PSA PHILOSOPHY OF SCIENCE ASSOCIATION

PHILOSOPHY OF SCIENCE

SYMPOSIA PAPER

Modeling Scaffolded Development into the Adjacent Possible Environment

James Griesemer

University of California, Davis, Davis, CA, USA
Email: jrgriesemer@ucdavis.edu

Abstract

I characterize a role for "environments" as ecological scaffolding of organism development in the evolution of novelty. I interpret Rainey's bacterial experimental system for empirically modeling evolutionary transition to multicellularity as an ecological-developmental problem in terms of a formal model of Kauffman's concept of evolution into the "adjacent possible." I propose a scenario to interpret scaffolds dynamically, treating them as organisms modeled in the same way as the developing systems they scaffold, rather than as fixed constraint boundary conditions. The scenario suggests avenues for mathematically modeling scaffolding dynamics.

1. "Environment" is a "thickety" concept

"Environment," like other challenging concepts in biology typically requires multiple, cross-cutting theoretical perspectives to serve a variety of scientific purposes. Biological nature is "thickety" rather than neatly organized into (nearly) decomposable levels (Wimsatt 2007; Griesemer 2021). In thickets, causal interactions "cross" boundaries set by descriptions from theoretical perspectives of phenomena occurring at those levels. Flows of energy or nutrients, climate parameters, predator-prey assemblies, species guilds, or communities each offer a different perspective on "environment."

Ecological processes "cross-cut" spatial or temporal boundaries of nutrient flows, climatic regimes, community assemblies, and ecological niches: Nitrogen or carbon atoms flow from prey to predators as community members migrate among habitat-types, reshaping habitat profiles of species niches. There is no single best perspective from which to characterize an ecological process or phenomenon; many are required.

We can think structurally about environment in terms of arrays of "resources," functionally in terms of fulfillment of roles in ecological or evolutionary systems or processes, or processually as having a dynamic of "its" own, comprised of yet more processes of cross-cutting interest in a focal process or system. Alternatively, we can

ignore all that and treat "environment" as merely the constraint that forms a shapeless context for some focal biological entity, structure, function, relation, or process.

One strategy for achieving greater understanding of environment as a concept is to restrict attention to a particular aspect and put off worrying about how that aspect relates to others, following one crooked branch through the thicket despite the whiplash of shifting causal mechanisms and theoretical perspectives. Here, the strategy is to restrict consideration of environments to those aspects directly affecting the biological development of a focal system or process in question. Phenomena "in the environment" of a system or process are treated as developmental scaffolds when those phenomena facilitate development in specific ways (Griesemer 2016).

Here, I sketch an approach to characterizing the role of ecological scaffolding in evolutionary transitions, understood as processes that change the way (level at which) *development* occurs. This is a twist on Maynard Smith and Szathmáry (1995), involving change in the way genetic information is transmitted. It emphasizes the integral role of development in reproduction and thus in transitions in individuality understood to involve new levels of development, while not denying the role of the evolution of inheritance systems that change the way "genetic" information, broadly speaking, is transmitted (Griesemer 2000a, 2000b).

I expand here upon the role for scaffolding characterized in the experimental system developed by Rainey and colleagues to explore ecological factors in evolutionary transitions (Rainey and Kerr 2010; Doulcier et al. 2020; Rainey et al. 2017). Treating ecological scaffolding of the kinds characterized in Rainey's experimental program dynamically and developmentally, as we treat the focal system, rather than as fixed constraints on system development and evolution, achieves a better appreciation of environmental contributions to evolutionary transitions. We should "eco-devo" our understanding of the dynamic role(s) of environment in evolutionary transition, not just characterize a structural or functional role for scaffolding.

This approach recharacterizes the conceptual landscape on a modeling platform for tracking the role of ecological scaffolding in the developmental dynamics of evo-devo processes. Here, I bring together conceptual resources drawn from theoretical, empirical, and philosophical literatures about evolutionary transitions and emergent phenomena in biology. One is Stuart Kauffman's idea about how to conceptualize environments in terms of what is adjacent to a system's actual environment (Kauffman 2000, 2019). A second is Rainey's bacterial experimental system for empirically modeling evolutionary transition to multicellularity (Rainey and Kerr 2010; Hammerschmidt et al. 2014; Black et al. 2020). A third is a dynamical model of correlated novelties formalizing Kauffman's picture of evolution as expanding into the adjacent possible (Tria et al. 2014; Loreto et al. 2016). The fourth is a conceptualization of scaffolding linking developing systems to aspects of their developmental environments (Griesemer 2016, 2021). Because one of these resources includes a formal model, the landscape suggests some directions for fruitful model development, although no explicit formal models are offered here.

