

Systemic Darwinism

Rasmus Grønfeldt Winther*

Philosophy Department, University of California, 1156 High Street, Santa Cruz, CA 95064

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Darwin's 19th century evolutionary theory of descent with modification through natural selection opened up a multidimensional and integrative conceptual space for biology. We explore three dimensions of this space: explanatory pattern, levels of selection, and degree of difference among units of the same type. Each dimension is defined by a respective pair of poles: law and narrative explanation, organismic and hierarchical selection, and variational and essentialist thinking. As a consequence of conceptual debates in the 20th century biological sciences, the poles of each pair came to be seen as mutually exclusive opposites. A significant amount of 21st century research focuses on systems (e.g., genomic, cellular, organismic, and ecological/global). Systemic Darwinism is emerging in this context. It follows a "compositional paradigm" according to which complex systems and their hierarchical networks of parts are the focus of biological investigation. Through the investigation of systems, Systemic Darwinism promises to reintegrate each dimension of Darwin's original logical space. Moreover, this ideally and potentially unified theory of biological ontology coordinates and integrates a plurality of mathematical biological theories (e.g., self-organization/structure, cladistics/history, and evolutionary genetics/function). Integrative Systemic Darwinism requires communal articulation from a plurality of perspectives. Although it is more general than these, it draws on previous advances in Systems Theory, Systems Biology, and Hierarchy Theory. Systemic Darwinism would greatly further bio-engineering research and would provide a significantly deeper and more critical understanding of biological reality.

biological theory | ecology | genetics | evolution | systems theory

There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that whilst this planet has gone cycling on according to the fixed laws of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

Ref. 1, p. 490.

Thus concludes Darwin's *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (hereafter referred to as *On the Origin of Species*). We interpret Darwin's "view of life" as a conceptual space consisting of three dimensions: explanatory pattern, levels of selection, and degree of difference among units of the same type. Each respective dimension is defined by a pair of poles: law and narrative explanations, organismic and hierarchical selection, and variational and essentialist thinking. Darwin's integrative theory linking biological structure, history, and function was nursed and reared within this logical space. During the 20th century, the poles of each pair came to be seen as mutually exclusive. Systemic Darwinism, emerging at the beginning of the 21st century, promises to reintegrate Darwin's view of life.

We are, in all likelihood, at a historical cusp of biological theory. Exponential progress is being made in developing new interdisciplinary ways of conducting experiments, gathering data, and articulating theory about systemic objects and processes at spatiotemporal scales and hierarchical levels ranging from tiny genomic systems to midlevel cellular and organismic systems to truly immense ecological/global systems. The rise of

Systems Biology is one such productive interdisciplinary research program (2, 3).

However, Systemic Darwinism provides a significantly more general and integrative perspective on complex biological systems than Systems Biology. First, it highlights the astounding ontological complexity of biological reality: dynamical self-organizing systems (composed of hierarchical networks of parts) are genealogical and can therefore undergo selection. Systemic Darwinism thus follows a "compositional paradigm" according to which complex systems together with their diverse hierarchical networks of parts—and not just base parts—are considered the focus of biological investigation.

Second, Systemic Darwinism emphasizes epistemic complexity. Although Systemic Darwinism does not seek to replace, or legislate over, ongoing local investigations across the biological sciences, it wishes to forestall radical fragmentation of biological theory. Its basic argument is that because biological systems are complex, a unified theoretical framework that coordinates, integrates, and even partially embeds a plurality of theories about systems is required to capture and manage this complexity. No single manner of analyzing biological complexity can provide a complete representation of biological reality. Insisting on the epistemic (i.e., explanatory and descriptive) completeness of any single theoretical abstraction would lead to dangerous reifications.

