Towards a More General Theory of Evolution by Natural Selection: A Manifesto

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In this manifesto for a more comprehensive account of evolution by natural selection (ENS), we draw on Hull's framework to expand the reach of Darwinian explanations. His approach is centered on the notions of interactor and replicator. He (and many others following him) defines the interactor in terms of cohesiveness. Often, such cohesiveness is cashed out by the vertical transmission to the next generation of the replicators that constitute the interactors. While we maintain the importance of the reciprocal influence of interactors and replicators (the differential extinction and proliferation of interactors leads to the differential extinction and proliferation of the replicators that produce them) central to Hull's framework, we downplay the importance of the cohesiveness of interactors and eliminate any need for lineage formation among them. This suggested revision of the interactor synthesizes various recent contributions in the field, and it allows the interactor/replicator framework to tackle more complex entities. Our approach, however, stands in stark opposition to the classical approach to ENS centered on lineage formation. In this paper, we present our view and argue that it should replace the classical approach in structuring future work in evolutionary biology.

1 Introduction

Providing empirical content to Darwin's theory of evolution by natural selection (ENS) amounts to determining what biological entities can be selected and explaining their traits and ecological interactions as a result of this selection. Probably because of Darwin's own emphasis on communities of descent (his interpretation of the species concept) and the organisms that compose them, it has been assumed by most researchers interested in biological evolution that the main

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entities of evolution are the ones that form *lineages*, i.e., entities capable of reproduction. Reproduction embodies the privileged causal role of parents in determining their offspring's traits, and this privileged causal role warrants drawing lineages across generations.

In recent decades, as genomic data has drawn our attention to the overwhelming richness of the biological world and the complexity of ecological interactions that permeate all systems where life is present, the focus on lineage-forming entities has come to constrain Darwinian explanations. The current, dominant version of the theory of ENS applies only to entities that form lineages. Hence, according to a common argument, all multispecies assemblages that are phylogenetic composites lie outside its scope. This argument has been used to deny, on a priori bases, that populations of multispecies biofilms, holobionts, or ecosystem communities, for example, evolve by natural selection as classically conceived (Doolittle and Inkpen 2018; Moran and Sloan 2015). In this short manifesto, we offer an account of ENS that encompasses complex entities across the biological hierarchy. To do so, we draw on Hull's (1980) *interactor/replicator* framework and synthesize contributions by various philosophers working with the theory of ENS to stress that there is an efficient, coherent, and simple way to broaden the scope of the theory. This requires giving more attention to the interactor in a way that downplays the often-assumed conceptual and causal priority of the replicator (or other similar notions referring to lineage-forming entities).

2 The "Classical" Approach to ENS

Peter Godfrey-Smith (2012, 2161) writes that "Evolution by natural selection is change in a population owing to variation, heredity and differential reproductive success …. [T]he criteria required are abstract; genes, cells, social groups and species can all, in principle, enter into change of this kind. For any objects to be units of selection in this sense, however, they must be connected by parent–offspring relations; they must have the capacity to reproduce."

He thus succinctly summarizes what he calls the "classical" formalization of ENS, based on Richard Lewontin's famous "recipe" approach, which is, in its 1985 version (as rendered by Godfrey-Smith 2009; see also Lewontin 1970):

(L1) There is variation in morphological, physiological, or behavioral traits among members of a species (the principle of variation).

(L2) The variation is in part heritable, so that individuals resemble their relations more than they resemble unrelated individuals and, in particular, offspring resemble their parents (the principle of heredity).

(L3) Different variants leave different numbers of offspring either in immediate or remote generations (the principle of differential fitness).

Put in this way, which is the way that most researchers now understand it, ENS requires the formation of lineages—a succession of parent-offspring relationships—and thus reproduction. Indeed, reproduction is the only way we can delineate generations while determining which individual entities are the offspring of which individual parents, thereby tracing lineages that satisfy L2. So ENS, according to the received or "classical" view (Godfrey-Smith 2009), just *is* differential reproduction, based on some property (that which is *selected*) that is heritable and can be legitimately attributed to the reproducing entity. Strictly speaking, this excludes biological entities that do not form lineages.

