5 Levels, Perspectives, and Thickets: Toward an Ontology of Complex Scaffolded Living Systems

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Overview

Complex systems appear to be hierarchically organized, and the idea of compositional levels of organization is one classic strategy to capture this type of complexity. However, compositional levels are inadequate for capturing the complexity of complexity. Wimsatt's ontology for complex systems—comprised of compositional levels, theoretical perspectives, and causal thickets—is mobilized in an argument that living developmental systems are typically scaffolded in ways that not only make them "interactionally" as well as descriptively complex, but with the effect that their system/environment boundaries change dynamically through the developmental process.

5.1 Introduction

Herbert Simon (1962, 1966/1981, 2002; cf. Callebaut 2007) offered a model and a parable to explain the intuition that evolved natural and designed artificial systems should be hierarchically structured in nearly decomposable, compositional levels of organization. I argue that Simon's model does not adequately represent the phenomena of his parable and that his parable does not appropriately illustrate his model. There is a missing ingredient: *scaffolding* explains how hierarchical order appears to arise out of complex nonhierarchical order, whether built up from fully decomposable aggregations or instead originating in interactionally complex, nondecomposable structures—"causal thickets"—that are "pruned down" (Wimsatt, 1974, 1997, 2007). In other words, there is a dynamical aspect of the parable that Simon did not consider that explains plausibly how the parable works better than what Simon says about it. My explanation for the appearance of hierarchy is epistemic: we tend to ignore developmental scaffolds in the environment when we describe the structure of scaffolded systems and thus see them (from some perspective or other) as neatly hierarchical, when in fact they are far more complex.

At the same time, the role I propose for scaffolding in Simon's parable *undermines* the applicability of Simon's model to his parable and therefore its applicability to his competitive evolutionary explanation favoring hierarchy, so we are back to scratch in explaining the appearance of hierarchical order in nature. In complicating Simon's picture in the

parable, then, we are also seeking a clue as to how to revise or substitute for the model he applied to evolution and thus a clue as to how to formulate an extended evolutionary theory (Laland et al., 2014, 2015; Müller, 2017; Pigliucci & Müller, 2010; Wray et al., 2014). Before we can get there, however, we will need to understand more about what Simon says and, importantly, what Wimsatt says in response to Simon about the complexity of complexity. I suggest the idea of scaffolding lends credence to Wimsatt's intuition that complex systems are often such tangles, such concrescences (Winslow, 2017) of causal processes that we tend to recognize hierarchical structure in those cases in which human interpreters have "pruned" the multiple perspectives in a causal thicket to reveal hierarchy as *simplifications* of actual causal order.

5.2   Simon's Argument for Hierarchical Levels of Organization

Simon says that real systems are not truly decomposable into strict compositional hierarchies. Instead, they are *nearly* decomposable. In so-called hierarchical systems, interactions among components across subsystems are weak relative to interactions of components within subsystems. If the former were zero, the system would be strictly decomposable and the behavior of the whole a mere aggregate of the behaviors of its components (see Wimsatt, 2007 pp. 274–312, on aggregativity).

In most physical systems, however, there is at least *some* interaction across subsystems. Covalent bonds *within* organic polymers are much higher energy than hydrogen bonds linking atoms *between* polymers, yet many hydrogen bonds can hold polymers together. Temperatures in corners of closed rooms of a building equilibrate faster than temperatures for each floor of many rooms or the whole building of multiple floors because gas molecules within rooms interact much more frequently and with higher energy than do those among rooms (via heat transfer through dividing walls or under closed doors). Cells of a multicellular organism or bacterial mat carry on their metabolic processes somewhat in isolation from their neighbors due to their bounding membranes, but there is exchange of material across membranes as well, regulated by various mechanisms.

We can think of near-decomposability as a criterion for *relational* dynamical specification of boundaries of objects or processes or as a criterion for biological units, "modules," or even "individuality." The ratio of among-to-within (sub)system interaction is a measure of degree of modularity and dynamical independence and thus a measure of the extent to which real systems are ordered hierarchically. Simon's insights about hierarchy and near-decomposability have gained renewed currency in discussions of modularity in evolutionary developmental biology (Callebaut & Rasskin-Gutman, 2005; Schlosser, 2004), where there is great need to conceptualize units of developmental construction as well as units of adaptive evolution.

At the heart of Simon's essay is a parable of two watchmakers, Hora and Tempus. They each make watches of 1,000 parts, but Hora's are put together in ten-part sub-subassemblies, which in turn are assembled into ten 100-part subassemblies, which in turn are assembled into a watch of 111 subassemblies comprising $10 \times 10 \times 10 = 1,000$ parts. Each component subassembly, like the whole watch, is stable (on the time scale of the assembly process). Tempus, on the other hand, puts 1,000 parts together and only the whole is stable. When the phone rings from a customer to order a watch, the watchmakers have to put down their

partially built watches to answer the phone, and the work under construction falls to pieces. Hora thrives and Tempus goes out of business because Hora only loses a subassembly-in-the-making while Tempus loses a whole watch in-the-making each time the phone rings.

While Simon's parable is clever, it does not support the mathematical model he offers to interpret it, nor is it an apt model of developmental construction. Most commentary focuses on what Hora's procedure adds compared to Tempus's. I ask a developmental question to challenge Simon's assumptions: how can either Hora or Tempus make watches *at all* given just the conditions Simon describes?

The argument is roughly that the homogeneous Poisson model Simon uses to describe mathematically how phone calls disrupt the work carries with it the assumption that the step-by-step processes of Hora and Tempus are the same. Yet they cannot be the same due to the very dynamical argument Simon makes because Hora's subassemblies of up to ten parts are internally stable while Tempus's are not. This means that Tempus must be doing something different from Hora when he puts parts together, so the formal model *of the individual steps* for Hora and Tempus should differ as well as the overall structure of the resulting watches. But if that's right, Simon can't apply the same Poisson model to both watchmakers step by step. I think that Tempus must be applying more sophisticated and extensive external *scaffolding* than Hora, either in how they hold parts with their hands or how they use external scaffolding jigs and clamps (which is what real watchmakers do). Without fancy scaffolding, it is hard to imagine Tempus could build a watch at all, phone call or no phone call.[1]

Thus, while Simon's formal model (cf. Simon & Ando, 1961) may be an appropriate heuristic null model for some purposes, developmental construction is not one of them. What Simon should have said about his parable is that "scaffolding" complicates, but may answer, the developmental question about construction dynamics for complex systems. Unfortunately, what Simon should have said about scaffolding (if he had recognized the concept)—that it leads to "interactional complexity" (i.e., causal interaction across different perspectives on the descriptive decomposition of a system into parts at different levels)—violates the assumptions of near-decomposability. Scaffolding undermines Simon's argument for nearly decomposable hierarchy as the core notion individuating entities of development (and evolution). This is a result due to Wimsatt (1974, 2007, chap. 9).