Thus, the integration and ideal unification of a plurality of biological theories investigating the same basic entities/processes—complex systems—are necessary for complete and nonreified scientific understanding and for effective means of intervention. That is, Systemic Darwinism harnesses epistemic complexity to analyze and control ontological complexity. It does this in two ways:

- 1.1.1. Each pole of each dimension—and each dimension itself—of Darwin's three-dimensional view of life is found to be productive for theory and practice. Systemic Darwinism makes Darwin's conceptual space whole.
- 1.1.2. Each of the three great 20th century mathematical biological theories remains essential for articulating a general theory of biological systems: the theory of dynamical self-organization [a theory of complex structure (e.g., 4–7)], cladistics [a theory of biological history (e.g., 8–10)], and evolutionary genetics [a theory of adaptive function (e.g., 11–13)]. Systemic Darwinism coordinates, integrates, and partially embeds these three explanatory theories, in part through the use of the conceptual space of 1.1.1.

Moreover, the historical arc of this argument is:

- 1.2.1. Darwin lays out the logical space of evolutionary theory in 1859.
- 1.2.2. As a consequence of conceptual debates in the 20th century biological sciences, the poles of each pair come to be seen as mutually exclusive opposites.

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*E-mail: rgwinther@gmail.com.

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1.2.3. New ways of thinking about genomic, cellular, organismic, and ecological/global systems at the beginning of the 21st century promise to restructure Darwin's view of life and to successfully integrate the 20th century's three main mathematical biological theories. (Again, these two efforts intertwine.) A communal and explicit articulation of Systemic Darwinism is necessary to achieve this.

In what follows, the three dimensions of Darwin's view of life are analyzed (*i*) in his work, (*ii*) in the 20th century, and (*iii*) in the context of 21st century Systemic Darwinism. In the conclusion, methodologies and directions useful for attaining Systemic Darwinism are briefly sketched.

Explanatory Pattern: Law and Narrative. The iconic view of science is that it fundamentally concerns mathematical laws (14, 15). These empirical generalizations and theoretical principles constitute the universal regularities of nature; moreover, they ground surprising and dangerous predictions. The more successful the law-based predictions of a science are, the more justified we are in believing its theories (16). In particular, physics is highly mathematical—consider the two great 20th century physical theories, Quantum Mechanics and Relativity Theory. Although an absolute consensus about the importance of laws and predictions in physics is lacking (17), mathematical laws are often interpreted as the basic building blocks of these explanatory theoretical edifices. This view is also important for the mathematical theories of Systemic Darwinism.

Systemic Darwinism also includes a contrasting yet complementary perspective on science. Darwinism involves the biological sciences of deep time, meta-change, and complex systems. First, our time is deep and punctuated time and not just the dynamical linear time of the state spaces that physicists canonically study; Darwinists investigate genealogical systems that are embedded in immense tracts of geological time. Second, our change is meta-change; Darwinists explore the evolutionary transformations of biological systems that themselves change (e.g., organisms). Third, our systems are not easily decomposable (18); Darwinists examine systems that are irreducibly complex. Deep time, meta-change, and complex systems—these are hardly preconditions for closed-form physical mathematical laws with strong predictive capacity.

Indeed, the types of explanations that were seen by many in the 20th century as the most appropriate for analyzing genealogy are not law-based explanations *sensu stricto* (“nomothetic”) but are instead narrative explanations (“ideographic”) (19–23). Evolutionary narrative explanations interweave causally related phylogenetic events of biological systems. Consider the structured narratives of the evolution of flowering plants, wings, or human brains. These articulated stories make explicit the historical patterns and processes of biological systems such as species; these narratives thereby produce scientific explanation.

Darwin was aware of both sorts of explanations. He repeatedly wrote about the laws of variation, reproduction, correlation, and heredity and even about the laws of natural selection, the struggle for life, divergence of character, and extinction. The last sentence of *On the Origin of Species* established an analogy between Darwin's evolutionary view of life and Newton's “fixed laws of gravity.” Furthermore, in another well known passage he noted:

It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and *dependent* on each other

in so *complex* a manner, have all been produced by *laws* acting around us.

Ref. 1, p. 489, emphasis added.

Even in an entangled bank—even in a complex system—laws act and produce. Laws govern.