Multi-level selection theory (MLST), as conceived by Lewontin and Godfrey-Smith (and many others, e.g., Okasha 2006) is similarly limited. MLST, in short, is the claim that ENS will

happen at any level at which some sort of differential reproduction can be attributed to entities with some sort of level-specific property, this property being passed from parent to offspring. Cultural practices, for instance languages, could in theory form lineages that evolve by natural selection: there need be no genetic underpinning.

One problem with the classical approach to MLST is that it relies on the possibility of designating discrete levels of organization in the biological hierarchy. Indeed, in that framework, only once such levels are identified can we know whether the level-specific conditions for ENS are realized. Yet biological interactions, including those affecting evolutionary dynamics, span levels and fail to respect boundaries set by accounts of hierarchy theory (Buss 1987; Bourrat 2015). While full-fledged arguments against level-based descriptions of the biological world are beyond the scope of this paper, the replicator/interactor dichotomy, meant to capture cross-level interactions, defines units of selection quite differently (Hull 1980).

3   The Interactor/replicator Framework

Moving away from the strict Lewontinian understanding of ENS, Richard Dawkins's (1976) proposed an alternative interpretation of the theory. As refined by David Hull (1980), and extended further by us here, this alternative decomposes the unit of selection into two underlying concepts: the interactor and the replicator. Accordingly, Hull defines ENS as any "process in which the differential extinction and proliferation of interactors causes the differential perpetuation of the replicators that produced them." Entailed by this definition is reciprocal causation (as in Svensson 2018), since the interactor's relationship to its environment influences the fate of replicators, and these in turn play a crucial causal role in the production of interactors.[1] This philosophical apparatus is of course only necessary when replicators and interactors are distinct, and less important when the interactor replicates (as in prokaryotes) or reproduces (as in sexual eukaryotes). Yet this is the major difference between Hull's view and the classical one: Hull's formulation allows for two different entities at different levels of organization to be integrated into a single evolutionary explanation. Indeed, multiple higher-level interactors can simultaneously "cause the differential perpetuation of the replicators that produced them."

Hull defines replicators and interactors rather narrowly, but as we will argue, such constraints may not be warranted in either case. Hull's central claim is that the relevant interaction with the environment (required for ENS) can take place at a higher level than that at which replication occurs, as long as replicators cause that interaction and as long as the interaction affects the rate of replication. In contrast, only cases where replication or reproduction and interaction can be attributed to the same entity meet the criteria of Godfrey-Smith's "classical" view.

Hull's alternative approach has been criticized for various reasons, but in part because it splits the "classical" ontological category, *unit of selection*, into two constitutive concepts, replicator and interactor. Godfrey-Smith (2014) summarizes this critique as follows:

> The quickest way to see that something is wrong [with Hull's framework] is to look at the Lewontin summary ["Lewontin's Recipe"] given earlier. This summary had problems of detail, but it describes all that is needed for evolution by natural selection. And in that analysis, there are not two kinds of things, but one: the

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[1]It has been brought to our attention that the interactor/replicator framework, as it stresses the reciprocal influence of interactors and their constitutive replicators, is similar to the classical approach to developmental system theory (DST), as articulated by Griffiths and Gray (1994). Our manifesto, however, should not be reduced to a rearticulation of DST, which is itself a rearticulation of Hull's framework. Indeed, DST explicitly stresses that developmental systems are forming lineages, while challenging that idea is the core of our argument.

> entities in the population that vary, inherit traits from their parents, and differ
> in reproductive success. If we have things with *those* properties, that is all that is
> needed. The passing on of "replicators" is one possible mechanism for inheritance,
> but it is optional. (45)

Godfrey-Smith is justified in rejecting the replicator/reproducer distinction: inheritance can occur in the absence of precise replicators (Brunet and Inkpen forthcoming). The presence of responsive ("interacting") reproducers is enough. In that way, the classical" framework can handle many instances in which "reproduction" entails only a minimal representation in offspring of the relevant parental properties, as long as lineages are formed and parents have a privileged causal role (in comparison to other individuals in the population) in determining the traits their offspring bear. That role need not even be genetic.

