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BIOLOGICAL EVOLUTION: FACTS AND THEORIES

A Critical Appraisal 150 Years After "The Origin of Species"

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Process and ontological priorities in evolution

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Abstract

Charles Darwin, a fervid admirer of Isaac Newton, nonetheless described evolution as a *process*, rather than as the action of laws upon objects. Against this bold initiative, the "Grand Synthesis" of Fisher and Wright and the ensuing discoveries in molecular biology ushered in the Neo-Darwinian scenario wherein ontological emphasis has reverted to material objects and mechanisms. Other life sciences, however, continue to lend themselves more naturally to description in terms of processes. The dynamics of ecosystems, for example, can be seen to rest upon a set of fundamental postulates corresponding to the attributes of processes. Mutuality stands at the ontological core of this perspective, known as "process ecology". By comparison, competition is seen to be accidental and derivative. Unlike in the Newtonian/Darwinian schema, selection in process ecology can occur internal to the system, rather than solely via the exogenous agency of "natural selection". The monist dictum of "survival of the fittest" appears to relate to only one side of a broader Heraclitean/Hegelian agonism. Such discrepancies with orthodox evolutionary theory suggest that a far richer picture of evolution (and the ethos that it informs) may be possible by reverting to Darwin's initial instinct to describe living nature primarily as process. Adopting the process perspective mitigates many of the ostensible conflicts between science and religion.

1. Evolution, process or law?

The contributions of Charles Darwin's *Origin of the Species* to scientific discourse have been monumental, and there is any number of reasons to celebrate the anniversary of its publication. For example, Darwin's work was among the first that introduced both change and history into science — considerations that were revolutionary at the time and remain controversial today. But in this essay I wish to focus upon one of Darwin's gifts to natural philosophy that is rarely emphasized — namely, the nature of Darwin's scenario for change as *process*.

Darwin's contributions undeniably were revolutionary, but Marshall McLuhan (1964) was wont to remind us how new ideas and inventions are usually perceived in the context of what went before. Now, the early nineteenth century saw an apotheosis of the consensus for a material/mechanical view of nature (Laplace 1814) that precipitated in the wake of Newton's *Principia* — although not following Newton's personal beliefs (Dellian 1992). Darwin himself was a great admirer of Newtonian methodology and aspired to become "the Newton of a blade of grass" (Depew and Weber 1995).

It is hardly surprising, therefore, that Darwin's theory for change was interpreted in terms of the prevailing Enlightenment metaphysic. Unfortunately, the phenomenon of process does not conform well to Newtonian thinking. The tendency thus was to force a fit by emphasizing and by reinterpreting those elements in Darwin's scheme that pivot upon the material and the mechanical. Signs of this drift are apparent in Fisher and Wright's "Grand Synthesis", the mathematics of which closely paralleled that used by thermodynamicists Boltzmann (1905) and Gibbs (1901) to describe the behavior of a statistical ensemble of non-interacting particles. The retro-fit was sealed by the stunning discovery and description of DNA/RNA as the material repository for biological history.

So complete has been this Newtonian revanchement that neo-Darwinian theory is considered today by many to validate the material/mechanical metaphysic. In my own country, for example, there is widespread resistance to the teaching of evolutionary theory in public schools. Some of this opposition comes from those who dispute the very facts of evolution — the "Young Earth Creationists". I would suggest, however, that an even larger number is worried more that neo-Darwinian theory is being used by some in the classroom as a Trojan Horse to inculcate youth with a hard materialism that is inimical to the values that those parents would prefer their children to adopt.

Almost forgotten by history and lost in the heat of this conflict is the reality that *process* is the very essence of the Darwinian scenario. Furthermore, upon the notion of process it becomes possible to construct a very different metaphysic as to how nature behaves. And science is desperately in need of new foundations. To wit, in my own field of ecosystem science each of the Newtonian foundations is violated in one way or another (Ulanowicz 1999). As a result, trying to apprehend living systems in terms of what Hans Jonas (1966) has called "an ontology of death" is as fruitless as pouring new wine into old wineskins.