Now, his main goal in 1859 was to establish the plausibility and empirical adequacy of descent with modification through natural selection. Descent with modification was represented—conceptually and in the only diagram in his 1859 book—as a Tree of Life [which, today, we know can be reticulated (24)]. With respect to classification, Darwin observed: “. . . I believe this element of descent is the hidden bond of connexion which naturalists have sought under the term of the Natural System” (ref. 1, p. 433). Furthermore, concerning embryology, Darwin wrote: “. . . community in embryonic structure reveals community of descent” (ref. 1, p. 449). Thus, genealogy is a fundamental explanatory principle of biological systems. The models for this sort of explanation are narratives rather than laws *sensu stricto*.

Darwin did not discuss predictive power in the physicists' sense nor did he ever attempt to formalize laws (Darwinists were to do that in the 20th century). However, his narrative-centered view of life still provides precious understanding. In a passage indicative of his colonial prejudices, he noted that “the study of natural history” will become “far more interesting” “when we no longer look at an organic being as a savage looks at a ship, as at something wholly beyond his comprehension; when we regard every production of nature as one which has had a history. . . .” (ref. 1, pp. 485–486). The integration of many causal historical factors in narratives produces scientific understanding.

Part of the ongoing research project of Systemic Darwinism is to determine whether its mathematical theories will ever own the strong predictive power characteristic of many domains of physics. For instance, the theory of self-organizing systems promises to produce fairly robust formal laws of the generally predictive patterns of ontogenetic processes (4–7, 25). Now, because of the complexity of such systems, single laws will at best only be weakly predictive; sets of laws, however, may yet turn out to be strongly predictive. Moreover, narrative explanations, broadly construed as articulated stories of temporally organized and causally connected events (19–23, 26), can be at least weakly predictive of both development (e.g., prediction of the gene regulation sequence of limb bud development) and genealogy [e.g., predicted/retrodicted “transitional fossils” that are subsequently discovered such as *Tiktaalik roseae* (27)]; at times, Darwin appealed to prediction in this weak sense (e.g., ref. 1, p. 126). Thus, Systemic Darwinism aims to be predictive and explanatory through the employment of both laws and narratives, in self-organization theory as well as in cladistics and evolutionary genetics.

In short, Systemic Darwinism productively intertwines mathematical laws/nomothetic explanations (as presented by the three mathematical biological theories of structure, history, and function) with narratives/ideographic explanations. Perhaps biological systems will turn out to be analogous to complex physical systems such as weather systems, where laws and narratives also intertwine. The integration happens in at least two ways. First, laws form part of the content of narratives; narratives grant an overarching theoretical framework for integrating laws. Laws and narratives are thus complementary. Second, and more deeply, the very distinction between laws and narratives will have to be rethought—perhaps they depend on and, ultimately, reconfigure each other.

Levels of Selection: Organismic and Hierarchical. For Darwin, the primary engine of evolutionary change was natural selection: “Furthermore, I am convinced that Natural Selection has been the main but not exclusive means of modification” (ref. 1, p. 6).

Natural selection is the only mechanism that can produce adaptations. By adding a further premise (admittedly contentious but one that Darwin seems to have held), namely, that natural selection often results in adaptation, it follows that most evolutionary modifications are adaptive. Darwin was indeed an adaptationist. Systemic Darwinism need not agree with him on this point; this issue (28, 29) should be explicitly and vigorously addressed (see *Section 4*).

Particularly in chapters 3 and 4 of *On the Origin of Species*, Darwin explicated selection in familiar terms: given limited resources, more organisms are born than can survive, so there is a struggle for existence. Varieties more “fit” to their environment leave relatively more offspring. Over time, there is thus cumulative change in the species. In chapter 4, he noted: “This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection” (ref. 1, p. 81). Evolution through natural selection has three individually necessary and collectively sufficient conditions: (i) phenotypic variation (ii) differential reproductive success and (iii) heritability (30). This is the recipe, the algorithm, for selected cumulative change in species.