However, Godfrey-Smith's narrow focus on reproducers leaves much of biology out. That is, it excludes entities that fail to form lineages. In contrast, the notion of interactor can be modified, we argue, to encompass such entities. Hull defines an interactor as an "entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential". Interactors often do form lineages: organisms, after all, are interactors for the genes that are their replicators. But interactors do not have to do this (replicate or reproduce, forming lineages), nor do they need to be especially cohesive in order to "cause the differential perpetuation of the replicators that produced them".

This is where we move beyond Hull's own perspective. For example, he argues that ecosystems seldom operate "cohesively" enough to count them as interactors. Indeed, often the species that make them up do have different evolutionary trajectories. Nonetheless, the frequent recurrence of an ecosystem type does foster the differential perpetuation of the species that thrive in that ecosystem and contribute to its making. We think that that is enough for recurring ecosystems to be treated as interactors.

For us, the ecological interactions leading to differential perpetuation of replicators can be accomplished at any level at which a replicator's expression makes a difference to its fate (its "perpetuation"). Consider multispecies biofilms whose interactions with the environment are determined in part by their capacity to produce extracellular polymeric substances. Some genes in some of the cells involved encode the production of this matrix, such that they can be said to interact with the environment at the biofilm level. Conversely, the presence of extracellular polymeric substances will have an impact on the replicators that form the biofilm (not only the ones that produce the substances). As such, multispecies biofilms can be conceived as interactors (Ereshefsky and Pedroso 2015).

We might then, according to our expanded form of Hull's formulation, allow that "differential extinction and proliferation of interactors" comprises not only (1) reproduction, as per Lewontin and Godfrey-Smith, so that the interactor is the same thing as the replicator/reproducer, but also (2) recurrence (re-production), as in the more and more frequent recurrence of ecosystems in which all necessary trophic levels are occupied *versus* those in which they are not, and (3) persistence. It's easy to see how more replicators could be produced by the successes of interactors such as ecosystems even if only (2) holds and there are no lineages of ecosystems.

Situation (3) refers to cases where the biological entities forming evolving populations fail to either reproduce or be re-produced. Van Valen's influential insistence that growth (or expansion, in his terms) can play an important role in ENS processes, comparable to reproduction (Van Valen 1989), must be taken into account. His insights ground powerful alternative approaches to evolutionary phenomena that a more traditional take reduces to differential reproductive output. For example, clade selection (Doolittle 2019; Neto and Doolittle 2022) or selection on clonal entities like quaking aspens (Bouchard 2008) could be conceived in this light.

The perennial problem with such situations is that the population will necessarily dwindle (with the most persistent entities increasing their proportion in the population, as the less persistent ones perish). While this certainly is ENS, it may indeed take further mechanisms for selection to produce complex adaptations (Papale 2021; Neto and Doolittle 2022). While we wish here to focus on (2) and do so below, it is important to note that (3) is also an option: increase in the *number* of interactors is not strictly required for ENS to obtain (Van Valen 1989).

Before turning back to MLST, an important consequence of our framework should be made explicit. In the classical perspective on ENS, units of selection (*sensu* Lewontin or Godfrey-Smith—that is, reproducers) *must* form a population. The same requirement is not to be imposed on our broadened interactors. A lone interactor, as long as it influences the differential persistence or replication of its constitutive elements, can be part of an evolutionary explanation (Dawkins 2004). Hence, arguments according to which an entity, such as Gaia, is incoherent within a Darwinian perspective because its population size is 1 can be rebutted through our approach: a lone interactor might be crucial to understanding evolution, and more specifically ENS, if it does lead to differential persistence/replication of its parts. While we leave the defense of a Darwinian Gaia open for further work, the closing section of the present paper explores the possibility of treating biogeochemical processes as interactors.

4   An Expanded Interactor/Replicator Framework, Rendering MLST Irrelevant

Here, we expand the reach of evolutionary theory beyond Godfrey-Smith's "classical" view and beyond the traditional interactor/replicator framework to cover entities that do not form lineages. Notably, clades, ecosystems, functional interaction networks (as in ITSNTS or ITSATS; Doolittle and Inkpen 2018; Bapteste and Papale 2021) and multispecies assemblages may be treated as interactors in the light of this more generous framework.

