectively stable state of a various collection of particular cell-types arranged in a particular spatial configuration – that is, in a fully developed morphological feature.
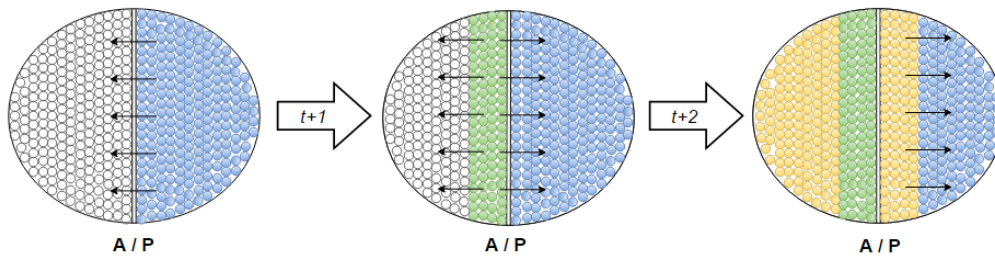

Figure 1: *Schematic two-dimensional representation of the early developmental stages of a multi-cellular imaginal disc constituting a module: 'A/P' denotes the anterior and posterior regions of the module, distinct bubble colours represent distinct cell-types, and arrows represent the causal/regulatory influence of one cell-type upon neighbouring cell-types. Over time, the cellular constitution of a module becomes increasingly compartmentalised and spatially discrete.*

It should by now be clear that if we wish to "capture the nature" of a developmental module, we must have recourse to its associated GRN, as knowledge of its elements and the relations among them sheds explanatory light upon the development of its associated morphological trait: if we want to explain the *why* and *how* of that process, we must appeal to the structural-causal mapping of its GRN. In doing so, we are citing its organised, connected collection of discrete parts as explanatory with respect to the possession of its characteristic feature. We are, in other words, showing the validity of defining the nature of a developmental module *qua* matter. But does such a definition *fully* capture the nature of a developmental module? That is, is there something yet left to account for with respect to offering the relevant explanatory utility which this definition fails to deliver? The answer, I think, is yes for, as I argue below, the *material* definition of a developmental module leaves one *uninformed* about its nature in an important respect.

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[12] For more on the regulatory "logic" found in GRNs, see Yeger-Lotem *et al.* (2004), and Alon (2007).

Modules & Morphospaces

Although I have been preliminarily modelling the causal output of a developmental module rather rigidly as a *singular*, fully specified morphological feature, a complication must now be made, as the full picture admits of rather more *flexibility*. For we now know that the morphological structure produced by a single developmental module, being underwritten by a specific 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; Gilbert & Epel 2015). As a result of "upstream" alterations consisting mainly of heterochronical and heteropical changes in inter-cellular signalling, a single developmental module is capable of producing a wide range of "downstream" qualitative alterations in its associated morphological feature with respect to its precise shape, size, pigmentation, etc. (Schlichting & Smith 2002; Aubin-Horth & Renn 2009). Thus, the morphological feature generatively specified by a single developmental module cannot be fully characterised by a single, particularised instance with respect to these qualitative and quantitative factors, but must instead be understood as a generalised collection of various qualitative and quantitative variations on that feature – this set of possible permutations is known as the feature's *morphospace*. For this reason, capturing the generative capacity of a single developmental module with respect to its associated morphological feature must involve modelling its "variational tendencies"[13], or its set of "developmental trajectories, [correlated with] the particular set of environmental conditions to which [it] is exposed"[14], to construct an "idealised type…constructed from ample and acknowledged variation"[15].

With this in mind, it's clear that "fully capturing the nature of a developmental module" must involve capturing its *rich* generative capacity to produce its *entire* morphospace. The pertinent question for our purposes is: can the *material* definition we've provided accomplish this? In order to answer this, we must look again to the causal story of development. We've already seen that one can model a fully developed morphological feature as a specific spatial arrangement of a collection of cells with specific genetic expression profiles. We've also seen that the developmental process involved in generating such a feature can be modelled as the temporal succession of states of the overall expression profile of the imaginal disc (itself composed of a number of individual cells' profiles), the transitions of which are governed by the regulatory logic specified by its GRN. Of course, we have thus far only modelled a *single* developmental trajectory towards the generation of a single variant of a morphological feature, and the phenomenon of developmental plasticity shows that *many* such trajectories are possible.