A set of questions immediately arises: at what level(s) is(are) the unit(s) that is(are) undergoing selection? Are the unit(s) that compete and undergo differential reproductive success classically defined organisms, families (i.e., groups of organisms) or even larger subpopulations of a species? Perhaps units are found at more than one level? Darwin addressed these questions in a piecemeal and incomplete manner. During the 20th century, they blossomed and a plurality of answers led to increasingly polarized general theories.

Although he focused on organismic selection, Darwin was moved by a very specific “difficulty on theory” in chapter 6 of his magnum opus: how can natural selection of organisms in the struggle for existence explain the evolution of sterility in the workers of social insects? That is, how can selection successfully act on organisms that never leave offspring? Here is Darwin’s answer:

[W]ith the *working ant* we have an insect differing greatly from its parents, yet *absolutely sterile*; so that it could never have transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked how is it possible to reconcile this case with the theory of natural selection? This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the *family*, as well as to the *individual*, and may thus gain the desired end.

Ref. 1, p. 237, emphasis added.

Sterile workers cannot and did not leave offspring. However, their kin, in particular their mother, did. The level of selection is the entire family. Darwin was willing to use group selection, and hence hierarchical selection more generally, to explain the acquisition and progressive accumulation of characters such as sterility in social insects and altruism in humans.

In *The Descent of Man and Selection in Relation to Sex* (31), Darwin argued that the appropriate level of selection for the evolution of human altruism was the human tribe, the group. Organismic selection cannot account for the existence of altruistic traits such as “patriotism, fidelity, obedience, courage and sympathy” (ref. 31, vol. 1, p. 166). These characters are hardly beneficial for the reproductive success of individual humans. However, higher level group (tribal) selection can explain human individual altruism. And how does this higher level process happen? Recall that evolution by natural selection requires heritable variance in fitness. Here, we have variation in the frequency of altruists of different tribes. Furthermore, tribes with a higher frequency of altruists

increase in relative size and relative number (i.e., have a higher reproductive success) for two reasons: (i) there is more intratribal sharing of resources, dictated by tribal norms and moral codes, and (ii) tribes compete with one another for limited ecological resources, including food, territory, and even dominion over other tribes, and those with higher frequencies of altruists are better able to secure limited resources. Finally, Darwin suggested, there is heritability of altruism (and selfishness). We thus have variance, differential reproductive success, and heritability (i.e., the three conditions for evolution through natural selection) of altruism at the tribal level.

This discussion became exceedingly important in the 20th century. The “levels of selection” debate involves strongly polarized positions. Genic selection, which is the logical extension of organismic selection, has perhaps been most strongly championed by Dawkins (32), building on the work of R.A. Fisher (see also 33). In contrast, there are biologists advocating hierarchical selection (34, 35), some of which take their inspiration from S. Wright’s “Shifting Balance Theory.” Both sides defend convincing models and arguments. Moreover, important connections between the two positions also exist (36). The nature of kin selection as either genic or hierarchical, or both, is also an ongoing dispute (36–38). Moreover, the levels of selection hierarchy have been explicitly expanded to include levels as large as species and even more inclusive clades of the Tree of Life (39–42). Darwin had also made reference to an upward expansion of levels of selection to varieties, species, and genera (ref. 1, p. 126; ref. 43, p. 238), but 20th century debates added significant formal and conceptual precision to the above questions.

A cogent solution to the levels of selection debate requires the hierarchical selection defended by Systemic Darwinism. Hierarchical selection subsumes genic selection—it is the more general model in that it includes genic selection as a limiting case when populations are extremely large, and gene interaction is negligible. Furthermore, hierarchical selection is productive in that it sheds light on how “individuals” of various types can evolve at levels other than the organismic level (i.e., not all individuals need be organisms [e.g., colonial individuals, symbionts/hosts, bacterial “metagenomes”]) (see refs. 24, 44–48). In this context, hierarchical selection, higher levels of individuality, and evolutionary transitions require an understanding of the mathematical theories of self-organizing developmental systems, cladistics, and evolutionary genetics. Moreover, note that the legitimate use of Ockham’s razor to deem genic selection a sufficient model for particular cases of selection is an empirical question. Recent evidence suggests that population structure and gene interaction are indeed ubiquitous (e.g., 49); hence hierarchical selection is more empirically adequate for most cases of evolution. However, genic selection can still play a heuristic role as a partial representation of complex biological reality that provides understanding through a powerfully simple, idealized, and limit-case model of selection.