Our approach is consistent with other recent interpretations of ENS and of the interactor. For example, Bourrat (2021) makes the interactor the ontological anchor of the theory of evolution by natural selection, suggesting, like Ereshefsky and Pedroso (2015) or Dupré (2017), that interactors might be important causal agents in evolutionary dynamics whether they form lineages or not. Lloyd's rigorous analysis of the unit of selection, decomposed into four underlying concepts, goes a considerable distance in this direction (Lloyd 2001, 2021). Our manifesto is meant to synthesize these contributions and anchor them in a general view of evolution, where the bookkeeping of genes (taken as crucial replicators), so common in contemporary evolutionary biology, acquires explanatory power through (and only through) the relationships these replicators have with a hierarchy of complex and nested interactors reaching up through reproducing entities like organisms and (arguably) species to non-reproducers like ecosystems and biogeochemical cycles (Falkowski et al. 2008; see next section). We thereby advance a perspective on evolution that stresses the crucial causal interactions that involve the entities we, following others, call interactors.

In a recent paper directly related to our argument, Papale (2021) describes how entities might increase in frequency in a population in the absence of lineages, the increase nevertheless being due to properties legitimately ascribed to entities causally interacting with their environment. He, following Charbonneau (2014), calls the underlying heredity condition "memory," and sees it as a population-level phenomenon that can be realized with or without lineage formation. This is how one can make sense of interactors sustaining ENS, which requires heredity, without necessarily forming lineages. It leads to a malleable approach to multilevel selection

where causation reaching across the hierarchy becomes relevant, whether a given level features lineage formation or not.

This contrasts with the traditional approach to MLST, which assumes the "classical" (lineage-dependent) understanding of ENS. Damuth and Heisler (1988, 407) define multilevel selection through the two related concepts MLS1 and MLS2: "Of interest in the former case are the effects of group membership on individual [particle] fitnesses, and in the latter the tendencies for the groups themselves to go extinct or to found new groups (i.e., group fitnesses)." In MLS1, only the individuals (or particles) are units of selection (in the classical sense), while in MLS2, the group (or collective) can also be taken as a unit of selection. In the "classical" framework, MLS is realized only if groups are also units of selection.

We can recast MLS1 in the interactor/replicator framework to articulate the difference between the classical take on multilevel selection and ours. Differential replication/reproduction of individuals or particles (the replicators) included in a collective or group is caused by a property attributable to the group (the interactor). Such a property might most obviously be the proportion in the group of a certain kind of replicator or reproducer particle (as in Wilson 1975), but it could be something else, an emergent[2] property at this higher level. We thus borrow from MLST the notion that there can be level-specific selectable traits, but we do not require that there be level-specific reproduction, which we see as essential to MLST as "classically" viewed. Indeed, MLS1 reduces levels higher than the ones being inquired into mere environmental conditions and MLS2 focuses on these higher levels only if they feature reproduction.

"MLS1 groups" in Heisler and Damuth's sense are thus equivalent to our non-reproducing "interactors," but they are not necessarily subject to ENS in their approach or Godfrey-Smith's. According to them, the success of these groups (if based on the proportion of particles of a given type and realized as the production of more particles of all types) can be cashed out in terms of the fitness of the particles (individual replicators or reproducers) that make them up, insofar as fitness is defined as differential replication/reproduction. Hence, it is only this particle-level fitness which is the focus of MLS1. For similar reasons, Godfrey-Smith's framework would warrant focusing on that level, as that is where lineages are formed.

But if subsequent generations of "MLS1 groups" are formed by random recruitment of particles and one type of particle, or a collection of types of particles, is repeatedly favored among such groups because it produces some group-level selectable benefit, groups will of necessity harbor an increasing fraction of such particles, and they will be on average increasingly productive of them. The populations of groups (interactors) too will evolve, in spite of constitutive groups not reproducing as units. This is fitness in the second sense mentioned previously (recurrence or re-production).