I suggest that typical living systems, the kinds Wimsatt (1974) identifies as "interactionally complex," are constructed or develop by means of exogenous scaffolding or by means of self-scaffolding events in the developmental process. A different approach to complexity and organization than one based on what Simon says, taking scaffolding interactions in the developmental and evolutionary origins of modules into account, is needed to articulate concepts of complexity and modularity suited to evolutionary developmental biology and extended evolutionary synthesis.

It is important to keep in mind that Simon framed his argument as a *contrast* between competing aggregative (Tempus) and hierarchical (Hora) systems of construction. Wimsatt's (1974, 2007, chap. 9) critique looks at how hierarchy emerges from failures of aggregativity in the complex interplay between epistemic descriptions of systems as comprising parts (Wimsatt's "K-decompositions") and ontic descriptions of systems of causally interacting parts (Wimsatt's "S-decompositions"). Interactional complexity involves causal interactions that "cross-cut" system descriptions in ways not recognized by Simon.

5.3 Wimsatt's Three-Tiered Ontology of Complex Systems

I propose a shift of perspective: that hierarchical organization be viewed as an *achievement* from the (ontological) top down, not something built from elemental building blocks from the bottom up. In my view, what is given, as William James said, is how nature appears to a baby lacking experience: "one great blooming, buzzing confusion" (James 1918, p. 488). Even human design doesn't proceed from the bottom up. To make a watch, car, or computer, you design from the top down in that designing and building must conjure a context and not just building blocks or at least a vision of system function that can be realized in a configuration of material parts.

Even without design, evolution works with *preexisting* organisms and environments, which form the "given" context in which evolution operates. Scientific investigations of nature must begin with humans entering into relationships with nature, which always already creates "causal thickets" in Wimsatt's sense, even if we have a theory by which to work some descriptive simplification on the phenomena. A theory may guide an observer, collector, or experimenter to move quickly from thickety experience to a more orderly, interpretable interaction by resolving, pruning, or reducing. However, the increased speed and confidence in how to approach a new problem or phenomenon when armed with a theory does not make "nature" any less of a thicket than it appears at the start of a new experience.

Where Simon might have started with his parable of two watchmakers would have been to set the scene of his investigation, just as he started his mathematical modeling by announcing presuppositions. To tell the parable, Simon might have imagined walking into the two watchmakers' shops to see how they make watches. There would be a mass of clutter and confusion (to those uninitiated in the habits of watchmakers) of jigs and clamps, tools and workbenches, the accoutrements of watchmaking. These would be noticed before the tiny watch parts. Look at a building or bridge under construction and the first thing you notice is the scaffolding, not the obscured building-in-formation. Watchmaking is as much about the scaffolding as it is about watch parts. A story or model that does not tell us *how* to put two watch parts together, only *that* they are, cannot tell us about the (dynamical) organization of watchmaking, only about the structure of (finished) watches. But the whole point of Simon's argument was supposed to be to open up the black box of watch *making* in order to consider why the finished products tend to have the structures they appear to. Simon just didn't open the box wide enough.

I think Simon's parable would be better articulated if it started from consideration of the workshop, not just of watch parts. In the same spirit, I draw from Wimsatt's work an articulated framework of concepts about complex systems to interpret dynamic adjustments of system/environment boundaries in developmental scaffolding processes. I think that most or all developmental systems, just as most or all systems of manufacture of artifacts, are in the class of systems Wimsatt calls interactionally complex.

In his 1974 critique, Wimsatt pointed out that there are two kinds of complexity relevant to Simon's argument (as Simon himself noticed in his discussion of descriptive vs. system complexity in the original paper). Wimsatt gives an elegant and penetrating account of a distinction between descriptive and interactional complexity (Wimsatt, 1974, 2007, chap. 9). Systems are descriptively complex when they admit of different descriptive "K-decompositions" (see Kauffman, 1971) of a system into parts from different theo-

retical perspectives. "Decompositions of the system into parts whose boundaries are not spatially coincident are more descriptively complex than systems whose decompositions under a set of perspectives are spatially coincident" (Wimsatt, 1974, p. 176, cf. 2007, p. 181). In nested hierarchical organizations, the boundaries of parts are contained in or coincident with those of more inclusive parts (at higher levels of composition). If different descriptive decompositions of a system give noncoincident spatial boundaries, the system is complex in a way that Simon's story of temperature equilibration of rooms in a building or parable of watches as systems of solid state parts is not. Wimsatt compares a piece of descriptively simple granite with a descriptively complex fruit fly (Wimsatt, 1974, see his figure 1; 2007, figure 9.1, p. 183).

A system can also be decomposed into subsystems of *causal* interactions ("S-decompositions"). Wimsatt describes interactional complexity in terms of the ratio of the strength of causal interactions among elements *between* interacting subsystems (as bounded by different parts decompositions) relative to the strength of causal interaction among elements *within* interaction subsystems. A system is interactionally simple if the interactions *within* subsystems tend not to cross the boundaries of K-decompositions and interactionally complex to the extent that they do (Wimsatt, 1974, figure 2; 2007, figure 9.2, p. 185).

Wimsatt revisited his distinction among three ontological notions or tiers in an ontological hierarchy: compositional levels, theoretical perspectives, and causal thickets, which he argues are required for "a full accounting" of the phenomena investigated by most sciences (Wimsatt, 1994, 2007, chap. 10, p. 194). He understands the relations between these categories of causation in terms of robustness of the entities that occupy them. One way to interpret Wimsatt's concept of object robustness across perspectives is by analogy with his views on perceptual robustness (Wimsatt, 1981). Objects detectable by means of different sensory modalities are more robust than objects detectable by fewer or a single modality. A mirage may be detected by sight, but perhaps not by touch, whereas a real pool of water can be detected by both. Wimsatt's perspectives are analogous to sensory modalities—both are "ontic" and both also deeply anchor representational successes and cognitive experiences relevant to our knowledge of causal systems. Perspectives and thickets reflect the messiness of ontology when robustness of the "objects, properties, events, capacities and propensities" (Wimsatt, 1981) at levels of organization weakens or fails. He characterizes compositional levels this way: "Levels of organization can be thought of as local maxima of regularity and predictability in the phase space of alternative modes of organization of matter" (Wimsatt, 2007, p. 209). Differently put, levels are maxima of detectability across sensory or perspectival modalities.

For Wimsatt, what it means for objects in this phase space to lack robustness is for the levels themselves to break down, to cease to be a mode of organization. Because robustness is both ontic and epistemic—a property of things in nature *and* a feature of our description and modeling of nature—Wimsatt understands levels, perspectives, and thickets as both ontic and epistemic. The two are hand in glove, but it makes little sense to think of one as the hand and the other as the glove. "Things are robust if they are accessible (detectable, measurable, derivable, definable, producible, or the like) in a variety of independent ways" (Wimsatt, 2007, p. 196), where independence is understood as independent probabilities of failure of the different means of access (Wimsatt, 2007, p. 197). To be an object is to be knowable robustly (Wimsatt, 2007).