Degree of Difference Among Units of the Same Type: Variational and Essentialist Thinking. Variation is a necessary condition for evolution by natural selection. According to Dewey (50) and Mayr (51), Darwin was crucial in moving us away from a Platonic-Aristotelian typological essentialism, where all tokens of the same biological type are interpreted as fundamentally identical and where the type is defined by an essential nature, to a variational thinking in which even similar biological material units exhibit myriad differences and are not strongly defined by essential natures. There is some truth to this account of the intellectual history, but it is clear that Darwin actually took both sorts of thinking very seriously. Systemic Darwinism also engages both variational and essentialist thinking.

Darwin emphasized variation. The first two chapters of *On the Origin of Species* document, respectively, “Variation Under

Domestication” (particularly in pigeons) and “Variation Under Nature.” Darwin reminded us that: “every one admits that there are at least individual differences in species under nature” (ref. 1, p. 468). In the first 1868 edition of *The Variation of Animals and Plants Under Domestication* (52), Darwin also recorded ubiquitous variation in domesticated organisms.

Moreover, in 1859, he wrote:

It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life.

Ref. 1, p. 84, emphasis added.

Natural selection is highly efficient—it works on every variation. It thereby produces adaptations in each lineage.

Darwin did not discard essentialist thinking, however. Following a long tradition, he noted that homologous organs [e.g., human arms, bat wings, porpoise paddles (ref. 1, p. 434)] have the “same pattern” (p. 457) across species, regardless of their purpose. According to typological thinking, this sameness of pattern is meant literally and indicates a deeper identity, a unity of type: “By unity of type is meant that fundamental agreement in structure, which we see in organic beings of the same class, and which is quite independent of their habits of life” (p. 206). As cases of unity of type, consider the general architectural and developmental patterns of vertebrates or arthropods. These patterns are the essence, and thereby define the baupläne or the archetypes, of these phyla (and of lower level clades within the phyla) (53). Now, Darwin accepted that this unity of type was abstractly characterized by the practicing biologist: morphology was the “very soul” of natural history (ref. 1, p. 434). However, Darwin’s great contribution in this context was to provide a purely historical and material explanation of the essential unity of type:

If we suppose that the ancient progenitor, the archetype as it may be called, of all mammals, had its limbs constructed on the existing general pattern, for whatever purpose they served, we can at once perceive the plain signification of the homologous construction of the limbs throughout the whole class.

Ref. 1, p. 435.

Archetypes are actual ancestors. Furthermore, extant homologies are the result of the inheritance of unity of type from ancestors: “on my theory, unity of type is explained by unity of descent” (ref. 1, p. 206). Very basically then, Darwin developed a notion of historico-material types.

Darwin insisted on the importance of variation for natural selection. Moreover, he emphasized archetypes and homologies as historical and material entities that could be abstractly characterized as types for pragmatic classificatory purposes. He was both a variational and an essentialist thinker.

In the 20th century, the tension between variational and essentialist thinking developed into the debate over the power of “constraints” on the operation of natural selection. Essentialist thinking tends to be structuralist. Here, structure refers both to unity of type and to self-organization (e.g., refs. 4–7, 25, 53–55). Structuralism is often opposed to functionalism, which focuses on variational thinking and natural selection (but see ref. 4 for a synthetic approach). The debate between structuralists and functionalists became particularly strong in the 1980s and revolved around the following questions: What is the nature and extent of architectural, developmental, and historical constraints on selectable variation? How much selectable variation can the hand, the eye, cellular metabolism, or the height of an *Arabi-*

dopsis thaliana plant exhibit? In short, how free or constrained is natural selection? The debate is ongoing (56, 57).