However, accommodating this involves no further complication - using the same GRN and its constitutive regulatory logic, we can model each of these trajectories as the developmental consequence of its "generative rules" being applied in the context of distinct initial developmental input conditions (Gurdon & Bourillot 2001; Tabata 2001; Mann & Carroll 2002; Müller 2008). In other words, the phenomenon of developmental plasticity reflects the fact that a single regulatory network is capable of delivering a variety of distinct morphological end-states according to a variety of distinct initial developmental conditions, as altering the initial network-state of a module has regulatory consequences (specified by the generative rules of that network) on the expression states of its cells which ripple "downwards" and "outwards" throughout an imaginal disc during the process of development.

So, modelling a module's flexibility with respect to its capacity to produce various developmental trajectories by defining it *materially* – that is, *via* its associated GRN – is easily done. However, a further complication arises when one considers that the morphospaces associated with developmental modules

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[13] Van Dassow & Munro (1999: 316)
[14] Pigliucci *et al.* (1996: 81)
[15] Love (2009: 57)

are not *merely* reflections of their developmental plasticity, but also of their *generative constraints*: for these systems are not *wholly* flexible, causally subject to every incoming environmental influence during the process of development, but instead reliably and repeatedly end that process within a well-demarcated range of particular states (Rasskin-Gutman 2005; Newman and Müller 2006; McGhee 2006; Wagner 2014). In other words, no module's morphospace consists of an ontologically exhaustive set of every possible qualitative and quantitative permutation on its associated morphological feature. Rather, the morphospace which characterises a developmental module is composed of a select set of *generatively privileged* permutations which arise within a wide-range of distinct environmental (read: causal) contexts. In this way, the character of a morphospace associated with a developmental module shows that nature delights in variety without indulging in it – morphological variation is allowed, but only within certain limits.

If "fully capturing the nature of a developmental module" involves capturing its rich generative capacity to produce its entire morphospace, then any adequate definition of that nature must be explanatorily relevant with respect not only to its generation of a certain amount of morphological variation, but also with respect to the specified constraints on that variation. What we require, in other words, is not only explanatory power with respect to a module's capacity to produce various distinct developmental trajectories, but also with respect to the limitations on that capacity. Importantly, note that understanding the latter allows us to understand, for any particular module, why *these* morphologies are *privileged*, and *why* they are so – something that cannot be achieved by simply appealing to any *single* developmental trajectory, nor to the entire *set* of privileged trajectories. Capturing this fact, I suggest, is crucial to capturing the *nature* of a developmental module.

Accomplishing this, as I will show, requires conceptualising these organismal sub-systems in a radically novel fashion, *via* the conceptual framework of *dynamic systems theory* (**DST**). Indeed, in doing so it requires, as I argue below, that we conceptualise developmental modules *holistically*, as *higher-order*, *dynamically directed* systems.

Dynamic Systems Theory: A Formal Science

The desire to more fully understand the *developmental constraints* of organismal systems was perhaps the founding motivation for the development of DST, a project begun in spirit by Waddington's (1957) posit of 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 such 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).[16]

In order to show the utility of DST in this respect, and in application to our current project, let us take stock. We have seen that the developmental process involved in a module's generation of a morphological feature can be modelled as the temporal succession of states of the overall expression profile of the imaginal disc (itself composed of a number of individual cells' profiles), the transitions of which are governed by the regulatory logic specified by its GRN. This fact forms the foundation of DST modelling, and the thought is: if we construct an abstract multi-dimensional state-space whose individual points represent particular disc-wide expression profiles (where each specifies the expression-state of each GRN element within each cell in the disc), arranged continuously (according to cellular expression values) on axes which represent a particular cell-type in a particular spatial region, we can model a particular

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[16] There are now a number of specialist journals which focus on holistic treatments of developmental phenomena – see, for instance, *Molecular Systems Biology* and *BMC Systems Biology*.