Wimsatt characterizes his ontological categories in terms of these ideas about complex organization. By levels of organization, Wimsatt means compositional part–whole relations in which wholes at one level function as parts at all higher levels (Wimsatt, 2007, p. 201). The "all" in this characterization expresses the sense in which decomposability or near-decomposability captures the relevant causal interaction aspect of the levels concept. His view of levels is something Simon could agree to. "I urge a view that Simon would share: that levels of organization are a deep, non-arbitrary, and extremely important feature of the ontological architecture of our natural world" (Wimsatt, 2007, p. 203).

But we can *describe* entities as residing at multiple levels of organization, so if the entities we can most easily identify are the most robust ones, "relations must hold between descriptions of the same object at different levels" (Wimsatt, 2007, p. 205). Because entities at higher levels of organization will have more parts with more degrees of freedom and emergent properties, the former will have "increased richness of ways … of interacting with one another" (Wimsatt, 2007, p. 205). By the same token, regularities at higher levels of organization will have more exceptions due to this increased number of ways of interacting. The "robustness" of objects begins to break down at higher levels as the exceptions overtake the rules. Because levels pick out maxima of regularity and predictability, their robustness "tends to make them stable reference points that are relatively invariant across different perspectives," and hence explanation tends to be "level-centered" (Wimsatt, 2007, p. 214).

When phenomena seem to occur "between levels," for example, Brownian motion (where entities of substantially different sizes interact), we tend not to recognize the clusters of objects (e.g., a dust mote plus the disturbing particles that cause it to display Brownian motion) "as entities" at all (Wimsatt, 2007, p. 215). We may give functional descriptions of such things, but "they" seem not to have "intrinsic properties," "since only levels have the intensity of different kinds of interactions among entities to fix unique sets of intrinsic properties as being causally relevant" (Wimsatt, 2007, p. 216). These points bear on the status of scaffolds: when a scaffold and what it scaffolds interact (combine), even when they are roughly of the same size, their functional roles are so different that we tend not to recognize the pairings as entities in their own right. We also tend to underestimate the strengths of interaction between them.

Wimsatt continues with the story of the breakdown of regularity: "As the richness of causal connections within and between levels increases, levels of organization shade successively into two other qualitatively different kinds of ontological structures that I have called, respectively, 'perspectives' (Wimsatt, 1974) and 'causal thickets' (Wimsatt 1976a)" (Wimsatt, 2007, p. 205). In particular, when interactions become complex in Wimsatt's sense, the "neat compositional relations break down," so "levels become less useful as ways of characterizing the organization of systems" (Wimsatt, 2007, pp. 221–222) and "other ontological structures enter, either as additional tools or as replacements," including perspectives. Indeed, "perspectives cannot be ordered compositionally relative to one another" as levels could (Wimsatt, 2007, p. 231).

Wimsatt's notion of perspectives recognizes that the state variables describing causal interactions of entities, organized as parts of a whole, may be salient to a class of observers because of the ways those observers (and, I would add, scaffolds), in turn, causally interact with complex systems (Wimsatt, 2007, p. 227). Moreover, the variables are not taken to be complete, so other perspectives are possible. However, for the problems and interests

of a class of observers (or scaffolds), a perspective may describe a complex system well enough for their particular purposes, while another perspective may describe the same system differently but well enough for other purposes, so more than one perspective might be "applied" to the behavior of a system at a time (Wimsatt, 2007, pp. 227–228). Thus, scientific practices for studying complex systems tend toward a form of pluralism, rather than forms of (apparent) monism with a reductionistic strategy applicable to the more robust entities occupying (typically lower) levels of a hierarchical organization. Similarly, a theory of the engagements of scaffolds in facilitating the development (or maintenance) of a complex system must tend toward a form of theoretical pluralism, because the dynamics of different sorts of scaffolding interactions will call for different "calculi" of combinations and permutations afforded by the many ways scaffolds might interact with their "targets."

With still further interactional complexity, even perspectives begin to fail: empirical problems become "cross-perspectival" (Wimsatt, 2007, p. 234). And when the boundaries between perspectives begin to break down, Wimsatt describes the situation as a "causal thicket." For example, what counts as a genetic perspective and what counts as a physiological perspective in phenomena of gene expression become entangled with questions of the nature of hereditary transmission (e.g., in research into transgenerational epigenetic inheritance). Is the methylation reaction leading to so-called epigenetic marking of DNA a chemical reaction, a physiological interaction, or a hereditary transmission? Or is it a causal interaction crossing all three of these perspectives on atoms, molecules, cells, and organisms? Another example is when biological entities participate in "culture": it becomes challenging to distinguish organisms as cultural or as biological phenomena and thus subject to sociocultural versus biological theories and perspectives other than by relying on reductionistic theories promising to map all phenomena to a lowest level of organization (e.g., genes), despite the many causal and compositional relations inherent in such "thickety" problems. Wimsatt motivates the notion of a causal thicket by appeal to those biological systems that have emergent psychologies, ecologies, socioecologies, and sociocultures (see figure 10.2 and its legend in Wimsatt, 2007, pp. 233–234).

5.4   Pruning Wimsatt's Causal Thickets: A Scaffolding Perspective

Most approaches to thinking about complexity are bottom-up, from some base notion of simple parts or simple systems. But if Wimsatt is right, evolved living systems are highly complex, entangled in (and as) causal thickets. Looked at from the top down, from top-tier causal thickets, we might consider the work done to understand these systems as a form of "pruning," of idealizing or abstracting away from some ontological perspectives in order to reveal the hierarchical structure "within" the system rather than only recognizing complexity in failures of aggregativity or robustness of the organized wholes on some account of hierarchical organization of the lowest tier of the ontology.

Wimsatt does *not* think that there is a natural (e.g., evolutionary) trajectory from levels to perspectives to thickets. He takes the ontological ordering of complexity and the breakdowns of regularity and robustness that form perspectives and thickets to be taxonomic rather than temporal (Wimsatt, 2007, p. 222). I am not so sure. Breakdowns and buildups of regularities can have a temporal dynamic in real systems. In my view, developmental scaffolding presents such a type of case. Scaffolding presents situations in which the

orderliness of compositional levels is disrupted dynamically by the association of scaffold and scaffoldee. The disruption is critical to taking the scaffoldee through developmentally unstable states to new ones affording further developmental possibilities not previously available (Bickhard 1992).

Viewed temporally, Wimsatt's ontology can be read as supporting a dynamical account of "developmental transition," following the pattern of accounts of evolutionary transition (Maynard Smith & Szathmáry, 1995, 1999; Szathmáry, 2015). A developmental transition is a contingently irreversible change in the way development can proceed. Some developmental transitions may mark what classical embryology calls "stages," although not in as theoretically principled a way as I have in mind for scaffolded developmental transitions (see Griesemer, 2016, 2018).