Systemic Darwinism allows us to reconsider the basic premises of this and other related discussions. For instance, current literature on the “natural kind” structure of homologies emphasizes the simultaneous importance of variational and essentialist thinking (10, 58–60). Both forms of thinking are needed as epistemic frameworks to effectively understand biological reality. This is consistent with Darwin’s views. Moreover, Systemic Darwinism highlights the importance of each pole for each of the mathematical theories: (i) the theory of dynamical self-organization finds patterns of variation, change, and instability (i.e., variational thinking) and of constraint, similarity, and robustness (i.e., essentialist thinking) in gene and cellular networks; (ii) cladistics classifies species (and higher level clades) using typologically defined homologies but also describes intraspecific and intraclade variation; and (iii) evolutionary genetics assesses the population structure of genetic variation and lack of genetic variation. As is also the case with the first dimension of Darwin’s view of life, we will ultimately need to rethink and reconfigure the very distinction between variational and essentialist thinking.

Systemic Darwinism. We have explored three dimensions structuring the logical space of Darwinism. These are defined by pairs of poles: law and narrative explanations, organismic and hierarchical selection, and variational and essentialist thinking. Darwin gave narrative explanation and variational thinking an analytical life that they had previously lacked. Moreover, he introduced the whole issue of levels of selection. In short, by identifying complementary poles of particular dimensions, he articulated a new biological conceptual space. To a large extent, this space allowed him to be the first to productively link biological structure, history, and function in a single theoretical structure. It is important to note that in addition to being an extraordinary scientist, Darwin is also a *trope*. Darwinism is an inordinately general, complex, and powerful theory, ultimately surpassing Darwin’s or any other individual’s greatest imagination.

Now, in attempting to reintegrate the Darwinian conceptual space explored in this article, Systemic Darwinism should ask the following questions (see also 1.1.1):

- 5.1.1. What are the appropriate relationships between mathematical laws and historical narratives?
- 5.1.2. How should we model the fitnesses of units, and of interactions among units, at different levels of selection in self-organizing genealogical systems?
- 5.1.3. How are patterns of variation, change, and instability, and those of constraint, similarity, and robustness, of parts and systems, relevant to the structure, history, and function of systems?

Furthermore, the three 20th century mathematical theories investigating structure (theory of dynamic self-organization), history (cladistics), and function (evolutionary genetics) have underspecified and indeterminate intertheoretical relations. Regarding the three mathematical theories examined in this article, Systemic Darwinism inquires (see also 1.1.2):

- 5.2.1. Under what conditions, and for what purposes, can and should we use these theories simultaneously?
- 5.2.2. How can and should we go about integrating, coordinating, and embedding them in general?
- 5.2.3. Does each theory describe different formal aspects of the same system, or does each provide unique criteria for identifying distinct systems that could partially overlap with the systems individuated by the other two theories (or both)?

These central questions regarding the Darwinian conceptual space and the plurality of 20th century mathematical biological

theories can be addressed by turning to the impressive amount of theory available on systems, complexity, and hierarchy. Systemic Darwinism draws on this work and invites collaboration. Current Systems Biology (2, 3, 61–65) is indeed an important research program for Systemic Darwinism. Powerful general conceptual methods are being developed in this context, such as conceptual continuity (66), modeling (67–69), abstraction (70), and understanding (71). These epistemic tools will be necessary for coordinating and integrating theoretical pluralism in Systemic Darwinism. Moreover, many of the abstract strands of Systems Biology grow out of earlier theoretical Systems Theory (72–78). This work was crucial in its time and can provide important formal tools (e.g., cybernetics, information theory, mereology, relational modeling) for a general biological theory. Systemic Darwinism is “dynamicist” (61) and “systems-theoretic” (3). The only qualification in this context is to note that Systems Biology and earlier Systems Theory concern primarily self-organization and lower levels of systemic hierarchies. These fundamental research areas have less to say about theories of history and function.