2. Prevailing metaphysics

Before going on, I should pause to enumerate the foundations of Enlightenment science. In doing so, I will circumvent the impossible task of describing the myriad attitudes that contemporary scientists believe concerning how nature operates. Rather, I will hearken back to the early nineteenth century — the height of Enlightenment thinking — at which time there prevailed a widespread consensus on how nature behaves. I submit that virtually all shades of current beliefs retain their roots in this formulation.

David Depew and Bruce Weber in their tome, *Darwinism Evolving* (1995), conveniently enumerate the basic assumptions:

> 1. Newtonian systems are causally *closed*. That is, only mechanical or material causes are legitimate, and they always co-occur. Other forms of action are proscribed, especially any reference to Aristotle's "final", or top-down causality.
> 2. Newtonian systems are *atomistic*. They are strongly decomposable into stable least units, which can be built up and taken apart again. Atomism combined with closure gives rise to the notion of reductionism, whereby only those causes originating at the smallest scales are of any importance.
> 3. Newtonian systems are *reversible*. Laws governing behavior work the same in both temporal directions. This is a consequence of the symmetry of time in all Newtonian laws.
> 4. Newtonian systems are *deterministic*. Given precise initial conditions, the future (and past) states of a system can, in principle, be specified with arbitrary precision.
> 5. Physical laws are *universal*. They apply everywhere, at all times and all scales. The key adverb here is "everywhere". In combination with determinism, universality leads many to believe that nothing occurs except that it be elicited by a fundamental physical law.

I hasten to add that no one today believes fully in all five tenets. For example, soon after Laplace (1814) had exulted in the absolute power of Newtonian laws, Sadi Carnot (1824) demonstrated the *irreversible* nature of physical *processes*. As I mentioned, Charles Darwin (1859) himself invoked history (i.e., irreversibility and indeterminism) into his narrative. Then at the beginning of the twentieth century relativity and quantum theories surfaced to cast serious doubts upon universality and determinism.

So it would seem that after two centuries of such erosion, the classical assumptions lie fully in tatters. Nevertheless, its frayed threads continue to hold enormous sway over contemporary science. Thus it is that closure is strictly maintained in the neo-Darwinian scenario of evolution (Dennett 1995). That atomistic reductionism continues to dominate biology is evident in the contemporary prominence of molecular biology. As for determinism, a surprising fraction of scientists today continues to eschew the reality of chance, contending instead that probability simply papers over an underlying determinacy (e.g., Bohm 1989).

3. Problems with biology

I would suggest that our inability to see beyond the material and the mechanical lies in our own narcissism, or more precisely in our preoccupation with ontogeny. As a matter of fact, when it comes to organisms, matters *do* appear so tightly constrained as to be almost mechanical. The emphasis upon mechanism leads many to look for the origin of life in the appearance of just the right molecules that suddenly and magically come alive. That is, we become intent on seeing first life only in the context of a mechanical transition from complicated dead molecules to highly constrained living beings — much like the dry bones in Ezekiel's vision that took on flesh and stood up.

If we were truly evolutionary thinkers, however, we would pay greater attention to Darwinian *process* and imagine the world prior to life as one in which constraints were inchoate and flexibility was rampant — a situation not wholly unlike what exists in ecosystems. Ecologist Howard Odum (1971), for example, argued that proto-organisms could arise *only* in the context of what might be described as a proto-ecosystem — one in which complementary reactions, such as oxidation and reduction, were physically separated in space and connected via physical transport. The activities associated with this large-scale dynamics could transfer in very natural fashion to smaller "dissipative structures", or proto organisms, in analogy with how large-scale hydrodynamic eddies spawn smaller ones. Ecological dynamics, therefore, appears to afford a far more fecund theatre in which to study non-Newtonian behaviors than does our usual preoccupation with ontogeny. This is because it is easier to discern that ecological dynamics are not determined by laws, but rather by processes (Ulanowicz 2009).