No matter how one characterizes complexity, our tendency to characterize origins in terms of simple, minimally complex systems entails that complexity can only increase over time. Moreover, if evolutionary transition is a process that creates new levels of organization with new units of selection, by composing biological entities at one level as parts of emergent wholes at a new level (Maynard Smith & Szathmáry, 1995; Szathmáry, 2015), then it would seem that Wimsatt's characterization of the increased degrees of freedom and emergent properties of wholes at the new level should afford more ways of interacting compared to the components at lower/earlier levels. I think it likely, although I cannot argue it here, that evolutionary transitions and what I am calling developmental transitions increase the degree of intersystem, cross-perspective interaction.

It would seem to follow, as new levels emerge in transition processes, that scaffold–scaffoldee pairs are just the sorts of entities that mark a breakdown of levels of organization into organisms and groups. Scaffolding bonds may be physical or social, but they are more intimate and serve developmental functions more fundamental than ordinary interactions among members of a group. Groups formed from scaffolding processes should look more like "individuals" than mere aggregates but less like individuals than organisms.

Differently put, the problem of temporal order in the ontological structure of nature looks different in light of evolutionary transition theory than from the perspective of a multilevel selection theory fixed by a static compositional hierarchy such as Richard Lewontin's (1970) interpretation of Darwin's principles and the units of selection. Note, however, that Hull's account of units of selection (Hull, 1980, 1988; see also Griesemer, 2005) recognized that levels of selection are dynamic and "wander" among the compositional levels as entities *at* levels dynamically come to satisfy or cease to satisfy Darwinian criteria. I think Hull's observation points to the dynamism of levels of evolution inherent in Wimsatt's story of "breakdown," not merely of descriptions, but of the hierarchical order of nature itself. What I add here is the thought that this same dynamism applies to the scaffolded development of organisms as well.

Because Wimsatt's notion of interactional complexity involves both epistemic (K-decompositions) and ontic (S-decompositions) aspects, one can see how his ontological ordering in terms of complexity might be read as taxonomic rather than temporal. Interactional complexity requires there to be multiple K-decompositions, and scientists may only produce those for systems already organized hierarchically. I do not, however, think it follows that there cannot be local causal progressions or trajectories between these ontological "states" of organization.

Wimsatt's view that the ordering is taxonomic only may be an artifact of his account having been formulated in terms of departures from Simon's account of hierarchy and near-decomposability, which Simon built on a physical theory of the organization of inactive matter. Simon only argues that hierarchically organized developmental systems (Hora-like modular constructions) should outcompete nonhierarchical developmental systems (Tempus-like aggregative constructions). Neither Simon nor Wimsatt offers an origin story of the two forms of variant organization. An origin story would include imagining the context in which construction can occur, such that the two kinds of systems might compete.

Simon, for his part, never seemed to inquire into the causes of the fixity of the starting conditions for his parable of the watchmakers or thus for the fixity of parameters of the model purported to describe it. I don't think Simon would have thought to ask how Tempus's workbench might be organized to make watches at all under the severe requirements of Simon's aggregative picture. Anyone who troubles to go into the "back room" of a workshop where such work gets done or into the yard of Wimsatt's "backyard mechanic" will find a causal thicket of parts, tools, scaffolds, and systems in various states of assembly, disrepair, or decay.

It may be that when scientists approach new problems or phenomena, they have a highly constrained, theory-guided perspective on how to make sense of what they experience, but that doesn't mean their *engagement* isn't messy and interactionally complex, at least at first, or that "the system" isn't so messy that it must be given an idealized description by the scientist as containing just the building blocks of interest while backgrounding everything else as context or environment or mere conditions.

Philosophers idealize this engagement when they neglect to consider the mess of multiple perspectives of science in practice: getting the grant, negotiating research permissions, organizing equipment and personnel, arranging to get into the field, setting up the lab in the first place, and whatever other "external," "social," "bureaucratic," or "merely pragmatic" conditions enable scientists to *justifiably* engage with "the phenomenon." That socioecological or sociocultural thicket is part of the phenomenon (no matter whether the discipline in question is anthropology, sociology, psychology, biology, chemistry, or physics). Until the mess is tamed and the thickety tangle of causes is pruned in an attempt to simplify the system and its description into a working empirical phenomenon from the perspective of the work to be done, the theory to be used as a guide will be no match for the phenomenon. Nor can a guiding theory succeed in targeting a focal level in "the" compositional hierarchy of elementary particles, atoms, molecules, and so on, until the thicket is pruned into a manageable shape (Wimsatt, 2007, figures 10.1, p. 224 and 10.2, p. 233). For a physics lab, the vibrations shaking the equipment and the trucks in the street outside the lab that are doing the shaking are all parts of the system until physicists intervene to impose physical barriers to vibration that "isolate" the phenomenon they are studying from its "surroundings."

That is merely an epistemic view of Wimsatt's ontology from the top down: while nature might be "organized" in levels, perspectives, and thickets, our human investigations of nature tend to progress from thickets to perspectives to levels: that is what it means to pursue a reductionistic research strategy (see also Bechtel & Richardson, 1993).

I aim to make a Wimsattian ontic claim as well: living things in general encounter "nature" as a process of entering causal thickets whose complexity they resolve, manage,

and indeed impose causal order upon by their actions and interventions. The picture here is that to enter a causal thicket without taming, mastering or coping with it is simply to be swept up by it and to survive by mere luck or perish in bewilderment, like William James's proverbial baby.

Perhaps, abstractly speaking, one might view interventionist accounts of causation, such as Woodward's (2003), as imposing conceptual order on causal networks first faced as causal thickets. The interventionist view can be used not only to interpret the causal character of a network of interactions but also to simplify it. An intervention "sets" the value of a variable in order to assess what relations change or not as a result of the intervention and can be used to infer causation in terms of that changed network structure. By the same token, intervention *simplifies* the network. To intervene, to "do" (Pearl, 2000; Pearl & Mackenzie, 2018), as opposed to infer or calculate, is to cut off part of a thickety network, insinuating an investigator-controlled cause as a substitute for a "natural" or "observed" input. If that natural input is at the head of a complex subnetwork, then the intervention has the effect of simplifying the network under investigation by pruning away the subnetwork upstream. To understand causes in this interventionist way is to simplify a causal network's thickety structure to the point where one can take a perspective or find a level at which to interact with "it."

The epistemic picture of Wimsatt's ontology, viewed from the top down, can be deployed as part of a heuristic strategy to look for how "ontic" developmental transitions can happen in the opposite direction to Wimsatt's description of breakdown from the bottom up. Breakdown occurs epistemically from levels to perspectives and perspectives to thickets, as scientists realize that their descriptions fail. But ontically, or we might say, "in practice," as scientists engage phenomena and intervene in order to understand and interpret, they prune causal thickets so that they can gain perspectives (plural) on phenomena and perhaps trace causes further to discover the sort of regularity Wimsatt thinks is characteristic of levels. At each of these transitions, we can look at them the other way and consider how interactional complexity might be exploited to impose functional order to achieve a form of dynamical autonomy, "as if" operating in more simplified causal circumstances—how, in other words, *additional* complexity in the form of a (developmental) scaffold might *simplify* causal circumstances of the developing entity, so that the developing system may develop effectively.