A key goal is to explore the evolution of novelty, understood to emerge from development into Kauffman's "adjacent possibles." Development is modeled here to

align with a formal model of Kauffman's idea, as "terminal addition" of sampled environmental resources to a growing sequence resulting from interactions between scaffolding environments and developing organisms.

Combining these ideas with a clear view of the developmental role of scaffolding improves our ability to make sense of thickety system-environment interactions when *both* system and environmental scaffold are dynamic "developers."

2. Kauffman's "adjacent possible"

Kauffman (2000, ch. 7) considers the set of kinds of organic molecules on or near the Earth. He calls this the "actual"—a reaction graph of all actual molecular kinds and linking reactions. He estimates there are hundreds of trillions of molecular species among the actual. He depicts reaction graphs with two kinds of nodes: bubbles indicating substrates/products, dots/boxes indicating reactions. Arrows depict flow from substrates, through reactions, to products.

Kauffman characterizes the "adjacent possible" as a set of kinds of organic molecules related in a particular respect and degree to the actual:

> The adjacent possible consists of all those molecular species that are not members of the actual, but are *one reaction step away from the actual* . . . [that] can be synthesized from the actual molecular species in a single reaction step from substrates in the actual to products in the adjacent possible. (Kauffman 2000, 142)

These possibilities are only *made* possible by moving to an actual state one step away. Kauffman aims to explain the origin and evolution of life on Earth and the prospect of general laws of nature governing the production of novelty and diversity. For his purposes, the spaces of adjacent possibles are *chemical*. He also describes human economic systems, which I leave aside.

My scope is narrower: biological development and the role of environment in evolutionary transition. To move from chemistry to biology, read the adjacent possible abstractly, as involving an activity of a process delimited by a mechanism. Mechanism sets the narrative "grain" characterizing particular (causal) activities of processes, specifying what constitutes "one step" away from "inputs," for example, proton transfer mechanisms that specify steps in organic condensation reactions of that type.

The adjacent possible forms a specific sort of "counterfactual environment": If these substrates were to enter a specific reaction that the known laws of chemistry permit but has not, so far, operated in the actual world, they would produce a specifiable, nonactual product. The actual is expanded into this adjacent possible when realizing such a possibility and thus incorporating that novel (kind of) product into the actual. A developing or evolving biological system produces some trajectory through an adjacently possible environmental space.

The adjacent possible renders dynamical laws "unprestatable" (Kauffman 2019, xi). What is adjacently possible *now*, relative to the actual *now*, is prestatable, so long as we can specify the process, activity, and mechanism singled out for description, for example by applying laws of chemistry to specify all the available reaction types and

thus possible products adjacent to the actual. Kaufmann's point is that moving from the actual *now* into that adjacent possible in the *next* moment (on a timescale specified by the activity) entails that there is a *further* adjacent possible accessible from *there* which will only be actualizable from *it*, not from the actual. We can't visualize or "prestate" what is two steps away because what counts as the environment, relevant process, activity, and mechanism *there* depends on what would be experienced in that adjacent possible, not what can be experienced or prestated in the actual. That further adjacent possible is *not* prestatable because its *accessibility* depends on what will or may happen in the future but has not yet happened and may indeed never happen. Kauffman's argument points to limitations of physical explanations leaving out of account the causal processes that set up boundary conditions; in biology: "the environment." What distinguishes the living world is that life makes and remakes its own constraints, so conditions beyond what are adjacent to the actual are not accessible.

We cannot condition futures beyond the immediate adjacent possible because those future adjacent possibles involve *novelties*, not just in the kinds or species that form an "activity graph" of the actual but also in the reaction (activity, process) *types* accessible from adjacent possible to adjacent possible as well. Consider that a particular condensation reaction might *reduce* the number and kind of molecular species that would then be actual, and thus in turn change the reaction *types* available there, even if we were confident that the laws of chemistry we know allow us to articulate all the reaction types there could be. It is not so hard to see why the *production* of further novelties from novelties is unprestatable. The very process of evolution into the expanding adjacent possible means that we cannot state the constraints, even if produced by the operation of laws, that govern evolutionary dynamics.