My esteemed colleague and friend, Stuart Kauffman, who preceded me to this podium has argued that not all of what we see in the living world is determined by known laws. Doubtless, some will persist in labeling his assertion another "God of the Gaps" argument. For who is to say that some biological laws, akin to those of physics, are not waiting to be discovered? Well, Walter Elsasser (1981) said as much in 1981. It was he who demonstrated that it was *patently illogical* to expect "laws" in biology analogous to those in physics. Elsasser's argument centered around the obvious heterogeneity in biological systems. That biological entities all differ in at least minor ways from each other makes it impossible to define homogeneous sets of biological entities. Early last century Alfred North Whitehead and Bertrand Russell (1913) demonstrated that the operation of laws in physics is logically equivalent to operations between perfectly homogeneous sets, i.e., groupings of entities that are totally indistinguishable from each other, such as a collection of electrons or hydrogen atoms. They showed that operations between tokens of two homogeneous sets always yielded, in determinate fashion, a member of yet another homogeneous set (*Figure 1*).

Figure 1. Operations between homogeneous sets are determinate.

By contrast, the same operations between heterogeneous groupings do not in general yield tokens of any single heterogeneous grouping (*Figure 2*). The results always exhibit some indeterminacy.

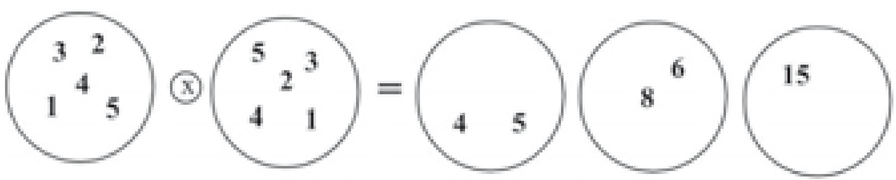

Figure 2. Operations between inhomogeneous groupings are indeterminate.

Of course, indeterminacy is hardly new. Variation is, after all, what keeps statisticians employed in biology. And, surely, one *does* observe statistical regularities throughout the living realm. Does that mean, however, that the spectre of chance is now under control — that we retain the advantage of prediction, albeit in a statistical sense? Once more, Elsasser answers rigorously in the negative by showing that probability theory does not apply universally to all chance phenomena.

Although rarely emphasized, conventional probability theory makes the tacit assumptions that chance events are simple, generic and repeatable. Elsasser (1969) demonstrated, to the contrary, that the overwhelming majority of stochastic events in biology are *totally* unique, never again to be repeated. If such an assertion sounds at first absurd, given the enormity and age of our universe, it happens to be surprisingly easy to defend. Elsasser noted that there are fewer than 10^{85} elementary particles[1] in the whole known universe, which itself is about 10^{25} nanoseconds old.[2] This means that, at the very most, 10^{110} simple events could have occurred over all physical time. It thereby follows that if any event has considerably less than 10^{-110} probability of re-occurring, it will never do so in any physically realistic time.

Now, 10^{110} is a genuinely enormous number. It might surprise some to learn, however, that it doesn't require Avogadro's Number (10^{23}) of distinguishable entities to create a number of combinations that exceeds Elsasser's limit on physical events. It doesn't require billions, millions or even thousands. A system with merely 75 or so identifiable components will suffice! It can be said with overweening confidence that any event *randomly* comprised of more than 75 distinct elements has never occurred earlier in the history of the physical universe. It follows, then, that in ecosystems comprised as they are of hundreds or thousands of distinguishable organisms, one must reckon not just with an occasional unique event, but with *legions* of them. Unique, singular events are occurring all the time, everywhere!

A necessary condition for applying probability theory to chance phenomena is that the events in question occur at least several times, so that a legitimate frequency can be estimated. Singular events, however, occur only once, never to be repeated. Any probabilities assigned to them transcend physical reality. Furthermore, these singular events constitute actual holes or gaps in the causal fabric. Akin to Heisenberg uncertainties or the Pauli Exclusion Principle, the singularities are a *necessary* part of nature, not some epistemological lacuna awaiting theoretical elaboration.