So non-reproducing interactors do increase in frequency in a population, and they do so in virtue of having legitimate interactor-level traits (properties), whether they form lineages or not.[3] To see this as a form of ENS requires a notion of heredity that can account for it being

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[2]Some of these properties are mentioned in Neto and Doolittle (2022). Of course, one might argue that all properties of higher-level entities have their ultimate cause in properties of the lower-level entities of which they are composed (a thoroughgoing reductionist position) and thus causation and selection (if seen as a causal process) always reside at the lowest level. But we still have "explanatory autonomy"—even if we lack ontological independence (Sterelny 1996). This is all that Heisler and Damuth's MLS1/MLS2 distinction claims, and all that we claim here.

[3]We must clarify our relationship to the presence of reproduction with lineage formation. We are very much aware that, in most biological cases that fit our general account of ENS, there will be lineage formation, at some level or another. Genes, after all, will be involved in most empirical case studies. Even at the level of interactors with too many parents, there is a way to make sense of them as being part of lineages, albeit complicated ones. Accordingly, instead of presenting the debate as being about the presence or absence of lineages, we could have

realized without lineage formation (the interactors do not form lineages); hence the importance of memory as described above. Certainly, in such cases, "book-keeping" accounts of ENS could be satisfied by looking at either the particles or collectives that we are tracking, but there is significant causality (without necessary reproduction) at the level of groups that calls for an approach to ENS that embraces it as well. Given the ubiquity of such causal interactions across the biological hierarchy, we believe understanding MLS requires looking into how cross-cutting multilevel and multidirectional causal interactions shape evolution. This contrasts with classical MLST, which analyzes levels independently of one another to establish whether a level, on its own, meets the criteria for ENS (Hull 1980).

Causation-embracing accounts of ENS depend on where and in what direction we draw causal arrows (Bouchard and Rosenberg 2004). Do groups interact causally with their environment in a way that determines their (and their components') fitness, more broadly defined (Bouchard 2008)? Certainly, "classical" versions of MLST might answer yes to this question, since the three ingredients in Lewontin's recipe are meant to hold at each level at which selection can occur, these levels and the three ingredients taken to be independent from one another. Yet the classical view holds all three ingredients to be necessary. Here we are in effect proposing that reproduction is *optional* for ENS and MLS. Causal interactions with the environment and variation among these interactions are thus the only necessary requirements. The situation minimally involves *reciprocal causation* (as in Svensson 2018) between replicators and the many overlapping interactors they are embedded in (including other replicators). To repeat Hull's (1980, 318) definition of ENS, it is a "process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them," to which we simply add "whether interactors form lineages or not."

5   How General Is Our Approach? the Case of the Nitrogen Cycle

Until now, we have shown that ENS applies to cases where biological entities, such as multi-species assemblages, may be conceived as interactors, whether they form lineages or not. Yet our formulation allows for an even broader use of the interactor concept. Indeed, we believe it can apply to abiotic entities. In this closing section of the paper, we show how we can conceptualize global phenomena, such as the nitrogen cycle, as interactors.

First, it must be noted that we do not think life to be a specific class of objects with distinctive characteristics (Mariscal and Doolittle 2000). If the theory of ENS is conceptually coherent with a given way to describe cultural, chemical or biogeochemical phenomena, we see no a priori reason to deny its application to them. The question of whether it is useful to do so is a distinct, empirically driven one.

Consider an example taken from the Earth System Sciences, the nitrogen cycle, which we use here because it has already been theorized as a unit of selection (without lineage formation; Doolittle and Inkpen 2018). Chemically, the biological nitrogen cycle converts N_2, whose atmospheric residence time is about a billion years, to NH_4 (ammonia) using nitrogenase (a highly conserved, oxygen-sensitive protein). Ammonia's oxidation to nitrite is a two-step reaction catalyzed by other prokaryotic taxa. Its further oxidation to nitrate is catalyzed by still other