What is beyond view may be possible but, in not being adjacent, it is difficult to "prestate" how it might figure in the evolution of such a system. Gravity plays an important role as a fixed constraint on the development of many multicellular organisms. A mother insect or frog may fix a fertilized egg to a rock or underneath a plant leaf, orienting embryological cleavage in Earth's approximately fixed gravitational field. A mother can also rotate an egg in the field relative to a moving abiotic substrate to maintain a fixed orientation in the field or, indeed, rotate the egg to change the egg's orientation to gravity. Whether a future substitution of mother for leaf or leaf for mother in future arrangements is prestatable as evolutionarily possible is the question. Lewontin (1978, 215) long ago made the point in resisting the notion of "empty niches" when biologists sought to characterize evolutionary adaptations as "solutions" to "environmental problems." Lewontin's critique of the idea that an environmental problem is to be solved by adaptation rested on the insight that evolution can change the problem as well as the solution. For Kauffman, evolutionary expansion into the adjacent possible changes what is "problematic" in ways that cannot be foreseen.

3. Rainey's experimental system of ecological scaffolding

An experimental bacterial system developed by Rainey and colleagues appeals to a role for ecological factors in evolutionary transitions from collections of reproducing

"Darwinian individuals" (Godfrey-Smith 2009) to reproducing collective individuals. They call this "scaffolding." I do not focus on their "cheater" hypothesis for evolutionary transitions (Rainey and Kerr 2010), but rather on the experimental system to address their emphasis on ecological scaffolding.

The system is characterized by a hypothetical ecological scenario: A "pond" with reeds growing out of the surface around which bacteria can aggregate in mats. Mats can manifest collective properties as discrete ecological entities when reeds are spatially separated. This may lead to fitness advantages or disadvantages among mats as well as among individual cells within mats through differential survival and reproduction at each level. Rainey and colleagues (e.g., Rainey and Kerr 2010; Hammerschmidt et al. 2014) developed mathematical models in which "cheaters" at the collective level in natural systems modeled by their experimental system may have become the "germlines." As Black et al. (2020, 427) put it, although Rainey's experimental system does not evolve true multicellularity because reeds remain necessary for the persistence of bacterial mats:

> Each reed allows establishment of a single microbial mat (the soma-like phase), with the spacing of reeds ensuring variation at the level of mats. Mats that collapse, for example, through physical disturbance, allow the possibility that an extant mat might, via production of a dispersing (germline-like) phase, increase its representation among the population of mats. The possibility of a selective process thus unfolds at the level of mats. (Black et al. 2020, 427)

Differentiation of roles into soma and germ is one hallmark of transitions to multicellularity on many accounts. "Cheaters" (dispersers) reap benefits of growth and survival in reed-organized clusters (e.g., access to oxygen at the surface interface) and escape their cluster to found new clusters around uncolonized reeds through cell-level migration and reproduction, unimpeded by constraints and costs of group living.

In the experimental system, vials containing growth medium serve as proxies for reeds in the hypothetical pond: Bacteria can cluster at the interface where the medium surface meets the vial wall. Vials in the lab serve as proxies for reeds in a pond, allowing experimenters to control "migration" between "reeds." Vials "scaffold" growth and stability of clustered cells, just as hypothetical reeds scaffold development of aggregating bacterial cells in mats. The vials are fixed constraints of the experimental system, supplied by the controlling investigator, just as reeds are fixed ecological constraints of the pond.

The only dynamism of the experimental bacterial environment is that vials and migrants come and go under strict control of the experimenter. In a natural pond with real ecology, reeds should be considered as developing, evolving organisms as well. An ecologist might *model* reeds as a fixed constraint of the bacterial system by focusing on the relatively short timescales of bacterial growth and reproduction in comparison to the longer timescales of reed growth and reproduction.

A further limitation of the experimental system environment (for present purposes) is that growth medium and vials function as *undifferentiated* environmental resources. The medium "recipe" is a constraint like the vial wall and medium/air interface (controlled by volume of medium): fixed by the investigator and controlled according to experimental protocol.