instance of the development of a morphological feature as a temporal trajectory through this state-space, ending in the expression-state representing that feature; the figure below illustrates this type of model with respect to a simplified GRN, represented on a two-dimensional state-space.[17]
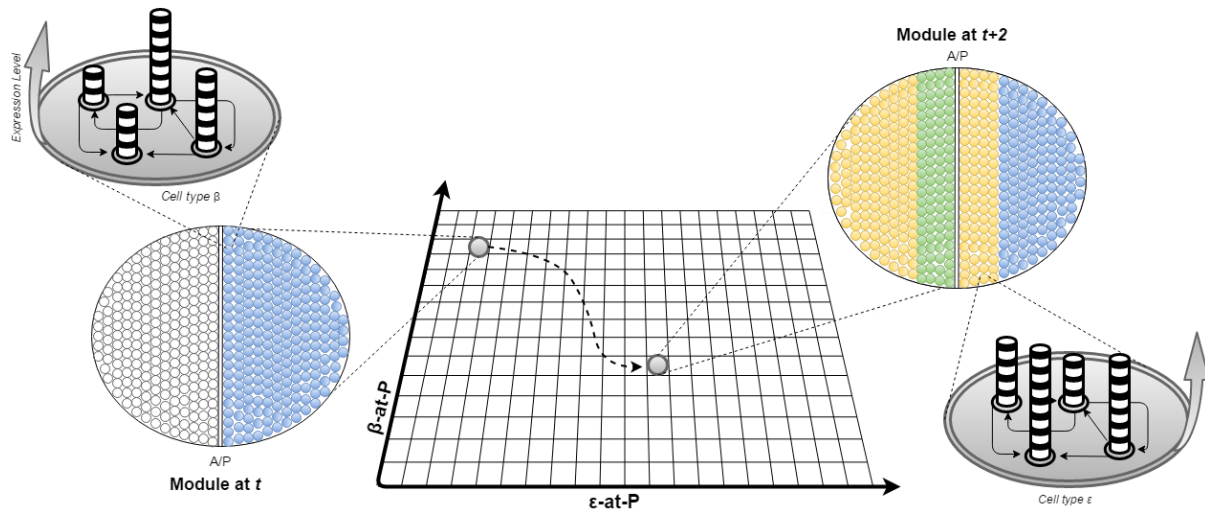

Figure 2: *Schematic representation of a single developmental trajectory of a module through a (truncated) abstract state-space, in reference to fig. 1. On either side, the 'module at t' and 'module at t+2' depict the spatial arrangement of two cell types (β and ε) within the imaginal disc with respect its anterior (A) and posterior (P) regions. Each cell type is represented as consisting of the module's GRN elements (depicted as elliptical bases), their regulatory connections (depicted by arrows), and their particular expression levels (depicted as stacked elliptical elements). In the middle of the figure, the temporal transition of the spatial arrangement of β and ε with respect to P is modelled as a trajectory through a two-dimensional plane whose edges represent unique disc-wide cellular GRN-expression states, arranged such that the distance between any two edges reflects quantitative similarity with respect to spatially-specific cellular expression. The 'module at t+2' here represents the expression levels of the module's GRN which constitute its developmental end-state.*

Accordingly, utilising the data derived from experimental evidence of the phenomenon of phenotypic plasticity, we can represent the generative progression of a variety of the module's possible developmental routes by tracing-out distinct trajectories through a single multi-dimensional state-space. The resulting picture provides a representation of the multiple developmental pathways, each defined by distinct trajectories through GRN expression-value space, which are responsible for the production of the various morphological permutations which comprise the morphospace of a particular module.

As theoretically interesting as this model may be, it yet fails to offer us a comprehensive understanding of the structural limitations on a module's capacity to produce these permutations. In other words, as I earlier put it, this representative framework doesn't offer any elucidation with respect to why *these* permutations are privileged, or *why* they are so. I think it's clear that examining more closely any *single* trajectory corresponding to such a permutation isn't going to do the requisite work, but nor will a similar scrutiny of the entire *set* – in the end, we're still left in the dark as to what singles *these* trajectories out from among many possible ones, and thus, *this* collection of disc-wide GRN expression values from among many possible multi-cellular expression configurations. However, a natural way forward should suggest itself: if we want to see why *these* pathways are privileged, we ought to compare them to a set of less developmentally fortunate ones.

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[17] For a (relatively) accessible introduction to how this mapping is done, both theoretically and with the aid of empirical data, see Huang (2009) and Wang *et al.* (2011).

