

Article

Applying the Prigogine view of dissipative systems to the major transitions in evolution

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Abstract.—Ilya Prigogine’s *trinomial* concept is, he argued, applicable to many complex dissipative systems, from physics to biology and even to social systems. For Prigogine, this trinomial—*functions, structure, fluctuations*—was intended to capture the feedback-rich relations between upper and lower levels in these systems. The main novelty of his vision was his view of causation, in which the causal arrow runs downward from dissipative structures to their components or functions. Following this insight, some physicists and biophysicists are beginning to apply terms formerly used mainly in biology, such as *evolution, adaptation, learning, and life-like behavior*, to physical and chemical nonequilibrium systems. Here, instead, we apply Prigogine’s view to biology, in particular to evolution, and especially the major transitions in evolution (MTE), arguing that at least the hierarchical transitions—the transitions in individuality—follow a trajectory anticipated by the trinomial. In this trajectory, formerly free-living organisms are transformed into “functions” within a larger organic “structure.” The Prigogine view also predicts that, consistent with available data, the increase in number of hierarchical levels in organisms should accelerate over time. Finally, it predicts that, on geological timescales, ecosystems and Gaia in particular will tend to “de-Darwinize” or “machinify” their component organisms.

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Introduction

It is well known that the mechanistic-reductionistic paradigm—explaining upper-level processes in term of lower-level mechanisms—has had a great deal of success in the physical sciences. But so has the macroscopic approach. Physics defines sets of processes and structures and formulates laws and principles that only make sense from a macroscopic viewpoint. These processes and structures do not exist at the microscopic level but rather—it is said—emerge from properties at that level. Thus properties like malleability, viscosity, friction between two objects, electrical conductivity, and so on, are all macroscopic properties that help us to describe and predict the physical reality we observe. And it is understood that these properties emerge from the microscopic level, whose parts do not possess them. We do not speak, nor can we, about the viscosity of an atom, for instance, or the friction between a molecule of cement and a molecule of the sole

of a shoe. At that level, we speak of electromagnetic forces. In fact, the most firmly established principles or laws in the physical sciences come from thermodynamics, which has historically started from such emergent properties (e.g., pressure or temperature).

The biological sciences try to be coherent with the physical sciences. It seems obvious that living beings comply with physical laws. But beyond that, physicists and biophysicists at least since Alfred Lotka (1922) have made important contributions to biology. The best known may be Erwin Schrödinger’s (1944) *What Is Life?*, but there is also the work of Kleidon and Lorenz (2005), Schneider and Sagan (2005), and Skene (2017). In ecology, important contributions have come from biologists taking a biophysical perspective, found in particular in the work of Odum and Pinkerton (1955), Margalef (1963, 1968), Ulanowicz (1997, 2009), Jorgensen and Fath (2004), and Jorgensen and Svirezhev (2004), as well as in the

macro vision of the Gaia hypothesis of Lovelock and Margulis (1974). These two views—from biology and physics—are complementary, each enriching the other.

Ilya Prigogine wrote many times that all complex dissipative systems are physical structures open to exchanges of energy, matter, and information. These systems are defined by three elements:

- **Structure:** The system as a whole, at the macroscale. Examples include Bénard cells, a candle flame, Jupiter’s Great Red Spot, and Hurricane Katrina.
- **Functions:** The parts or units within the system whose processes and relationships causally determine the structure and in turn are stabilized by the structure.
- **Fluctuations:** The variations in matter and energy flow at the level of function, variations that are either enhanced or diminished, stabilized or eliminated, by their interaction with the flow of matter and energy through the larger structure.

In Prigogine’s view, there are internal feedbacks—causal flows of energy and matter—between each trinomial element and the other two elements of the system, shown schematically (e.g., Prigogine 1977b) in Figure 1. This pattern of interaction can be recursive, leading to a positive feedback.