A parent might help a child learn to ride a bicycle by *adding* training wheels (or running alongside while loosely holding the back of the seat). In this way, the parent scaffolds the child so that the uncontrolled minor fluctuations moving the rider out of balance do not lead to a catastrophic fall as the child shifts her weight and attention from street to handlebars, to legs, to parent, and back again in a trial-and-error attempt to maintain balance while pedaling forward. The addition of the parent to the "system" of child and bicycle creates a whole thicket of interactions that cross-cut perspectives on the mechanical, interpersonal, infrastructural, and organismic aspects of a child-operating-a-machine-in-the-street. At the same time, some of those interactions add constraints in the bicycle-child-parent system that screen off or prune some causes, freeing the learner from some thickety features that may not even be apparent to an observer (e.g., the choice of which street the parent guides the child down so as to avoid that dog on a leash in the next block that is likely to bark and scare the child into a dangerous wobble).

What I am gesturing at here is the notion that reading Wimsatt's ontology from the top down also suggests an *epistemic* perspective on the conduct of inquiry focused on "preparing" phenomena by pruning nature to fit perspectives. This reading suggests looking at causal thickets and tracing certain specific interactions pointing toward those causes or constraints that have "scaffolding effects" (i.e., consequences for delimiting or changing the boundaries between what is system and what is environment). Developer and scaffold join together to achieve a developmental effect for the developer, but in the process, their interaction causes a developmental transition to a new, "hybrid" compositional level *of the duo* that persists at least temporarily while the developmental process operates.

My example was a case of learning. Learning can be interpreted as a kind of developmental process. I view development quite broadly as any process in which new capacities are acquired, refined, or actively maintained. In other work, I characterize *biological* development as a process in which a capacity to *reproduce* is acquired (Griesemer, 2000a, 2014a, 2014b, 2016). The theoretical perspective I seek considers the role of scaffolding in biological development. In a sense, I offer a refined idealization of what Waddington called the "*epigenetic* environment"—but rather than picking out *all* environmental factors operating in development, I pick out just those that play a scaffolding role.

5.5   Dynamic System/Environment Boundaries

The problem with treating system/environment boundaries as fixed that is raised by the phenomenon of scaffolding has to do with ways in which interactions between a developing system and its scaffolds can themselves develop and evolve. In my view, developmental scaffolds, to do their work of facilitating development, *change* the system/environment boundary *while they are in interaction*, which means we cannot use static representations of causal relations and fixed structure of complex systems to capture the dynamism of system/environment relations. Scaffolding systems are cases, like Brownian motion, of phenomena that seem to occur *between* levels (Wimsatt, 2007, p. 214). We can interpret these changing system/environment boundaries as dynamical transitions to a new, higher degree of complexity and level of developmental organization. The combinations of scaffolds and scaffoldees are at least temporarily "at" a new level of developmental organization. These may only be transient, and the release of a developing system from a scaffold may represent the return of the system to a "lower" compositional level marked by the regularity we associate with system "autonomy" (see Moreno & Mossio, 2015).[2] Because understanding transient levels of organization is itself a conceptual boundary problem in which the orderliness of interlevel relations used to characterize things and their environments breaks down into conceptual thickets, we must view the conceptual landscape from multiple perspectives that track system/environment divides differently.

Students of phenotypic plasticity often endorse a "norm of reaction" view of phenotypes to express the idea that phenotype results from interactions with environment rather than by gene determination, so variation among environments as well as variation among genotypes (and phenotypes) must be tracked to express phenotypic outcomes. On this view, the range of possible environments an organism might experience in its development must be considered. But in development, organisms experience *sequences* of "developmental environments," and "genomes" (in a properly expanded sense) experience *sequences* of

scaffolding interactions (or their containing systems do). What conventional norm of reaction diagrams plot as "locations" on x- and y-axes are, in my view, *vectors* of changing quantities or qualities in development (Griesemer, 2016, 2018; compare figure 5.2A and 5.2B in this chapter). We need something akin to Waddington's full epigenetic landscape picture, or more, to represent it (figure 5.1A and 5.1B).

Nevertheless, norm of reaction diagrams are still genotype-centered descriptions, tracing genotype effects across alternative environments and into alternative phenotypic outcomes.[3] A more dynamic representation of developmental reaction norms is needed to represent these sequences of environments, phenotypes, and genomes as vectors in open, contingent, dynamic landscapes. Even Waddington's epigenetic landscape took genes to be pegs, working via gene expression and interaction in ways that render the *landscape* dynamic but the foundation as static: as pegs fixed in some static, abstract foundation so the landscape could change against this fixed scaffold as an organism developed. So long as the scaffolding is abstracted away, the calculus of population genetics holds the promise of a complete, if highly idealized, dynamical theory, in the sense that all "nongenetic" causes impinging on development are encapsulated (and marginalized) in the "error" or "environment" term of its equations.

One thing Waddington got right is that the temporality of the epigenetic environment in interaction with genes over the course of development is crucial, although there are (at least) two different relevant senses of environment: epigenetic and selective environments. He speculated that these concepts could be brought together by someone with greater mathematical ability than he had (Waddington, 1974, 1975, chap. 26). What I reject, though, is the notion that there *is* any fixed foundation to anchor genes in their interaction with environments: *all* of the elements of a developmental system can change, at different rates relative to one another, and what counts as the boundary of the system may also change.

5.6   A Developmental Scaffolding Reaction Norms Perspective

I propose a shift of perspectives on norms of reaction to bring the concept of scaffolding into the picture of interactionally complex systems. The perspective seeks to integrate traditional norms of reaction representations of genotype × environment interactions without the gene-centrism. I start from a Waddington-like epigenetic landscape perspective on development but without the abstraction of separate developmental and selective environments and without the abstracted fixed foundation from which genes may act.

I view biological development as the acquisition of a capacity to reproduce (Griesemer, 2000a, 2000b). Typically, this involves multiple stages of acquiring developmental capacities in a sequence until a capacity to reproduce is acquired. To become reproductive, for a metazoan, for example, may entail gastrulation, which in turn entails blastulation, which in turn entails cleavage from a fertilized egg. Each of these "stages" of development involved acquiring new capacities that resulted in part from changes in gene expression but also cell movements, tissue differentiation, and much more that affords the capacity to get to the next stage in the sequence.

Reproduction, on my view, is progeneration (propagule generation) of material entities with parts carrying a capacity to develop (Griesemer, 2000a). This functional, capacity-centered account is intended to be sufficiently abstract as not to be constrained to any

particular mode of development evolved in extant life or constrained even to cellular life. Some molecular systems must have been developmental systems if cellular life was to have *evolved* (through a Darwinian process entailing entities that can reproduce) from "proto-biological" molecular systems (Griesemer, 2014b; Griesemer & Szathmáry, 2009).