Given the representative machinery of our multi-dimensional state-space, we can do just that, as mapping out a trajectory on this space only requires our picking a state (a disc-wide cellular GRN expression profile) and iteratively applying the associated GRN regulatory logic to derive its temporally successive states. In other words, "determining the next move" of a developmental trajectory within state-space from any state requires a simple *conditionalising* process: for any particular regulatory network, by plugging in a specific set of expression values for the members of that network, and applying the activities of the causal connectives which constitute its regulatory logic, we can derive its members subsequent expression values. Thus, because the regulatory logic of a GRN effectively acts to assign a Boolean function to each state within this state-space, we can vectorise any single state and trace the directionality of temporally successive states within that space (Wang *et al.* 2011; Davila-Velderrain *et al.* 2015). We can, in other words, plot any possible developmental trajectory for a particular imaginal disc.[18]

If we do so, after a significant number of iterations, we find that the collection of these trajectories exhibit interesting properties. Firstly, we find that localised collections of trajectories follow similar curvatures through state-space: they appear to "stick together", bending around similar regions of that space. Secondly, we find that multiple trajectories end in the same general areas in state-space: these regions appear to "attract" trajectories from various originating points within that space. As one may have guessed, these regions correspond to the disc-wide expression states that define the various morphological permutations which comprise the module's morphospace.
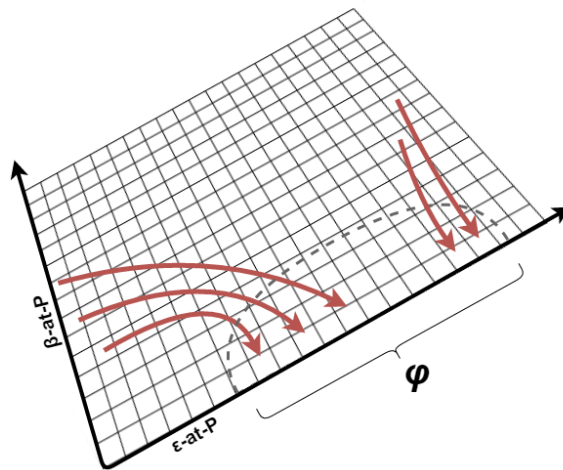

Figure 3: *Schematic representation of a simplified, two dimensional state-space depicting a small selection of a module's developmental trajectories. This truncated state-space represents the disc-wide cellular expression levels of the module with respect to two cell types (β and ε) in a particular spatial region (posterior, P). Multiple individual trajectories (depicted as arrows) from distinct initial conditions converge on a general region (φ) of developmental end-states with quantitatively similar spatially-specific disc-wide cellular expression values (with respect to ε and P).*

Notice that taking a "bigger picture" look at the characteristics of this state-space reveals precisely the features we were interested in, for here we see *privileged* permutations *qua* attractor-regions (e.g. *φ* in *fig. 3*) and *constraints* on possible permutations *qua* curvature structures on that space. What we want to know then is: what explains this *shaping* of state-space? We've seen that the developmental transition from any particular point in state-space to the next is determined by a kind of Boolean function which utilises the

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[18] This is of course a rather complex task, given that performing it requires taking into account *multiple* cells, their spatial *arrangement*, and both *intra-* and *inter-cellular* regulatory interactions.

GRN's regulatory logic operating on the particular expression profile of the GRN elements which define that state. However, the transitions between states in this space is not reflective of merely simple analytical operations – for note that the transition-function in question is a *regulatory* one, and so each step within a single trajectory is a step toward disc-wide regulatory *stability*. In other words, although the state-to-state transitions within that space take place according to the aforementioned Boolean model, each step throughout developmental time is in fact a transition from a *less* stable disc-wide expression profile to a *more* stable one, given the relevant regulatory structure. So, from any origination point within that space, the subsequent state-transitions which comprise its trajectory follow the multi-cellular expression profile of the disc's "search" for *regulatory stability*, where the relevant GRN elements' expressions "even-out" in such a way that their collected values no longer cause further significant inter-network expression alterations.