4. From laws to processes

By Elsasser's reasoning, determinism is decidedly *not* a universal characteristic of nature. I should hasten to add, however, that physical laws nonetheless remain inviolate. It's simply that no conceivable combination of the four force laws of

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1 Today the figure is put at closer to 10^{81}.

2 A nanosecond is one-billionth of a second — the timescale of atomic reactions.

physics and the two laws of thermodynamics can possibly be stretched to cover all the possible changes amongst a complex system having, say, 35 loci for incremental change. Any particular parametric specification of laws will be satisfied by a *very large* multiplicity of possibilities. Laws continue to constrain complex biological phenomena, but they are insufficient to *determine* results. That which specifies outcomes must lie elsewhere.

As Darwin indicated, that which specifies outcomes is process. In order to maintain rigor, however, it becomes necessary to define "process" more precisely. Accordingly, we take the following as our operational definition (Ulanowicz 2009):

> *A process is the interaction of random events upon a configuration of constraints that results in a non-random, but indeterminate outcome.*

Now, the juxtaposition of "non-random" with "indeterminate" is perhaps a bit confusing, so it should prove helpful to consider a simplistic example of a process called Polya's Urn (Cohen 1976). This exercise begins with a collection of red and blue balls and an urn containing one red ball and one blue ball. The urn is shaken and a ball is blindly drawn from it. If that ball is the blue one, a blue ball from the collection is added to it and both are returned to the urn. The urn is shaken and another draw is made. If a ball drawn is red, it and another red ball are placed into the urn, etc. The first question to arise is whether a long sequence of such draws and additions would culminate in a ratio of red to blue balls that converges to a limit. It is rather easy to demonstrate that after some 1000 or so draws, the ratio indeed converges to the close

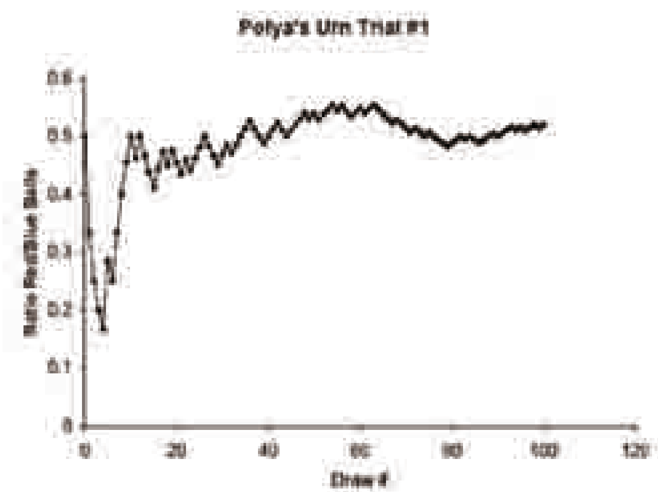

Figure 3. Polya's Urn, Trial #1 after 100 draws.

neighborhood of some constant, say 0.54591, as shown in *Figure 3*. That is, the ratio becomes progressively *non-random* as the number of draws grows.

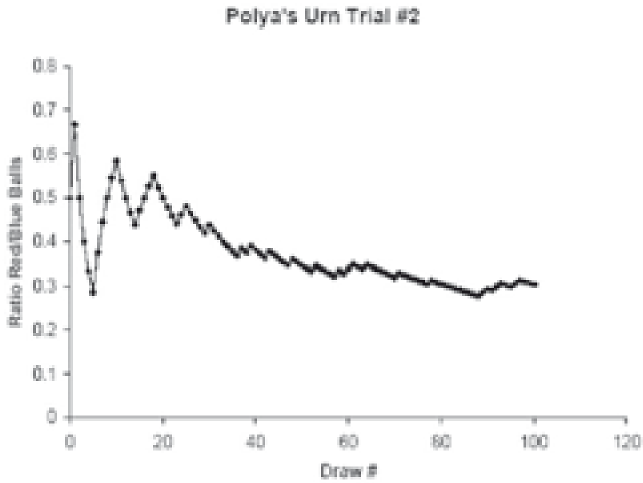

Figure 4. Polya's Urn, Trial #2 after 100 draws.