As I have argued previously,

Most developmental processes are facilitated rather than autonomous in the sense that the aid of an "external" process interacting with the developing system makes easier, or more likely, or with lower fitness cost, the acquisition, refinement or exercise of a new developmental capacity (Caporael et al. 2014). I say "external" because on traditional accounts of compositional levels of organization, the scaffold is one thing, the thing scaffolded is another thing, and the pair in interaction may or may not be treated as a thing at a higher level. (Griesemer, 2018, p. 155; see also Caporael et al., 2014a; Griesemer, 2014a, 2014b; Wimsatt & Griesemer 2007)

Scaffolds are typically treated as parts of the environment that facilitate development. They add constraints, guidance, coordination, timing, and (in some cases) safety or "fitness modulation" to a developmental process, sending it down a different and more (or less) felicitous developmental pathway than it otherwise would have gone without the scaffold. Think of scaffolds as specific triggers, switches, models, templates, or constraints that operate at branch-points of developmental trajectories in Waddington's epigenetic landscapes of developmental possibilities. Temperature triggers that drive development toward male versus female adult forms in turtle species with temperature-dependent sex determination are scaffolds set up by mother turtles, since the depth at which eggs are laid in beach sand cavities are determined by parental digging activities together with ambient environmental temperatures (Valenzuela & Lance, 2004).

Waddington imagined whole epigenetic environmental contexts of developing systems represented by balls rolling down landscapes, shaped by gene expression ("chemical tendencies which the genes produce") (figure 5.1A). The three dimensions of such landscapes are X: phenotype, Y: inverse of developmental probability given gene expression, and Z (into the plane of the figure): time. In some images (figure 5.1B), the landscape was portrayed from "underneath" as a system of gene pegs pulling gene expression guy-wires shaping the landscape into a (relatively stable) surface (Waddington, 1957, figures 4 and 5, pp. 29 and 36).[4] To depict developmental scaffolding, I combine Waddington's two representations (figure 5.1C) and add the "pull" of developmental scaffolds as abstractly anchored environmental factors that interact with genes to shape the epigenetic landscape. In the example above of temperature-dependent sex determination, mother turtle and ambient temperature are both pegs pulling from the sides of figure 5.1C, just as the baby turtle's genes are pegs pulling from below to create a window of environmentally regulated developmental opportunity for steroid hormonal control of gene expression, in this case.

Now we can idealize Waddington's landscape to consider not the whole landscape and trajectory but just those points in the landscape at which scaffolds mark and guide developmental trajectories (figure 5.1D). In this image, we can represent Waddington's notion of a selective environment as similarly temporally extended and dynamic, operating over the whole epigenetic landscape (rather than only on the end-state adult phenotypes) as a sequence of fitness functions representing a changing fitness surface overlying the epigenetic landscape. This representation idealizes the selective environment by depicting it as operating only through the fitness-modulating effects of scaffolding interactions. That is,
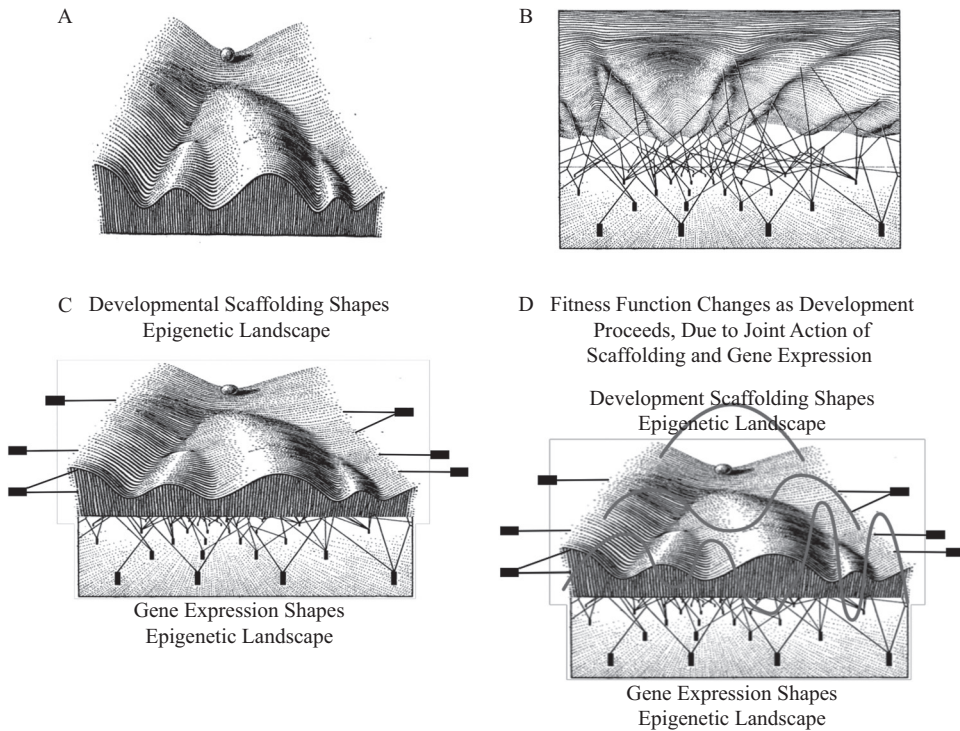
Figure 5.1
Waddington's epigenetic landscape. (A) Waddington's original depiction of the epigenetic landscape. The ball represents an organism at the beginning of its ontogeny. As it develops, it rolls down the landscape following a trajectory of favored paths (troughs). Alternative paths are possible, although more or less probable. (B) The underside of Waddington's landscape is underpinned by genes (pegs) in an undefined abstract foundation. The genes pull the epigenetic landscape into a shape due to gene expression (guy-wires), which manifests "chemical tendencies which the genes produce." (C) Waddington's figures (1A, 1B) fused together, with the addition of developmental scaffolds (pegs to the sides), which also pull the landscape into shape by facilitating development through interaction with the developing system. (D) Fitness functions superimposed on Waddington's landscape, representing time slices of a fitness surface extending over the whole epigenetic landscape. Figures 5.1A and 5.1B (and elements of 1C and 1D) are copyright 1957 from *The Strategy of the Genes* by Conrad Hal Waddington. Reproduced by permission of Taylor and Francis, a division of Informa plc.

it does not represent the full complexity of the fitness surface but rather locates *developmental transitions* in fitness at developmental scaffolding "events."

From this perspective, developmental processes can be narrated as sequences of scaffolding interactions through which systems acquire new developmental capacities. The exercise of these new capacities advances developing organisms through epigenetic landscapes in their trajectories from birth to death. Along the way, scaffolds may modulate the fitness functions that describe natural selection operating among variant developmental systems in selective environments (figure 5.1D). These might be modeled as actual selective environments operating among variants in a population or as potential selective environments defined over the developmental possibilities of a given developing system, where the near-future developmental outcomes (of the rolling ball at $t+1$, given that it was at t) may afford different selective values to the developmental states that would be reached with or without a given scaffolding interaction.