With this in mind, we can add another aspect to our state-space: each state can be given a *stability measure* which specifies the GRN elements' expression values tendency to substantially shift (given the relevant regulatory logic) to a subsequent state (Kim & Wang 2007; Bhattacharya *et al.* 2011); in effect, in this process, we are properly vectorising the state-space, in that the arrows we earlier assigned to each state now have a direction *and* a kind of magnitude. In DST modelling, this aspect is represented by assigning each state a particular *elevation* value (along another dimension), where the *higher* the elevation value, the relatively higher level of expression *instability* of the state – i.e. the more likely the disc-wide expression values of its GRN elements will shift (again, given the relevant regulatory relations in operation).[19] Once we have done so, our abstract state-space is now a structured *topology* complete with high hills and low-lying basins with various gradient measures connecting them.
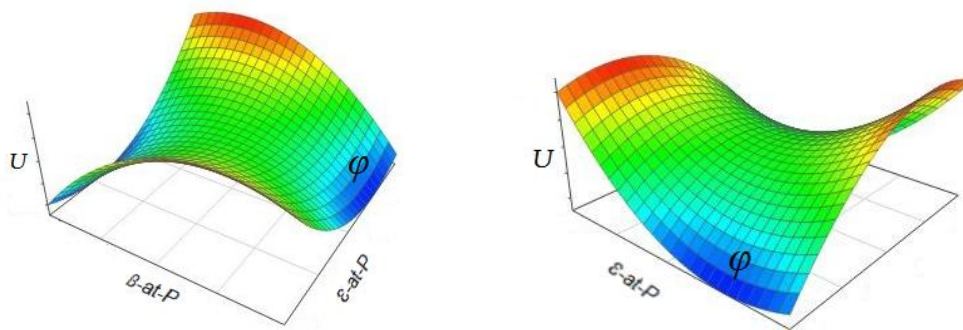

Figure 4: Schematic topological representation of the state-space from fig. 3. The third dimension (U) reflects the elevation level of any particular disc-wide spatially-specific expression profile for any specific coordinate, itself a measure of the relative regulatory stability; here, a higher U-value and warmer colouration are inversely correlated with regulatory stability. φ, denoting a set of quantitatively similar developmental end-states with respect to ε-type expression profiles within the posterior compartment of a module (P), is shown as a low-lying basin within state-space. NB. although representing a complete such topology for a particular module would require a rather complex, multi-dimensional state-space, the same principles at play in this schematic would apply.

With this stability-based topological mapping of our state-space in hand, we can now understand the process of the development of a particular module in a novel fashion: if we depict the state of the module as a kind of frictionless orb, we can model the temporal succession of various distinct states of the module throughout the process of development as the dynamic trajectory of that orb through a pathway geometrically constrained by the topological ridges and valleys of the system's Boolean regulatory

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[19] Technically, assigning an elevation value involves stochastic simulation of *groups* of cells, etc. – but I pass over this complication here. See Bhattacharya *et al.* (2011) for the finer details.

configuration. This novel modelling puts us in the position to understand more clearly why, for the corresponding morphospace of a particular module, *these* morphological permutations are privileged, and *why* they are so: they represent disc-wide patterns of *regulatory stability* with respect to intra-module cellular expression states which "carve-out" wide, low-lying basins in the topology of state-space, and their privilege consists in the fact that the dynamics of the process of development is shaped and constrained by the geometric curvature of that topology (Kitano 2004; Huang 2009; Huneman 2010). In this way, the framework of DST affords us a more complete picture of the rich generative capacity of a developmental module - for it not only allows us to understand a module's ability to produce the varied morphological permutations which comprise its associated morphospace, but importantly also the causal-*cum*-structural "shape" of that capacity with respect to both the developmental privileging of and constraint on those permutations. Thus, by utilising the conceptual resources of DST we are able to more fully "capture the nature" of a developmental module, having been equipped with the explanatory resources necessary to account for the multi-faceted character of the developmental process of its associated morphological trait.

Importantly however, note that in order to have this rich understanding of the nature of a developmental module, we have had to *abstract away* from its compositional particularities and their mechanistic interactions in an appeal to a *higher-order structure* which is neither a compositional part of the module, nor strictly reducible to any such part (or set of such parts).[20] Of course, this process of abstraction required an initial appeal to its compositional elements and their mechanistic arrangement in order to define a network and its associated regulatory logic, but the resulting topology from which we have drawn the aforementioned explanatory prowess (a) is itself constructed purely from a set of functionally defined, weighted Boolean connectives which (b) form a continuous mapping over an exhaustive set of various iterations on the values of those compositional elements and their causal connectives. In as much as functionally defined operators are unable to qualify as "proper parts" of a biological system, (a) entails that this topology cannot be strictly understood as a contributing to the constitution of a module. Furthermore, given that a highly abstract, functional mapping which plots the interrelation of every possible configuration of an entire system is incapable of being bijectively assigned to the set of elements which compose that system, (b) illustrates the irreducibility of a topology to such a set; here, you might say, 'the possible' outstrips 'the actual'.