That the system does not converge closely to 0.5000 prompts a second question, namely, what would happen if the urn were emptied and the starting configuration recreated? Would the subsequent series of draws converge to the same limit as the first? It almost certainly will not. After a second 1000 draws it might approach a limit in the vicinity of 0.19561 (*Figure 4*). The Polya process is clearly *indeterminate*.

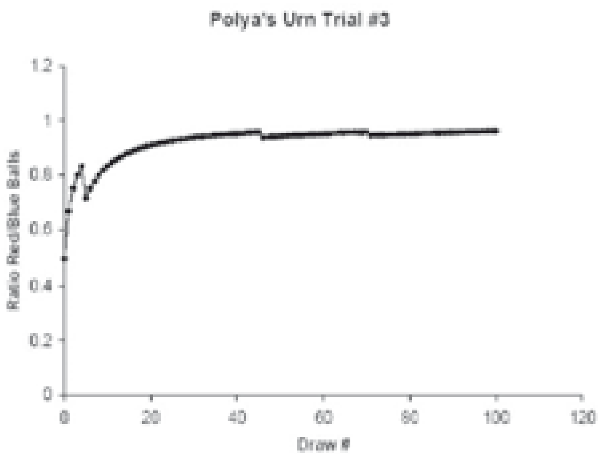

Figure 5. Polya's Urn, Trial #3 after 100 draws.

Repetition of the process many times reveals that the ratio of balls is progressively constrained by the particular series of draws (history) that have already occurred.

We note further that some histories converge to behaviors that are difficult to distinguish from mechanical, law-like dynamics interrupted by occasional noise, as in *Figure 5*. The possibility thus arises that scientific laws might be limiting forms of prior, less constraining processes (Chaisson 2001).

For later reference, we emphasize three features of this artificial, simplistic process:
(1) It involves chance.
(2) It involves self-reference.
(3) The history of draws is crucial to any particular series.

5. Order from natural processes

Of course, Polya's Urn is but an artificial process. Gregory Bateson (1972), however, provided a clue as to how natural processes could impart order to noisy affairs. He noted that the outcome of random noise acting upon a feedback circuit is generally non-random. Following his lead, I now draw your attention to a particular form of feedback — autocatalysis (Ulanowicz 1997). By "autocatalysis" I am referring to any instance of a positive feedback loop wherein the direct effect of every link on its downstream neighbor is positive (*Figure 6*).

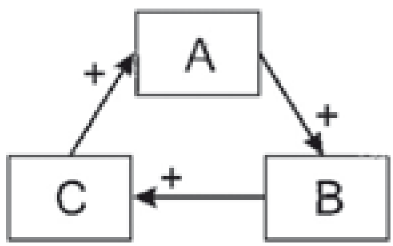

Figure 6. A three-component autocatalytic configuration of processes.

A convenient example of autocatalysis in ecology is the community that forms around the aquatic macrophyte, *Utricularia* (Ulanowicz 1995). All members of the genus *Utricularia* are carnivorous plants. Scattered along its feather-like stems and leaves are small bladders, called utricles (*Figure 7a*). Each utricle has a few hair-like triggers at its terminal end, which, when touched by a feeding zooplankter, opens the end of the bladder, and the animal is sucked into the utricle by a negative osmotic pressure maintained inside the bladder. In nature the surface of *Utricularia* plants is always host to a film of algal growth known as periphyton. This periphyton serves in turn as food for any number of species of small zooplankton. The autocatalytic cycle is closed when the *Utricularia* captures and absorbs many of the zooplankton (*Figure 7b*).