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opted for a more nuanced perspective involving reproduction. In that more nuanced perspective, lineage formation is always present, but lineages are more or less diffused (and it is a matter of degree). This alternative would be compatible with general accounts of reproduction (e.g., Griesemer 2000) that broaden the scope of this concept and, concurrently, with the "classical formulation" of ENS. We steered away from that avenue, in the present paper, because we wish to center general accounts of ENS away from reproduction and the difficulties tied to Lewontinian or recipe-like approaches to ENS.

prokaryotes (nitrifiers), which also reduce CO_2 to organic matter. Anaerobically, additional microbial taxa use nitrite or nitrate to oxidize organic matter, ultimately releasing N_2 into the atmosphere again. Many microbial taxa are involved, making their living as parts of this cycle. These taxa can be widely separated in space and time: the nitrogen cycle is far from cohesive.

The nitrogen cycle *interacts* with the abiotic environment and other cycles studied by Earth System scientists. The carbon cycle, for instance, is necessary for the recycling of a second major constituent of living things, without which the nitrogen cycle would not exist. Of these Falkowski et al., in a paper aptly entitled "The Microbial Engines That Drive Earth's Biogeochemical Cycles" wrote:

> Earth is ~4.5 billion years old, and during the first half of its evolutionary history, a set of metabolic processes that evolved exclusively in microbes would come to alter the chemical speciation of virtually all elements on the planetary surface. Consequently, our current environment reflects the historically integrated outcomes of microbial experimentation on a tectonically active planet endowed with a thin film of liquid water. (1034)

The ecological and selective interactions that orient the evolutionary dynamics are not necessarily tied to a specific lineage, to specific populations of reproducers or replicators (nonetheless allowing for bookkeeping at the level of replicators, the genes or taxa involved). As detailed above, past versions of the interactor/replicator framework implied that interactors should be cohesive entities, and Hull went as far as suggesting that an interactor should be characterized by the vertical transmission of its constitutive replicators, thereby maintaining a tight association with Lewontinian approaches to ENS. This restrictive criterion, however, conflicts with the idea that interactors are entities that influence the differential reproduction/replication of their parts. To generalize the theory of ENS, it suffices to center the account of the interactor on the latter criterion rather than vertical transmission of reproducers/replicators. By doing this, we believe that processes such as the nitrogen cycle can be conceived as interactors.

It should also be noted that interactors can be nested. Just like there might be populations of genes within populations of organisms where evolutionary dynamics pull in different directions, there might also be nested interactors, and some of their constitutive replicators may also overlap. This suggests that, instead of thinking of a neat hierarchy of levels of organization, evolutionary inquiries would benefit from identifying the nested interactors and how the ecological interactions they are involved in will influence differentially the propagation of nested replicators/reproducers. Instead of levels, the biological world can be divided into ontological categories, and evolutionary studies can be centered on interactors.

Acknowledgments

Literature cited

Bapteste, Éric, and François Papale. 2021. "Modeling the Evolution of Interconnected Processes: It Is the Song and the Singers: Tracking Units of Selection with Interaction Networks." *BioEssays* 43 (1): 2000077. https://doi.org/10.1002/bies.202000077.

Bouchard, Frédéric. 2008. "Causal Processes, Fitness, and the Differential Persistence of Lineages." *Philosophy of Science* 75:560–570.

Bouchard Frédéric, and Alex Rosenberg. 2004. "Fitness, Probability and the Principle of Natural Selection." *British Journal for the Philosophy of Science* 55:693–712.

Bourrat, Pierrick. 2015. "Levels of Selection Are Artefacts of Different Fitness Temporal Measures." *Ratio* 28:40–50.

Bourrat, Pierrick. 2021. *Facts, Conventions and the Levels of Selection*. Cambridge, UK: Cambridge University Press.

Brunet, Tyler, and Andrew Inkpen. (Forthcoming). "Return of the Interactor." *British Journal for the Philosophy of Science*.

Buss, Leo W. 1987. *The Evolution of Individuality*. Princeton: Princeton University Press.

Charbonneau, Mathieu. 2014. "Populations without Reproduction." *Philosophy of Science* 81:727–740.

Damuth, John, and I. Lorraine Heisler. 1988. "Alternative Formulations of Multilevel Selection." *Biology and Philosophy* 3:407–430.