Even with these fixed constraints, their use in Rainey's experiments reveal an important role for nonliving, nondynamic ecological scaffolds in eliciting a transition to multicellularity. However, the hypothetical reeds in a pond have additional properties not modeled by Rainey's experiments. Because reeds are living, developing, evolving things, there is opportunity for coevolutionary, codevelopmental dynamics between bacteria and reeds. My interest is even more specific: How should we understand situations in which scaffolds are not merely fixed constraints but rather are active guides in system development, making "choices" that influence development, survival, and reproduction?

Put differently, how should we characterize environment if it does more than generates organism-constructed selective feedback to its niche-constructing organisms; what if parts of environments can function as *developmental* scaffolds, shaping developmental outcomes and modulating fitness effects in populations (Griesemer 2021)?

Three ideas help articulate a developmental scaffolding platform for extending Rainey's experimental system:

(1) development includes *extracting (sampling)* environmental resources incorporated into the developing system. Development is not only a reconfiguration or reorganization of existing parts but also assimilation of food, experiential learning, and active behavior engaging environments. Development entangles metabolism, growth, and other life activities with differentiation. Griesemer (2000a) characterizes development abstractly as acquiring a capacity to reproduce. We might characterize this developmental entanglement in acquiring capacities to metabolize, grow, differentiate, and persist to reproduce in part through sampling environmental resources. Ecological scaffolding contributes to development when it facilitates reproduction and to metabolism, maintenance, repair, growth, and differentiation when it facilitates persistence.

Kauffman's adjacent possible concept offers a way to specify "developmentally relevant" aspects of environment: those adjacently possible resources available for sampling for a system to "develop into." Scaffolding makes/shapes this availability. The adjacent possibility concept can help "eco-devo" evolutionary transition because scaffolding can drive changes in the level at which development moves into the ecologically adjacent possible.

(2) a *differentiated environment* in which some potential resources for system development are "familiar," some "novel." A resource is familiar if the developing system has encountered it before and previously incorporated a sample into itself as part(s) or experiences through learning. A resource is "novel" if it has not been encountered and incorporated by the developing system before. Two meanings are distinguishable: Items or experiences new to a particular system are *novel* to it, while items or experiences new to *all* systems are *innovations* (Tria et al. 2014, 1). This idea will be explored by interpreting Tria and colleagues' (Polya Urn) formalization of Kauffman's "adjacent possible" as a model for a *developing* system.

(3) *developmental scaffolding* of a system can be interpreted as a kind of mechanism that biases sampling and incorporation of familiar and novel resources into the developing system. This biasing changes the way(s) a developing system experiences "the environment" and creates a new *level* of developmental organization—the collective of scaffold and developer.
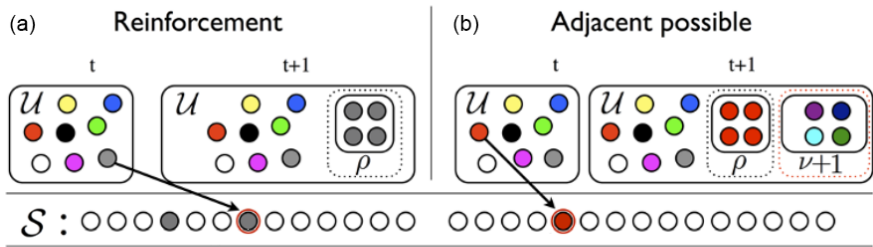
Figure 5 | Models. Simple urn model with triggering (a), (b) and urn model with semantic triggering (c), (d). (a) Generic reinforcement step of the evolution. An element (the gray ball) that had previously been drawn from the urn $\mathcal{U}$ is drawn again. In this case one adds this element to $\mathcal{S}$ (depicted at the center of the figure) and, at the same time, puts ρ additional gray balls into $\mathcal{U}$. (b) Generic adjacent possible step of the evolution. Here, upon drawing a new ball (red) from $\mathcal{U}$, $v + 1$ brand new balls are added to $\mathcal{U}$ along with the ρ red balls of the reinforcement step that takes place at each time step.

Figure 1. Tria model. Modified from Tria et al. (2014, 5), Figure 5 to omit panels 5c, 5d, with permission under Creative Commons License 4.0. https://creativecommons.org/licenses/by/4.0/. Figure in color online.