Prigogine’s view is that the trinomial of Figure 1 can be applied to any sufficiently complex dissipative system and that all of these systems must comply with it.* We will call this view *Prigogine’s conjecture*. Assuming the conjecture is correct then, as all biological systems are dissipative and very complex, any biological theory that describes biological systems, from bacteria to the biosphere, should aim to be consistent with it, just as such systems should be consistent with other principles of physics. Prigogine used this trinomial to explain how dissipative systems evolve. We will use it to explain the continuous and accelerated increase

*The trinomial does not apply to every physical or chemical dissipative system. For instance, a rock falling through the air is a dissipative system that does not have all the causal relations of the trinomial.

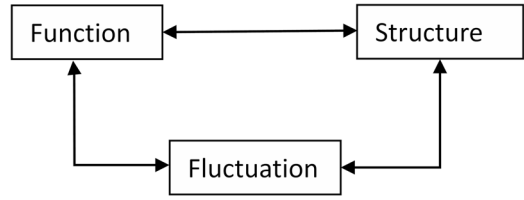


FIGURE 1. The “Prigogine trinomial.” In complex dissipative systems, each element of the trinomial is in mutual interaction with the others. The double arrows refer to the causal feedbacks among the three members of the trinomial.

in hierarchy in the history of life, the trajectory marked by the major transitions in evolution (MTE).

We start with a qualitative formulation of Prigogine’s vision of complex dissipative systems. We then generalize the trinomial in a “recursive” form that gives rise to a nesting of trinomials and show how this form illuminates certain features of the MTE and contributes to the ongoing discussion in the literature. At the end of that section, we offer a justification for what we acknowledge is the unusual approach we are taking to large-scale biological trends, through the physics of dissipative systems. Finally, at the end, we consider the possible consequences for how we understand the evolutionary process at each level and speculate on the possibility of applying the trinomial to ecosystems and Gaia.

The Physics behind Prigogine’s Trinomial

Dissipative structures are open systems with self-organizing behavior that hover in organizational macrostates far from thermodynamic equilibrium. This is achieved by the absorption of an energy flow (in physics terms, exergy) and the dissipation or dispersion of that energy, exporting entropy outside the system while reducing the gradient that generated the energy flow (Glandsdorff and Prigogine 1971; Brooks et al. 1989; Weber et al. 1989; Salthe 1993; Toussaint and Schneider 1998; Jorgensen and Svirezhev 2004; Schneider and Sagan 2005). Thus, for example, a hurricane is a macroscopic structure that self-organizes in a heat gradient, a column of warm air rising from equatorial oceans. It absorbs energy from the upward

flow of warm air, and it releases that energy in the rotary motion of the air mass that constitutes it. It is dissipative in that its motion acts to dissipate or reduce the heat gradient between the upper and lower atmosphere, in the process exporting entropy to the surrounding air mass (see, e.g., the discussion of the thermodynamics of hurricane behavior in Emanuel 1999).

In the Prigogine view, the gradient maintains the structure, but also causes it. More precisely, the structure arises when fluctuations occur in lower-level processes and are amplified by the system. In the hurricane example, the fluctuations are parcels of air that by chance move in the same direction. The gradient amplifies these movements to produce local coherent rotary motion, entraining other parcels, whose movements are further amplified, ultimately producing the macroscale vortex. It is the fluctuations that break the initial symmetry—warm air rising uniformly from the ocean surface—and their amplification that gives rise to the macroscale structure, the hurricane.[†]

Hurricanes have substantial structural complexity: an eye, an eye wall, a periphery rich in local thunderstorms, occasionally spalling off tornadoes. These are the parts of the system, or what Prigogine would have called its “functions.” Living systems have many more, of course. But in both, the source of the complexity is the nonlinear coupled relationships and the rich self-generated feedback cycles present in their coupling with their external environments.

Thus, for Prigogine, the cause of the structure, of the large-scale order, is the amplification of small-scale fluctuations. And what makes this order through fluctuations stable is the exchange of energy with the external world. One could say that the large-scale structure is the “aim” or “goal” of the system, in that the structure arises predictably, over a large range of different

small-scale fluctuations, and it is implicit, so to speak, in the initial conditions, the gradient. It is brought into existence by the gradient, “feeds” on the gradient, and is maintained by its contribution to dissipating it.