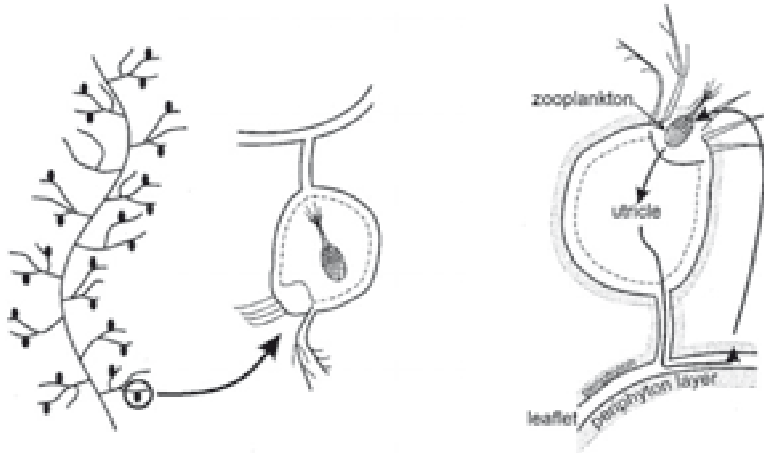

Figure 7. (a) Stem of *Utricularia* with closeup of utricle. (b) The autocatalytic processes inherent in the *Utricularia* system.

A seminal feature of autocatalysis is that it exerts selection pressure upon all of its components and any of their attendant mechanisms. Any change in a characteristic of a component that either makes it more sensitive to catalysis by the upstream member, or a better catalyst of the element that it catalyzes, will be rewarded. Other changes will at best be neutral, but more likely will be decremented by the feedback. A very important aspect of selection is that it re-enforces changes which bring more material or energy into a participating element, resulting in what can be called (in Newton's word) "centripetality" (*Figure 8*).

I believe that one cannot overstate the importance of centripetality to the phenomenon of life. Conventional Darwinism, for example, conveniently overlooks

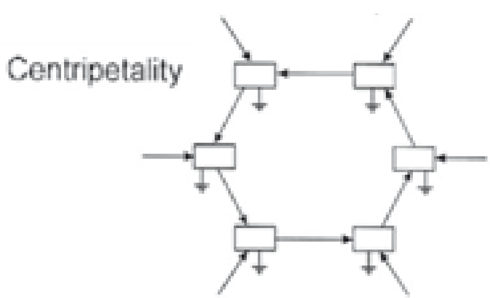

Figure 8. Autocatalysis induces centripetality.

the role of "striving" in evolution (Haught 2003). While all the various organisms are competing with one another in epic struggle, one is pressed to ask what accounts for their drive? Such striving is considered epiphenomenal to most Darwinian accounts, but here's what Bertrand Russell (1960) had to say on the topic:

> *Every living thing is a sort of imperialist, seeking to transform as much as possible of its environment into itself and its seed … We may regard* the whole of evolution *as flowing from this 'chemical imperialism' of living matter.* (Emphasis by author)

It is clear that by "chemical imperialism" Russell is identifying centripetality; and, from the perspective of systems ecology, he correctly places it at the very core of evolution.

Equally important is that centripetality is a prerequisite for competition. Without the generation of centripetality at one level, competition cannot arise at the next. Mutuality is essential; competition is an accidental consequence. To see how centripetality induces competition, we regard the sequence in *Figure 9*. In the second graph element D appears spontaneously in conjunction with A and C. If D is more sensitive to A and/or a better catalyst of C, then the ensuing dynamics of centripetality will so favor D over B, that B will either fade into the background or disappear altogether. That is, selection pressure and centripetality can guide the replacement of elements.

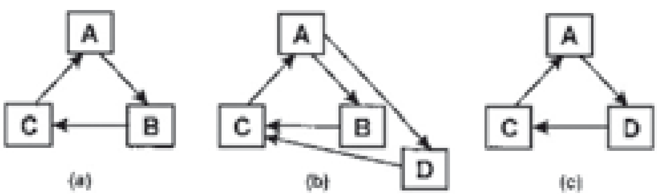

Figure 9. Centripetality induces competition.