Bias in this developmental sense will be explored next by extending Tria's formalization to include a dynamic scaffold that *biases the model's sampling scheme* altering the probability that a particular subset of familiar or novel environmental resources are presented to a developing system for sampling and incorporation.

4. Tria model of Kauffman's adjacent possible

Kauffman's picture of the adjacent possible has been formally modeled (Tria et al. 2014; Loreto et al. 2016; cf. Kauffman 2019). Here, I adapt the Tria model by interpreting their *visualization* of the model as a simple representation of scaffolding environment *and* developing system. The Tria model's "rich-get-richer" sampling scheme in a Polya's Urn model is exploited to characterize development as the urn is articulated in a new way.

Polya's Urn involves sampling items with replacement (colored balls in Tria et al. 2014). A sequence of trials generates a sample, S, as an ordered set of sampled balls. When a ball is randomly sampled from the urn, it is replaced in the urn and a specified number of additional balls of the same color are added to the urn. This reinforces— increases the probability—that balls of that color will be sampled in future trials. Rich-get-richer is a kind of evolutionary modeling where sampled variants become favored by their "selection." Here, I interpret S as a developing "organism." Tria et al. (2014) adapt Polya's Urn to model Kauffman's adjacent possible in the following way (Figure 1a).

In addition to sampling with replacement and reinforcement, Tria et al. (2014) add an "adjacent possible" step: When a sampled ball has a color not so far represented in the *sample*, in addition to reinforcing it as before by replacement plus additions of the

same color, additional balls are added with colors not so far included in the urn (Figure 1b). Sampling creates an adjacent possible sampling space for the sequence of trials to "develop into." Tria et al. (2014) develop additional variations of the model (not shown in Figure 1), for purposes not of concern here.

I interpret the Tria model visualization of the sample sequence as itself a model of a developing system, S, and the urn as a model environment, U. In their model, the system's "development" results from randomly sampling the environment and incorporating environmental resources (colored balls) into the extending sample/developmental sequence.

To build out the conceptual landscape, we add two ideas: Ecological scaffolding plays a developmental role by biasing the sampling process to be in some way "developmentally appropriate" when incorporating particular resources at particular stages, and a well-mixed urn becomes organized through sampling bias in ways that represent an adjacently possible scaffolding *environment.*

The second idea was proposed by Tria et al. (2014) and further modeled by Loreto et al. (2016), who showed that the sampling scheme of the Tria model is equivalent to a random walk on a special undirected graph comparable to Kauffman's chemical reaction graphs. Encountering a new color in the Urn model is equivalent to a random walker visiting a previously unvisited node, making accessible a further graph fragment of adjacent, unvisited nodes.

5. Eco-devo scaffolding in the Tria model

Now we extend the Tria model to reveal a *dynamic* environmental role with scaffolds modeled as developing systems in that same environment, but with different accessibility relations to resources than the scaffolded system has.

Interpret the Urn environment, U, as a resource space in which scaffolded "developers," S_i, in an evolving population, S_n, sample resources to incorporate as they develop. Divide resources into two developmental kinds: familiar and novel. Suppose the environment is organized so that some resources are packaged in particular subsets (structures) with respect to the two kinds. Anything in U that biases resources available for sampling could be a "scaffold," as with Rainey's experimental air/medium/vial interfaces. Scaffolds are modeled as particularly ordered subsets of environmental resources, so in the modified Tria model, they can also be modeled developmentally by the same kind of process that produces focal developer, S.

In Tria's model, sampling is random with respect to U. In the modified scenario, environmental scaffolds "organize" the environment so that developer sampling of resources is random with respect to a *biased subset* of U, presented by a scaffold, for random sampling by S. In Tria's model, this is a bias in ball colors a developer can sample from/"develop into."

In a Tria model visualizing sample sequences as developers, sampling can be interpreted as metabolizing "food" resources incorporated in development. Converting environmental into developmental resources may be time sensitive: deleterious if consumed (sampled) at the wrong time, nutritious if consumed at the right time. Replacement in the Polya Urn scheme can be understood as returning "waste" products to U by excretion or death and decay of "organisms."