Waddington's epigenetic landscapes represent the space of developmental possibilities for each state at each time but only incompletely insofar as they do not explicitly represent scaffolds that also have "guy-wires" pulling the landscape into a shape or constraint system, as Tavory et al. (2014) point out in their characterization of "social-developmental" landscapes. In figures 5.1C and 5.1D, I have added these scaffolding "guy-wires" as additional causal interactions crossing from the theoretical perspective of ecology to that of development.

Importantly, in considering the place of scaffolds in the epigenetic, social-developmental, or any other causal thicket-like landscape of causal factors that cross perspectival boundaries between ecology and development (e.g., if organisms' active behavioral choices co-construct their environments as their environments co-construct them), we can consider two ways of understanding and interpreting the implications. One mode relies on the kind of abstraction Waddington used to represent genes as conceptually *outside* the developing system, pulling on the landscape to shape developmental trajectories. In that mode, scaffolds are just an additional, interacting source of developmental constraint coming from the environment rather than from internal constraints. Waddington's abstraction reflected his desire to integrate development into the then-current neo-Darwinian gene-centric picture rather than to present an alternative theory incompatible with neo-Darwinism. Another interpretation recognizes the interaction of a scaffold with a developing system as generating a new developmental system—one with the scaffold as a *part*. Two balls (organisms) rolling down the (possibly transformed) landscape may temporarily join to form a hybrid developing duo and then perhaps separate.

In many cases of developmental scaffolding, the short temporal duration of the interaction relative to the duration of embryogenesis or the whole life trajectory of a developing organism may lead us to treat the scaffold as "environmental," especially if the resulting acquisition of a new developmental capacity of the system leaves it morphologically largely unchanged after the scaffolding interaction has ceased. People rarely judge gradual or slight phenotypic or parts change to constitute numerically distinct individuals. But for theoretical purposes, this might be a mistake if the change in developmental *capacity* marks a necessary condition for further development, or a seemingly slight deflection in capacity has the potential to produce a substantially different developmental outcome, as Waddington's landscapes were meant to illustrate.[5]

Examples of gradual change, in which the scaffold is likely to be treated as environmental, rather than as part of the developing system, might include the use of a fixed substrate as anchor for a stage in a developmental process. A rocky surface can scaffold pupation in insects. Inanimate triggers or conditions may scaffold a developmental response at an appropriate time in development (e.g., when a temperature profile in the sand triggers temperature-dependent sex determination of developing turtle offspring). These triggers or environmental conditions function as scaffolds when they are set up as triggers through the effects of scaffolding agencies that select among environmental variations.

The picture I have in mind is one in which organisms develop in *sequences* of developmental environments (the time steps in Waddington's diagram) rather than in *alternative* environments as described contrastively in norms of reaction diagrams in terms of, typically, a single parameter of measurable environments, for example, temperature or altitude (compare figures 5.2A and 5.2B). The point is that environments are processes, just as are developing systems and as is natural selection. All are distributed over the whole life
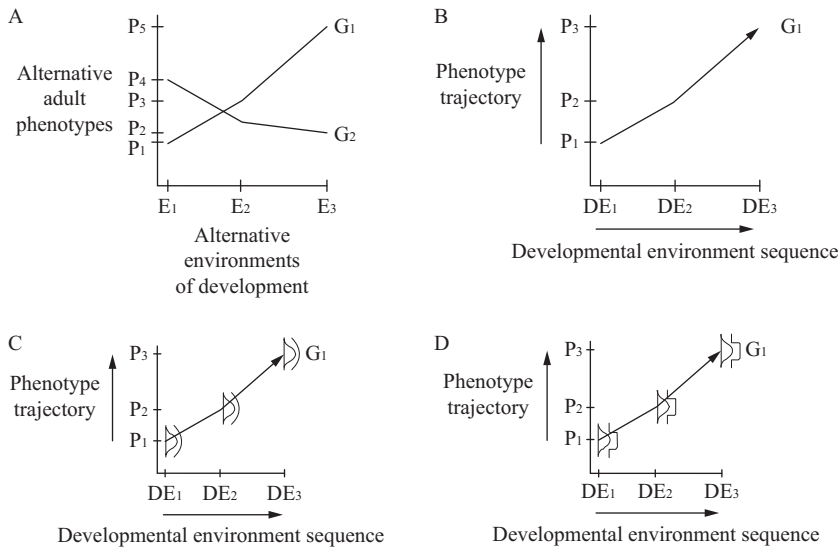
Figure 5.2
Conventional and developmental norms of reaction diagrams. (A) Conventional norm of reaction diagram showing the adult phenotypes (vertical axis) of organisms of genotypes G1, G2 as they would develop in alternative environments, E1, E2, and E3 (horizontal axis). (B) Developmental norm of reaction showing the developmental trajectory of an organism with genotype G1 through a sequence of developmental environments marked by developmental scaffolding events $DEi = \{DE1, DE2,$ and $DE3\}$ (horizontal axis). The phenotype also displays a trajectory through states $Pj = \{P1, P2,$ and $P3\}$ (vertical axis). (C) Same as B with phenotype distributions around Pj and (Gaussian) fitness function superimposed. (D) Same as B, but with a fitness function modulated (changed in shape to be more permissive of phenotypes farther from Gaussian optimum) due to developmental scaffolding.

trajectories of living organisms. They can, for very specific purposes, be idealized as occurring at points in life trajectories, but these are idealizations that may yield a misleading picture of system/environment boundaries as static. By not taking for granted what counts as system and what counts as environment when we first encounter a new phenomenon, we might look upon some aspects as scaffolding that changes the boundary *between* what might otherwise be identified as system and what as environment.

In this vein, recognition that a scaffold is interacting with a developing system amounts to identifying a mosaic or hybrid system. This "new" system would have to be recognized as creating a new system/environment relation as well, since a piece of the environment has become a part of the system. Conventional norm of reaction diagrams cannot (fully) capture what happens in the genotype × environment interaction of this developmental hybrid system. What counts as "environment," including both developmental and selective environments, changes at different points in scaffolded development. What is system at one point in development becomes a part later when a scaffold "joins" it. How selection operates may also change as scaffolds shift developmental trajectories from what they otherwise would have been (Griesemer, 2016, 2018). As different scaffolding interactions take place over the course of development, what count as system and environment depend on whether one takes the perspective of the scaffold or that of the developer or, rather, of the duo. On this reading, conventional norm of reaction diagrams are "adultocentric," in that they display adult phenotypic outcomes of development in possible alternative environments (Griesemer, 2014b, 2019; Minelli, 2011). An alternative "developmental reaction norm

diagram" would take the environments of a norm of reaction to be the sequences of environments experienced and created by scaffolding interactions: a developmental sequence or vector in an epigenetic landscape. In figure 5.2C, time slices through Waddington's landscape are represented to show developmental trajectories of phenotypes subjected to local fitness surfaces (developmental transition probabilities). In figure 5.2D, the fitness surfaces of figure 5.2C are *modulated* due to the action of scaffolds at those points in development.