However, important resources for a theoretical framework for mathematical theories of genealogy and natural selection can be found elsewhere. Hierarchy Theory, generally construed, has developed concepts important for Systemic Darwinism such as (i) the distinction between genealogical and ecological hierarchies (41, 79, 80), (ii) the notion that “biological evolution is an entropic process” (ref. 81, p. xii), and (iii) the explicit concept of large multicausal developmental systems, described either as systems of cointeracting genes and environmental conditions (82–84) or, more generally, as systems of hierarchical networks of mutually coconstructing and interacting parts (41, 82; see also refs. 85, 86). Moreover, proponents of general Hierarchy Theory have articulated critical conceptual methods such as dialectical thinking and identification of inappropriate modeling reifications (82, 87–90). Regarding dialectical thinking, the argument is that seemingly mutually exclusive dichotomies can be turned into complementary and interpenetrating poles (82, 83), as Systemic Darwinism attempts to do with the three dimensions explored in this article. Concerning reification, the worry is that although mathematical modeling is powerful, a plurality of methodologies and “clusters of models” (88) are necessary for avoiding the reification of particular models and theories. In short, general Hierarchy Theory is useful for theories and models of history and function.

Systems Biology, Systems Theory, and Hierarchy Theory provide rich resources for a Systemic Darwinism that (i) can make Darwin’s view of life whole and (ii) can coordinate, integrate, and partially embed the three 20th century mathematical biological theories of structure, history, and function here explored. Each individual theory is necessary but not sufficient for a full and empirically adequate understanding of complex biological ontology, just as each blind man provides only a partial perspective of the proverbial elephant. Dialogue among theories and among modeling perspectives within each theory [e.g., Fisherian and Wrightian perspectives in evolutionary genetics (90)], is essential, just as the elephant story can be transformed to imagine blind wise women dialoguing with one another in order to understand, communally, the nature of the complex elephant. Ignoring key and legitimate abstractions can

lead to limited understanding, short-sightedness, and the stalling of theoretical and empirical research at the community level. Thus, although each mathematical theory will continue making independent progress within its own domain, dialogue among them is essential for the articulation of Systemic Darwinism.

Systemic Darwinism insists on the centrality of the compositional paradigm and the possibility of providing a general mathematical framework for the biological sciences. The entities/processes of study of biological mathematical theories are networks of units at a variety of spatiotemporal scales and hierarchical levels rather than individual atomistic units at just the basement level. Thus, biological systems are much more like social systems than solar systems. Moreover, biological mathematical theories are more similar to computer science programs than to physical theories.

Two final qualifications are in order. First, full Systemic Darwinism must explore (i) other dimensions and (ii) other mathematical theories. Other dimensions also tend to follow the historical arc noted at the end of *Section 1*. Three such dimensions are defined by the following poles: (i) genetic and ecological explanations, (ii) microevolution and macroevolution, and (iii) deterministic and stochastic dynamics (e.g., refs. 79, 82, 91). Furthermore, theoretical ecology (92) and analytical paleobiology (93) are other important mathematical theories to be explored even if they are perhaps less axiomatized and “axiomatizable”.

Second, we may not be able to attain our regulative ideal. There may be hidden unresolvable tensions or other currently undiscovered reasons that impede attempts at unification. Because Systemic Darwinism is work in progress, we do not yet know. However, even partly unified (i.e., disunified), general, and ongoing Systemic Darwinism embedding different biological theories would greatly further both our theoretical understanding and the effectiveness of our interventions. Furthermore, to avoid a higher level “reification regress,” Systemic Darwinism should probably also eventually be compared with other sorts of unification platforms that may be on offer. These are exciting times for biological theory, and much work lies ahead of us.

In conclusion, let us return to the beginning of our story, to 1859. Given Darwin’s own concerns with (i) the “whole organization” (ref. 1, p. 143) and “reproductive system” (ref. 1, p. 131; structure), (ii) the “natural system is a genealogical arrangement” (ref. 1, p. 479; history), and (iii) the “perfection of . . . coadaptation” (ref. 1, p. 3) and the “web of complex relations” (ref. 1, p. 73; function), he might very well have applauded the efforts of Systemic Darwinism. By focusing on complex systems and their hierarchical networks of parts, strong dichotomies can be rethought as complementary and interpenetrating poles, and theories can be integrated.

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