Let us pause here to consider the ramifications of this ontological inversion. Although many feel it impossible to proceed from an existential "is" to a normative "ought", the ethos of a human community often is coupled with how it perceives nature. Thus, while emphasis upon competition is likely to promote that form of behavior, quite another prescription might follow from the recognition that mutual beneficence (the drive behind centripetality) lies at kernel of life. Corresponding moral directions are likely to be as disparate as those espoused by Thomas Huxley and Giovanni di Fidenza.

Returning to the sequence in *Figure 9*, we see how C might be replaced by E and A by F, so that in the long run, the lifetime of the autocatalytic configuration can exceed that of any of its components or their attendant mechanisms. Such supervenience by the whole over its parts explicitly contradicts the Newtonian dictum of *closure* (Clayton 2004). In fact, the other Newtonian postulates fare no better. We mentioned earlier how *determinism* is a chimera in complex systems. The asymmetric directionality in autocatalysis makes the system highly *irreversible*. The fact that each component develops in the context of its co-participants renders them all highly co-dependent over the course of time, so that the organic complex is no longer amenable to *atomistic* decomposition. Finally, the domain of any individual process is hardly *universal*, being circumscribed in time and space and subject to mitigation by processes at other levels.

6. An ecological metaphysic

As they pertain to ecosystems, all five Newtonian postulates appear ill-fitted to the description of living dynamics. The time is ripe for an entirely new, but wholly naturalistic, metaphysic — an ecological metaphysic, so to speak. In particular, the new metaphysic requires that we shift our focus from laws and objects to configurations of processes. Here we invoke the three features of the Polya process that I earmarked earlier — namely that process requires chance, self-influence and history.

Our first postulate establishes chance as a reality:

(1) *Radical Contingency*: Nature in its complexity is rife with singular events.

Organic systems are constantly being exposed to unique contingencies, but due to the self-stabilizing properties of autocatalysis, most of these events do not upset the prevailing dynamics. A miniscule few, however, may carry a system into a wholly different mode of *emergent* behavior – now perceived as an entirely *natural* phenomenon (Ulanowicz 2007).

The strictures of closure and atomism do not allow systems to maintain their integrities and grow (Ulanowicz 2009). By contrast, autocatalytic action, a particular form of self-influence, is capable of imparting form and pattern to nature. Accordingly, we replace closure and atomism by allowing for

(2) *Self-Influence*: A process in nature, via its interaction with other natural processes, can influence itself.

Thirdly, in place of reversibility we recognize, as did Darwin, that the system must retain some record of its past configurations, that is, it must possess a

(3) *History:* The effects of self-influence are usually constrained by the culmina-

tion of past such changes as recorded in the configurations of living matter.

In a scientific world bent on materialism, our conception of history tends to be dominated by DNA and similar molecular forms. But our analysis of competition suggested that the first records of organic history were more likely written into the topologies of stable, long-lived configurations of processes.

These three postulates, then, constitute a natural platform from which to cast an ecological perspective on life. In addition, the precepts spawn two corollary tenets: The first is that agency in the developmental scenario resides more with configurations of processes than with objects. Life itself is closely identified with configurations of processes. For example, Enzo Tiezzi (2006), Professor of thermodynamics and part-time hunter, asked what was different about a deer that he had just killed from the one which had been alive three minutes earlier? Its mass, form, bound energy, genomes — even its molecular configurations — all remained virtually unchanged immediately after death. What had ceased with death and was no longer present was the configuration of processes that had been coextensive with the animated deer — the very agency by which the deer was recognized as being alive.