Suppose the scaffold is no mere biaser but also sensitive to the "developmental state" of the sample sequence being built, in presenting a *particular* subset of novel colored balls depending on the current state of the sample. A developmental scaffold may have the ability to monitor the system it scaffolds, as parents monitor offspring for this "right time" (Bickard 1992), biasing the developer's interaction with environment in an age- or stage-appropriate way.

Some novel colors are "developmentally appropriate" (in a particular color range, say) while others are less so. A colored ball is familiar or novel to a sample depending on whether it has already been sampled or not. Interpreting the sequence of trials as the developmental sequence of an "organism," S, novelty of resource sampled is analogous to movement of a developing system in an "epigenetic landscape" (Waddington 1957). The scaffold operates by biasing the sampling process in ways analogous to Waddington's gene-peg "guy-wires" pulling the landscape into a shape (Griesemer 2021).

Now scaffolds are modeled as developers, "Ss," in a slightly different sampling environment, U-Ss. The result of S's random sampling from *subsets* of environmental resources biased by scaffold, Ss, is system development more developmentally appropriate than if S had sampled the full environment, U, at random.

If this kind of biased sampling/development occurs in the context of a population, Sn, of developers, Si, and scaffolds, Ss, such that differential bias among scaffolding processes in U results in developer variation, some variations may be more or less favored in an evolutionary process. Differential scaffolding among members of a population of developers may result in fitness-effect *modulation* of the impact of random sampling of environmental resources on developmental processes (ibid.). Fitness effects of differential scaffolding with respect to what is developmentally appropriate to each developer at each sampling trial may result in differential system survival or reproduction.

Now we can conceptualize Kauffman's adjacent possible in terms of developmental scaffolding in the modified Tria model. Scaffolding generates an adjacent possible for a developing system, S, at time, t, where the scaffold, Ss, is a structured part of U that functions to bias the presentation of a subset of *novel* environmental resources thus made accessible to S to randomly sample. The formal sense of adjacency is that resources in U-Ss are only made available for sampling by the scaffold, not merely because they are present in U. The sense of possibility is that novelties are presented for sampling in this scaffolded way, never experienced before and only made available at the "right time," when the scaffold detects that the window of appropriateness to development at that stage has opened and not yet closed.

Returning to Rainey's experimental system, scaffolding reeds in the pond *also* develop and reproduce. This is not a feature of experimental implementation in fixed-constraint glass vials and controlled nutrient medium in Rainey's experimental setup. The modified Tria model shows a path to modeling *dynamic* hypothetical reeds in a pond.

Imagine reed development as acquiring straight, left or right bending tops, affecting (through a mechanism not modeled) how reeds scaffold bacterial mats assembling at their air-water-stem intersections. Left-bending stems tend to scaffold by presenting novel environmental resources to a developing system in the "blue" range of ball colors when the last ball sampled by S was blue-ish. Right-bending stems

tend to scaffold by presenting novel environmental resources to the developing system in the "red" range of ball colors when the last ball sampled by S was blue-ish. Straight stems tend to scaffold by presenting novel environmental resources to the developing system in the "gray" range of ball colors, regardless. These scaffolds would differentially affect development in ways that are more or less appropriate, depending on what advances development appropriately at a time when a blue ball has just been incorporated into the sequence.

A developmental monitoring mechanism of the reeds would presumably involve detection of what environmental resources (colors of balls) S has sampled so far or most recently. While order in the sample sequence (developmental process) probably matters in developing organisms, a simple tracker of colors sampled would suffice to model familiar versus novel colors.

Conclusion

We need a more detailed scenario about viable developmental pathways and mechanisms to fill out the reed pond story. Hopefully, the main point is clear enough. In Waddington's epigenetic landscape, a developing embryo (ball) poised at the top of the sloping landscape, can roll down toward maturity following different pathways. Which way it rolls, which (successful, viable) developmental outcome will result, is "unprestatable." Scaffolding modulates developmental outcomes through regulation of environmental resources available for sampling and incorporation. Fitness-modulating effects in populations of scaffolded developers may in turn provide clues to what future development holds, if only in the nearby sense of what is adjacently possible.

The aim has been to reinterpret and modify features of Tria's model of adjacent possibility to articulate a dynamic role for ecological scaffolding. A modified, biased sampling model would characterize evolutionary transitions to a collective level of scaffolded ways of developing. Whether these are contingently irreversible evolutionary transitions in Maynard Smith and Szathmáry's sense requires further investigation.