Note further that, in utilising the explanatory resources afforded by our topological understanding of a developmental module, we have had to conceptualise it as a higher-order, *dynamically holistic* system: these are resources granted to us only by modelling the system's causal activity as an iterative operation on a continuous, integrative mapping of its entire collection of possible system-wide state-values. Indeed, each point in the collection that comprises a complete state-space is intimately connected to its neighbouring points to form a smooth gradient contour so that the resulting geometry of that topology – and thus its dynamic "flow" – cannot be attributed to any particular GRN element, nor the entire GRN, but only to the system *as a whole*, by taking into account its exhaustive set of possible disc-wide expressions states (Jaeger & Monk 2015). For within that topology, each individual vector is merged into a *holistic* dynamic structure, and it is this integrated flow (and not the specification of any underlying operating mechanisms) which plays an explanatory role with respect to the multi-faceted developmental of the module's characteristic morphological feature *via* system-wide stability measures and their resulting topological curvature.

What's more, the flow which characterises this higher-order structure doesn't just represent the dynamic activity of the system acting *as a whole* (as "one"), but as a whole with respect to *its directedness toward certain states*: the flow of the system, characterised by its vector-summed stability measures, presents a topology whose geometrical configuration *directs* a module's process of development *toward* certain

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[20] See Levy & Bechtel (2013) for a good discussion of this general sort of abstraction process in biological modeling.

morphological end-states *qua* disc-wide expression patterns of regulatory stability.[21] For the system's causal progression, represented as the temporal traversal of that process through the two-dimensional state-space of disc-wide expression profiles, is no random walk – it is *guided by* (and *restricted by*) the three-dimensional contours of its holistically-defined topology *toward* certain developmentally *privileged* morphologies. Importantly, this "goal-directedness" which bestows explanatory utility with respect to morphological development is attributable only to that topology, and thus the to the system *as a whole* – as we have seen, the stability-measure which defines that topology cannot be gleaned from the mere specification of the module's GRN, or any single iteration of that GRN within a possible disc-wide expression state, or even any particular developmental trajectory guided by the regulatory strictures of that GRN.

Hylomorphic Modules: Explanation & Ontology

With all of the above in mind, the point I wish to make ought to be clear: in order to have a sufficiently rich understanding of the nature of a developmental module and its associated generative capacity, we have had to appeal to a *holistic* conception of its system-wide *causal structure* in which its various possible developmental trajectories *toward* particular morphological end-states are *dynamically united*.

Importantly, although this higher-order causal structure to which we must appeal is in an intimate way metaphysically tied-up with the mereological make-up of a developmental module, as its constitutional elements specify the module's possible expression profile (which define its corresponding state-space) and the regulatory logic which governs the temporal transitions between them, the preceding discussion has strongly indicated that this abstracted causal structure is importantly *conceptually independent* of that make-up, in that each state which comprises its space is defined *functionally* (as a weighted Boolean function), and the resulting topological structure, *qua* functional mapping, is conceptually independent of the mechanistic particularities of the activities of the module's GRN elements. This is further evidenced by the fact that a wide variety of permutations in the mereological make-up of a module which are nonetheless causally connected by the same regulatory architecture will result in that system's higher-order, topological structure being unchanged: thus, a particular *geometrical-cum-dynamical mapping* cannot be conceptually wed to any particular set of constitutional elements (Gilbert & Bolker 2001; Jaeger & Monk 2015).[22] Indeed, the now popular evo-devo project of individuating homologue-specifying developmental modules *via* processual definitions, itself grounded in the overwhelming evidence that *distinct* GRNs have underwritten the *same* developmental modules over time, depends upon this fact (Rieppel 2005; Brigandt 2007; Love 2009; Wagner 2014).[23]

Furthermore, although this higher-order structure is conceptually distinguishable from the diverse array of its mereological underpinnings, it cannot for that reason be regarded as a mere heuristic artefact, as an appeal to its nature licences unique *explanatory* and *predictive* power with respect to the causal structure of the process of morphological development.[24] As we have seen, understanding the process of the development of a particular morphological feature as a dynamic traversal through a topological

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[21] Interestingly, Von Dassow & Munro (1999: 310) briefly note in passing the conceptual similarity between the causal privileging of end-state morphologies in DST models and an Aristotelian form of "goal-directedness".