Secondly, one can discern two opposing propensities in ecodynamics. Autocatalysis supplies the animation for systems to grow and maintain themselves. Opposing this drive is the well-known effect of the second law to degrade and dissipate existing structures. This perspective is hardly new. Diogenes reported how Heraclitus saw nature as the outcome between agonistic tendencies that build-up as opposed to those that tear-down. The direct conflict between these drives ameliorates at higher levels, however: Without the action of radical contingency, novel structures could never emerge. Conversely, larger, more constrained structures perforce dissipate more resources.

The three foregoing postulates and the two derivative observations constitute the crux of what I have called, for want of a better term, "process ecology" (Ulanowicz 2004, 2009).

7. Ontological priorities

Again it must be emphasized that these new postulates in no way abrogate any scientific laws or phenomenology that have accrued over the past three centuries. Experience with homogeneous, rarefied and weakly-interacting systems led, however, to a framework of knowledge that was found wanting whenever variety and complexity overwhelm the ability of law to specify outcomes. Most elements of the classical framework now appear as special, degenerate cases of more general processes, in analogy with how material and the laws of force are purported to have precipitated out of inchoate processes in the wake of the Big Bang (Chaisson 2001).

As with the relationship between mutuality and competition, the perspective of process ecology reorders numerous ontological priorities (Ulanowicz 2009): Process, long the stepchild in scientific discourse, now appears more fundamental than either law or material objects. Before material as we know it came to be, process was. Attributes formerly thought universal now appear circumscribed: determinism applies to a vanishingly small class of rarefied phenomena. Atomism is possible only in the purely physical realm. Monist dictums, when pursued to the extreme lead inevitably to dire consequences in a world that arises out of dual, contrasting propensities. Causalities emanating from small scales must now share the stage with supervenient influence from higher levels. Natural selection can act within a system and not just from beyond its perimeter. History is of fundamental importance. True chance quite naturally gives rise to the emergence of new phenomena. The dynamics of life are qualitatively different from that of non-living matter. Etc., etc…

8. Process ecology and theology

I wish to make it very clear that nothing I have discussed violates the constraints of methodological naturalism. There is nothing in process ecology that *in principle* would bar a metaphysical naturalist from accepting the whole of it. If what I have said happens to discomfit some, it is likely because the ecological perspective challenges cherished beliefs that some bring with them into science — especially the strict materialism that has proved such an effective weapon against transcendental convictions.

That minimalist materialism, however, excavated a gaping chasm between the transcendental and science — an abyss that swallowed the phenomenon of life. It is my hope that a process-oriented framework will allow science to address life in a direct and more rational way than hitherto was possible under the outworn metaphysic. I stress as well that bridging the chasm in no way impugns the freedom of those who wish to maintain their distance from the numinous. It simply recognizes life for what it is — a dynamic that is qualitatively different from the dead physics in which it is immersed.

It should surprise no one that any platform used to raise life out of the netherworld also mitigates several ostensible conflicts between science and believers (Ulanowicz 2004). As already noted, emergence fits comfortably into process ecology; and, by way of corollary, free will does likewise. Of course, theodicy (the problem of evil and suffering) has not been obviated, but its complexion has changed. In a world of dual dynamics, the complete elimination of petty evil and its attendant sufferings would foreclose all possibility for evolutionary change. Evil is thus seen as a problem of magnitude, rather than ontology (Ulanowicz 2004; Keller 2005; Jackelén 2009; Callahan 2003). Finally, any metaphysic that entails abundant "wiggle room" in nature (Hefner 2000) is one that cannot preclude Divine intervention. Intercessory prayer no longer defies rationality.

I would like to conclude by exhorting believers neither to fear evolution nor to try to discredit it, but rather to embrace it. Darwinian thought, freed from its procrustean box, celebrates life as distinct from death. It is too wondrous a story to be allowed to devolve into a game among little pieces of matter. Above all, I would recommend the necessity to perceive evolution as Darwin first portrayed it — as process. That perspective frees humanity from the "cosmology of despair" (Haught 2000) so fashionable in today's academic circles and allows one to entertain again a cosmology of hope.

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