It was observations of the thermodynamics of physical-chemical systems that led Prigogine to state:

There are three aspects which are *always* linked in dissipative structures: the *function* as expressed by the chemical equations, the space–time *structure* which results from the instabilities, and the *fluctuations*, which trigger the instabilities... [in combination these can be said to generate] order through fluctuations. (Prigogine 1977b: p. 272, italics added)[‡]

For Prigogine, statistical fluctuations at the microscale are amplified by macroscale gradients giving rise to flows of energy and matter exchange between the environment and the structure, as well as within the structure (Prigogine 1977b). In addition, the system responds with internal changes, changes in the functions, to external fluctuations at the macroscale. In physics, these include fluctuations in temperature, density, and pressure gradients; in chemistry, concentration gradients; or in biology, changes in the environment, such as available resources (Prigogine 1977a).[§]

The Trinomial.—Ultimately, Prigogine sought a common basis for all complex dissipative

[†]Prigogine here is thinking about structures like hurricanes and chemical clocks as well as biological systems. In all cases, the claim is that the macroscale level—what he calls the “space–time structures”—can be understood as the product of the dynamics of functions at the micro-level. Thus, for a hurricane, these are the equations of meteorology, for a chemical clock the chemical equations of molecular reactions, for a biological system the equations of biochemical reactions or other microbiological principles. In other words, the functions can be understood in terms of lower-level “physical” equations, the standard ones used in each of the relevant disciplines.

[§]The use of the term “fluctuations” may be a little bit confusing. Prigogine uses it to describe the initial small fluctuations occurring at the microscale, but he also uses it to describe changes in large-scale external gradients, material or energetic. Gradient might be a better word for our purposes, but the word suggests a static relationship, and Prigogine was interested in the more dynamic aspects. In any case, the common theme is change, at a variety of different scales. Here we will make clear from our usage the scale to which we are referring.

[†]A recent paper by Chartier et al. (2021) shows that a hydraulic instability (a fluctuation, in Prigogine’s terms) is amplified by physical forces that cause some germ cells to grow and others to shrink in volume in the germline cells of *Caenorhabditis elegans* nematode. Then programmed cell death eliminates the shrunken cells, further amplifying the differentiation process, as required for proper development in the *C. elegans* embryo. Another word for this process, in which small-scale fluctuations are amplified and stabilized, might be (as suggested by an anonymous reviewer) “synchronization.”

structures, ranging from the classic “Bénard instability” (Prigogine 1977b) to organisms and human societies. And that common basis was the fluctuation–function–structure trinomial (Fig. 1). Prigogine thought of the trinomial as a bridge uniting the sciences, uniting the physical with the biological, social, and human (Prigogine 1982).

However, although he used the trinomial frequently as a heuristic, he did not fully formalize it, even qualitatively. He did not describe the causal relationships one by one with generalizable examples in a systematic way, and the reason may have been that the physics of “far-from-equilibrium” systems had not been fully worked out in quantitative terms. Thus, for him, the trinomial was less a formal physical principle and more a great intuition, his “conjecture,” that he would defend for decades.**

Still, from his multiple writings, we can try to clarify the causal relationships of the trinomial in an explicit way. Thus, for example, he wrote that the functions can be considered the “microstructure” of the system (Prigogine 1977a). As examples, he used the molecules in the convection of Bénard cells, the thousands of coordinated enzymes in a cell, the neural cells in a brain (Prigogine and Stengers 1978), and individuals in a society. And the large-scale spatial or space–time organization corresponds to the “macrostructure,” which here we call simply the structure. In his terms, a small-scale fluctuation causes a local modification of a function [in other words: fluctuation → function], such that, if the regulatory mechanisms are inadequate, modifies the larger structure [fluctuation → structure] as well.

However, there is more to the causal story. The causal arrows do not all run upward, with fluctuations and functions affecting structure. The dissipative structure also reacts to changes in the environment, acting downwardly on its parts, affecting the trajectories of the fluctuations that occur at the microscale and sometimes reorganizing the functions to

accommodate the new external regime [structure → fluctuation, and structure → function] (Prigogine and Stengers 1978).