Genes are developmental constraints that interact in complex ways with scaffolds to change what counts as the developing system. The upshot is that the *units* of development may change with each successive scaffolding interaction. Scaffolds work by forming mosaic or hybrid developmental systems on some time and size scale defined by the interactors who form them. The salient processes during a scaffolding interaction cannot be reduced to effects of genes, even if the results of interaction can be calculated mathematically as "marginal" effects of genes in one (or more) contributors to the process. Marginal effect values cannot predict future developmental results because scaffolds, even if they are organisms, do not necessarily follow Mendelian or Darwinian dynamics in their functional-causal roles as scaffolds. We know from cultural evolutionary models that modes of cultural transmission and selection (e.g., social learning) need not follow standard gene dynamics, and scaffolding could be viewed as one generalization of "culture" in the context of development extending to many forms of developmental interaction inside organisms as well as to interorganism "ecological" interactions.

If the principles governing the dynamics of these mosaic/hybrid developmental systems are neither strictly Mendelian nor Darwinian, it is an open question whether there is a coherent theory to be had, assuming theory requires a "calculus" that is mathematically simple to operate, like population genetics. Moreover, it is not obvious that extended inheritance theories on my view of reproduction and development will look anything like an "expansion" by merely adding terms to a standard population genetics equation. This mirrors my understanding of the state of play in the debate over extended evolutionary synthesis: proponents charge that the modern, neo-Darwinian theory is inadequate, while skeptics wonder what form a proper theory *could* possibly take if the aim is to model a causal thicket where causal variables cross genetic, developmental, and ecological perspectives (Laland et al., 2014; Wray et al., 2014).

Perhaps recognizing the character of the conceptual challenge can provide insight into shaping a solution or at least guide us to instructive phenomena from which to prune the eco-devo-geno-evo thicket[6] into some semblance of explanatory, multiperspectival order. Or, alternatively, perhaps we will be forced to recognize that thickets by their nature, resist the regimentation of algebraic equation theories-as-usual, and conclude that thicket scientists must seek some other form of theoretical order.

The challenge can be sharpened considerably by diving deeper into the technical apparatus of Wimsatt's ontology of complex systems. He has offered hints, such as suggesting that we study the phase space represented by his epsilon, measuring the degree of interactional complexity, but against what other parameter? What would a Wimsattian phase plot for scaffolded development look like? Once we have the dimensions of a suitable phase space for the temporal dynamics of developmental transition, I think we will be on the path to an expanded and hopefully more explanatory configuration space for living

systems that might answer Simon's question: why do the systems we see in nature tend to be (or look like they are) hierarchically organized?

5.7   Conclusion: Toward a Theory of Developmental Transitions

I sketched a developmental scaffolding perspective on phenomena that seem to display a breakdown of perspectival order, forming causal thickets in Wimsatt's sense. I have been pursuing an epistemic project, deploying the notion of causal thicket to reflect on the problem of identifying units or components of perspectival order from the top down rather than from the bottom up as failures of hierarchical order. The project is to find and understand patterns among scaffolding interactions, classify them into kinds, and explore whether new forms of theory can describe, predict, and explain these patterns. The units of development become units of interaction; a "process ontology" for them would take interactions to be primary. The material realizations of these developmental interactions are what I have been calling mosaics or hybrids.

New theoretical possibilities open up by embracing the scaffolding perspective resulting from the top-down epistemic strategy. Maynard Smith and Szathmáry characterize evolutionary transition in terms of changes in the way genetic information is transmitted before and after a transition, noting that the relevant sorts of changes involve "contingent irreversibility," that is, a low likelihood of return to the earlier mode of transmission (Maynard Smith & Szathmáry, 1995, 1999; updated in Szathmáry, 2015). I characterized their account in terms of transitions of reproducers rather than replicators (Griesemer, 2000b). Here, I suggest that the ways in which scaffolds contribute to mosaic/hybrid developmental systems look like "nongenetic" "parents" of those systems in a sense analogous to the very different *developmental* contributions of egg and sperm in sexual reproduction. An extended genetics on my view would need to count not just other organisms as developmental "parents" but also the diverse scaffolds that play developmental roles. This may stretch the notion of inheritance beyond credulity, but inroads can be made by a turn to process (e.g., Jaeger et al., 2012). In some cases, scaffolds cause "developmental transitions," marking contingently irreversible changes in the way developmental capacities can be acquired. Developmental transitions display analogous contingent irreversibility.

The value of describing transition as a matter of contingent irreversibility is to underscore that not just any sort of scaffolding event plays the relevant kind of role in a new or extended Darwinian theory: developmental transitions may be relatively infrequent in development, just as evolutionary transitions are presumably infrequent in evolution, or they may be so common as to occur multiple times in each life trajectory. Not every adaptive change or major evolutionary innovation such as the evolution of flight, or terrestriality, marks an evolutionary transition, nor does every developmental scaffold have the dramatic effects of, say, gastrulation.

What I seek is an account of developmental scaffolding that can classify, describe, and maybe explain eco-devo-evo patterns of developmental transitions across a wide range of developmental systems. Some of those systems may be ones we presently consider to operate in causal thickets that resist evolutionary explanations, like many aspects of socioculture, sociodevelopment, and sociopsychology. It may be that they will always resist

because they genuinely are not evolutionary phenomena. But it is well recognized to be hard to answer that question using tools developed by a theoretical biology designed to handle hierarchies of biological organization grounded in a gene's eye perspective. That perspective begins to lose its grip in the face of Wimsatt's ontology and the new perspectives proposed by extended evolutionary synthesizers and has little to say in the face of causal thickets, other than to offer an in-principle reductionism that gets us nowhere.

Acknowledgments

Notes

1. It is an interesting question whether Simon's analysis applies to "soft" materials such as living cells or only to solid-state machines and artifacts. As well, it is important to consider whether Simon's analysis applies equally to development and evolution. I do not have space to address these questions here. My argument here is that Simon's model and parable do not sit well together, so neither can be a good guide to thinking about the complexity of complex living systems even if there are disanalogies between solid-state and soft materials, assembly and biological development, or development and evolution. Thanks to James DiFrisco for pressing these points.

2. Jan Baedke wonders whether this account, reversing Wimsatt's "tiers" epistemically as pruning thickets rather than emergence from failing levels, applies to situations other than compositional levels. I think it may, for example, apply to scaling phenomena but would require a very different analysis beyond the scope of this essay.

3. Sonia Sultan (2015, 2017) has recently called for a reassessment of the genotype concept in light of her views on phenotypic plasticity.

4. As Jan Baedke points out, Waddington's pegs could be generalized from genes to developmental factors, but I will not characterize them as such here in order to distinguish exogenous environmental scaffolds from genes as kinds of developmental factors and to take special note of the shift of perspective on the relation between genetic factors and environments that I propose on norms of reaction.

5. It should be emphasized that merely necessary conditions for the possibility of development, like environmental oxygen for aerobic metabolisms, are not developmental scaffolds because their presence/absence does not per se mark transitions in developmental capacities (although in evolutionary history, they may once have done).

6. The problem is worse than this since behavior is yet another relevant perspective, so the thicket is really etho-eco-devo-geno-evo.

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