[22] Thus, in accord with the classic Aristotelian picture, 'form' will be *multiply realisable* – the "one over many" - in at least an explanatory sense. See Mitchell (2012) for a comprehensive look at the phenomenon's various incarnations in contemporary biology.

[23] For an account which more explicitly defines homologous morphological structures in the framework of DST, see Striedter (1998).

[24] Even if the explanatory virtues provided by higher-order, dynamic models must ultimately somehow "bottom out" in the activity of mechanisms (as Kaplan & Craver (2011) argue), it's not clear that this detracts from their having genuinely novel explanatory power (Bridgandt 2015); for an opposing view, see Kaplan (2015). I discuss these issues in Austin (2016b).

mapping of expression stability affords a novel, non-mechanistic explanation of the *shape* and *structure* of a module's developmental capacity: this is an explanatory oblation purchased by an appeal to a module as a higher-order, dynamically integrated system, rather than by its mere characterisation as a specific set of "entities and activities" (Huneman 2010). But this understanding also provides novel, non-mechanistic *predictive* power with respect to that process, for the particularities of the higher-order, pseudo-kinetic curvature of the system's stability topology licences inductive inferences regarding both the probability of the module following particular developmental trajectories (under certain conditions, and more generally) and the probability of the module producing particular morphological permutations (under certain conditions, and more generally). This prowess is exhibited perhaps most prominently in cutting-edge cell biology, where the regulation and re-programmability of cell fate is analysed *via* the higher-order topological dynamics of stem cells (Bhattacharya *et al.* 2011; Li & Wang 2013), but it is present (and increasingly so) in the study of everything from plant morphology (Álvarez-Buylla *et al.* 2008) to carcinogenesis (Kaneko 2011).

Thus, in satisfaction of the twinned goal I earlier introduced, I have shown not only (a) that a higher-order, holistically dynamic, goal-directed structure can be conceptually distinguished from the particular vagaries of a developmental module's mereological underpinnings, but also (b) that by appealing to this structure, one is afforded a wealth of unique explanatory resources with respect to the generative capacity of that module and its associated morphospace. In other words, to return to our original formulation, I've shown that fully "capturing the nature" of a developmental module requires not only having a grip on its specific constitutive collection of genetic elements and the particular arrangement of their causal connectives, but also on the dynamically directed topology of its higher-order causal structure. Or, to put it yet another way: it is a job which requires an appeal to both matter *and* form.

While providing a plausible, empirically informed vindication of the Lockean definitional project of hylomorphism in the biological realm – which has been the sole aim of this paper - is no trivial task, one might yet wonder what the metaphysical worth of this toil is: what does a successful defence of (a) and (b) tell us, for instance, about the *ontology* of organisms? In line with the purpose of this paper, as stated in §1, I have intentionally remained silent on this issue in the hope that the results of the discussion might be of applicable value to a wide variety of specific accounts (of the kind earlier mentioned), and not stand or fall on the posits of any particular ontology. And although for that reason I have refrained from giving those results any ontological gloss, I think it's instructive to end by briefly more explicitly noting the ways in which they aren't in any way inimical to, and in fact offer conceptual support to, the typical ontological claims of contemporary hylomorphism.

Note first that showing that (a) is true is a prerequisite for attempting to defend the truth of the central claim of hylomorphism – that fully capturing the nature of an entity requires an appeal to both matter and form: whatever your particular ontological commitments, if the nature of entities cannot be shown to be at the very least *conceptually* bipartite, that claim is clearly off the table. Of course, (a) being true only secures the conceptual independence of form from matter, and one might reasonably expect a project which aims to aid the cause of hylomorphic ontologies to do better: wouldn't showing that form is also *existentially independent* from matter be of more use? In this instance, the answer is no. For although hylomorphism conceptualises entities as ontological *unities* of form and matter, this is a unity which is not taken to be established by metaphysically tying together – either through "composition or connection" (*Metaphysics VIII*, 6) - two existentially separate sub-entities. And because hylomorphism denies the very possibility of the existence of *uninformed* matter, or *immaterial* form, a call for the truth of something more robust than (a) betrays a fundamental misunderstanding of the doctrine.