References

Bickhard, Mark H. 1992. "Scaffolding and Self Scaffolding: Central Aspects of Development." In *Children's Development within Social Contexts, Vol. 2 Research and Methodology*, edited by Lucien T. Winegar and Jaan Valsiner, 33–52. Hillsdale, NJ: Erlbaum.

Black, Andrew J., Pierrick Bourrat, and Paul B. Rainey. 2020. "Ecological Scaffolding and the Evolution of Individuality." *Nature Ecology & Evolution* 4 (3):426–36. https://doi.org/10.1038/s41559-019-1086-9

Doulcier, Guilhem, Amaury Lambert, Sivia De Monte, and Paul B. Rainey. 2020. "Eco-Evolutionary Dynamics of Nested Darwinian Populations and the Emergence of Community-Level Heredity." *Elife* 9 (e53433):1–39. https://doi.org/10.7554/eLife.53433

Godfrey-Smith, Peter. 2009. *Darwinian Populations and Natural Selection.* New York: Oxford University Press.

Griesemer, James. 2000a. "Development, Culture and the Units of Inheritance." *Philosophy of Science* 67 (S3):S348–68. https://doi.org/10.1086/392831

Griesemer, James. 2000b. "The Units of Evolutionary Transition." *Selection* 1 (1-3):67–80. https://doi.org/10.1556/select.1.2000.1-3.7

Griesemer, James. 2016. "Reproduction in Complex Life Cycles: Toward a Developmental Reaction Norms Perspective." *Philosophy of Science* 83 (5):803–15. https://doi.org/10.1086/687865

Griesemer, James. 2021. "Levels, Perspectives, and Thickets: Toward an Ontology of Complex Scaffolded Living Systems." In *Levels of Organization in the Biological Sciences*, edited by David S. Brooks, James DiFrisco, and William C. Wimsatt, 89–109. Cambridge, MA: MIT Press.

Hammerschmidt, Katrin, Caroline J. Rose, Benjamin Kerr, and Paul B. Rainey. 2014. "Life Cycles, Fitness Decoupling and the Evolution of Multicellularity." *Nature* 515 (7525):75–79. https://doi.org/10.1038/nature13884

Kauffman, Stuart A. 2000. *Investigations.* New York: Oxford University Press.

Kauffman, Stuart A. 2019. *A World beyond Physics: The Emergence and Evolution of Life.* New York: Oxford University Press.

Lewontin, Richard C. 1978. "Adaptation." *Scientific American* 239 (3):213–30.

Loreto, Vittorio, Vito Domenico Pietro Servedio, Stephen H. Strogatz, and Francesca Tria. 2016. "Dynamics on Expanding Spaces: Modeling the Emergence of Novelties." In *Creativity and Universality in Language*, edited by Mirko Degli Esposti, Eduardo G. Altmann, and Francois Pachet, 59–83. Cham: Springer International Publishing.

Maynard Smith, John, and Eörs Szathmáry. 1995. *The Major Transitions in Evolution.* Oxford: W. H. Freeman Spektrum.

Rainey, Paul B. and Benjamin Kerr. 2010. "Cheats as First Propagules: A New Hypothesis for the Evolution of Individuality During the Transition from Single Cells to Multicellularity." *Bioessays* 32 (10):872–880. https://doi.org/10.1002/bies.201000039

Rainey, Paul B., Philippe Remigi, Andrew D. Farr, and Peter A. Lind. 2017. "Darwin Was Right: Where Now for Experimental Evolution?" *Current Opinion in Genetics & Development* 47 (December):102–9. https://doi.org/10.1016/j.gde.2017.09.003

Tria, Francesca, Vittorio Loreto, Vito Domenico Pietro Servedio, and Steven H. Strogatz. 2014. "The Dynamics of Correlated Novelties." *Scientific Reports* 4 (1):1–8. https://doi.org/10.1038/srep05890

Waddington, Conrad H. 1957. *The Strategy of the Genes: A Discussion of Some Aspects of Theoretical Biology.* New York: Macmillan.

Wimsatt, William C. 2007. *Re-Engineering Philosophy for Limited Beings: Piecewise Approximations to Reality.* Cambridge, MA: Harvard University Press.