Dawkins, Richard. 1976. *The Selfish Gene*. Oxford: Oxford University Press.

Dawkins, Richard. 2004. "Extended Phenotype—But Not *Too* Extended: A Reply to Laland, Turner and Jablonka." *Biology and Philosophy* 19:377–396.

Doolittle, W. Ford. (Forthcoming). *Darwinizing Gaia*. Cambridge, MA: MIT Press.

Doolittle, W. Ford. 2019. "Making Evolutionary Sense of Gaia." *Trends in Ecology and Evolution* 34:889–894.

Doolittle, W. Ford, and Andrew Inkpen. 2018. "Processes and Patterns of Interaction as Units of Selection: An Introduction to ITSNTS Thinking." *Proceedings of the National Academy of Science USA* 115:4006–4014.

Dupré, John. 2017. "The Metaphysics of Evolution." *Interface Focus* 7 (5): 20160148.

Ereshefsy, Mark, and Makmiller Pedroso. 2015. "Rethinking Evolutionary Individuality." *Proceedings of the National Academy of Science USA* 112:10126–10132.

Falkowski, Paul G., Tom Fenchel, and Edward F. Delong. 2008. "The Microbial Engines That Drive Earth's Biogeochemical Cycles." *Science* 320:1034–1039.

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

Godfrey-Smith, Peter. 2012. "Darwinism and Cultural Change." *Philosophical Transactions of the Royal Society B* 367:2160–2170.

Godfrey-Smith, Peter. 2014. *Philosophy of Biology*. Princeton: Princeton University Press.

Griesemer, James R. 2000. "Development, Culture and the Units of Inheritance." *Philosophy of Science* 67:S348–S368.

Griffiths, Peter E., and Russel D. Gray. 1994. "Developmental Systems and Evolutionary Explanation." *Journal of Philosophy* 91:277–304.

Hull, David L. 1980. "Individuality and Selection." *Annual Review of Ecology and Systematics* 11:311–332.

Levins, Richard, and Richard Lewontin. 1985. "Adaptation." In *The Dialectical Biologist*, 65–84. Cambridge, MA: Harvard University Press.

Lewontin, Richard C. 1970. "The Units of Selection." *Annual Review of Ecology and Systematics* 1:1–18.

Lloyd, Elizabeth A. 2001. "Units and Levels of Selection: An Anatomy of the Units of Selection Debates." In *Thinking about Evolution*, edited by Rama S. Singh, Costas B. Krimbas, Diane B. Paul, and John Beatty, 267–91. Cambridge, MA: Cambridge University Press.

Lloyd, Elizabeth A. 2021. *Adaptation.* Cambridge, UK: Cambridge University Press.

Mariscal, Carlos, and W. Ford Doolittle. 2020. "Life and Life Only: A Radical Alternative to Life Definitionism." *Synthese* 197:2975–2989.

Moran, Nancy A., and Daniel B. Sloan. 2015. "The Hologenome Concept: Helpful or Hollow?" *PLoS Biol* 13:e1002311.

Neto, Celso, and W. Ford Doolittle. 2022. "A Chemostat Model for Evolution by Persistence: Clade Selection and Its Explanatory Autonomy." *Philosophy of Science* 90 (1): 21–38. doi:10.1017/psa.2022.11.

Okasha, Samir. 2006. *Evolution and the Levels of Selection*. Oxford: Oxford University Press.

Papale, François. 2021. "Evolution by Means of Natural Selection Without Reproduction: Revamping Lewontin's Account." *Synthese* 198:10429–10455.

Sterelny, Kim. 1996. "Explanatory Pluralism in Evolutionary Biology." *Biology and Philosophy* 11:193–214.

Svensson, Erik I. 2018. "Reciprocal Causation in the Evolutionary Process." *Evolutionary Biology* 45:1–14.

Van Valen, Leigh M. 1989. "Three Paradigms of Evolution." *Evolutionary Theory* 9:1–17.

Wilson, David Sloan. 1975. "A Theory of Group Selection." *Proceedings of the National Academy of Science USA* 72:143–146.