That said however, vindicating the conceptual independence of form aids in supporting the ontological claims of hylomorphism in only a limited fashion – namely, by securing a metaphysical foundation for them. Showing that (b) is true, on the other hand, may go some way further in that task. If

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(b) is true, and the higher-order dynamic structure of developmental modules licenses *irreducibly novel* explanatory power with respect to the ontogenic processes of its mereological make-up then plausibly, given that explanation often traces causation, we may have *prima facie* reason for thinking that structure possesses irreducibly novel *causal power*. Importantly, while this sort of move is certainly defeasible, any proposed annulment of it on the grounds that "existential dependence *entails* causal ineffectuality" ought to be dismissed.[25] Not only would this sort of objection beg the question against hylomorphism, but as its defenders have been at pains to point out (Rea 2011; Koons 2014; Jaworski 2016), the *emergent* properties of entities which are typically acknowledged to existentially depend upon their 'realisation bases' are often assigned causal roles, and treated with ontological sincerity – a practice now widely adopted in contemporary developmental biology (Boogerd *et al.* 2005; Mitchell 2012; Salazar-Ciudad & Jernvall 2013; Pigliucci 2013).

If the holistically higher-order dynamic structure of developmental modules can be understood as a *causal* structure then, in line with the 'Eleatic Principle' ("to *be* is to *be powerful*") – widely adopted among neo-Aristotelians in the defence of dispositional realism – we have good reason for thinking it represents a fact about the *ontology* of those modules.[26] Indeed, the recent surge in support for adopting a Whiteheadean 'process ontology' in the philosophy of biology can be seen as a reflection of the growing consensus that such mechanistically irreducible, higher-order causal structures must be understood as genuinely "carving at the joints" of organisms (Henning & Scarfe 2013; Dupré 2013; Jaeger & Monk 2015).[27]

Putting particular ontologies aside however, the more general lesson I wish to draw from the preceding discussion is that both (a) and (b) being true not only reflects the assumption in contemporary developmental biology that this *formal* structure is no mere metaphor, or philosophical phantasm, but also functions as the conceptual soil in which a neo-Aristotelian hylomorphic ontology might flourish. That said, though the further question as to whether and to what extent any of the ontologies currently on offer bear philosophical fruit is no doubt an important one, it is an enquiry I leave for another time.

Summing Up

Though the neo-Aristotelian congregation has grown considerably in recent years, most of its members have hesitantly refrained from adopting a doctrine historically central to its metaphysical catechism, and understandably so – for while many have demonstrated its theoretical plausibility, few have offered a compelling account of its empirical viability. Throughout this paper, by focusing on the biological realm, and appealing to recent theoretical advances therein, I have attempted to do just that. To that end, I've argued that the hylomorphic claim that fully "capturing the nature" of a biological individual requires an appeal both to it *qua* an organised, connected collection of discrete parts and *qua* a dynamically directed higher-order holistic structure can be given empirical content. In doing so, I've focused on a particularly important class of biological sub-systems with the hope that, given their role as developmental building blocks, the account can eventually be generalised to a higher-level hylomorphic account of organisms.[28]

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[25] There are of course other, independent reasons one might have for rejecting that move – see Robinson (2014) for a recent critique.

[26] The principle originated in Plato's Sophist, and was reintroduced in to contemporary debates by Armstrong (1997).

[27] Waddington (1969) himself, the progenitor of the 'epigenetic landscape' concept, professed to being deeply influenced by Whitehead, as Gilbert and Bolker (2001) note. More recently, Hall (2013) has characterised the contemporary topological models of DST as having a natural home within a Whiteheadean ontology.

[28] The conceptual resources utilized here may even be applicable to a hylomorphic account of biological 'natural kinds', the first steps of which are undertaken in Austin (2016a).

While that crucial work yet lies ahead, the hope is that this paper has shown it a task worth its toil by making a compelling case that the hylomorphic creed is one worthy of contemporary conviction.

Acknowledgements

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