Thus, in physical systems like a Bénard cell array, a modest increase in the temperature gradient imposed from outside causes an increase in the rate of rotary motion of the fluid within each cell [structure → function] and therefore a change in the microstructure, that is, in the trajectories of the fluid molecules within the cell [structure → fluctuation]. Similarly, a change in the seasons causes a deciduous tree to change the configuration of its parts, a loss of leaves [structure → function], which in turn demands a change in the microstructure, in the concentrations and movements of materials within the tree [structure → fluctuation]. There is a difference, obviously, between these two systems. The responses in the Bénard cell array are purely physical, and those of the tree have also been engineered by the evolutionary process. But Prigogine would point out that because organisms are dissipative structures, this kind of top-down causation did not have to be engineered from scratch. Rather, it is primitively present in all dissipative systems, in all biological systems, and therefore available for the evolutionary process to co-opt and fine-tune.

Top-Down Causation.—This last relationship is what closes the trinomial and makes positive feedback possible. And it is actually the most difficult to recognize, in that it adds something forbidden by the classical reductionist paradigm, namely, a simultaneous “backward” or top-down causation. The standard bottom-up style of explanation may be the most common in biology. But in certain areas, such as discussions of the origin of cells from abiotic chemistry or the emergence of the brain from neurons, top-down language routinely appears. In these systems, when the macro-level structure is forming or formed, we speak of the “thousands of enzymes coordinated by the cell or the neurons coordinated by the brain.” Top-down causation is not always explicitly acknowledged, but it is often implicit in the language used. Where it commonly appears explicitly is in the various systems-theoretic approaches in biology, such as those of Maturana and Varela (1973; also Varela et al. 1974), Rosen (1991,

**Perhaps in much the same way, the “Kepler conjecture,” concerning the packing of spheres, was initially formulated only qualitatively, and then required centuries of mathematical development to become a quantitative scientific theorem (Hales et al. 2017).

1994), Reid (2007),^{††} Ulanowicz (2009), and Shapiro (2013). This is entirely appropriate in biology, Prigogine would argue, because biology is dealing with systems that are both dissipative and highly connected, systems in which the parts combine to form unified wholes (Prigogine and Nicolis 1971). And to the biologists who might justify a preference for the bottom-up style of explanation with an appeal to physics, the science which in reductive thinking underlies all others, Prigogine would point out that top-down explanation is routine in physics for many purely physical-chemical dissipative systems. “Despite what some biologists unconsciously say,” he remarked at one point, “our science [physics] that they think they invoke is no longer Laplace’s” (Prigogine and Stengers 1975, p. 67, English translation from Spanish).

Indeed, recent work in nonequilibrium thermodynamics and on physical and chemical microsystems has been using the language of top-down causation for quite simple systems—much simpler than biological ones—even adopting language that is usually reserved for biology, such as adaptation and the capacity for self-organization (England 2015; Perunov et al. 2016; Horowitz and England 2017; Kachman et al. 2017; Ropp et al. 2018; Kedia et al. 2019). Simple physical systems are said to exhibit life-like behavior (Colomer et al. 2018; te Brinke et al. 2018) and even to show some anticipatory predictive capacity (Zhong et al. 2021; M. Jacob, J. M. Gold, and J. L. England unpublished data). In physics, the Prigogine conjecture is alive and well.

Complexity and Hierarchical Structure.—Systems with the structure underlying the trinomial, have—beyond the stability present in

any dissipative system—two more essential characteristics: the potential for historical-evolutionary change and for increase in hierarchical structure. We focus on the second here. The more complex the dissipative system is, the more defined its hierarchical structure can become. And this in turn creates the potential for an evolutionary feedback (Prigogine 1977b). That is, complex, hierarchical dissipative structures can become the foundation for even higher-level structures. In terms more familiar in biology, the hierarchical complexity—or what has been called the “vertical complexity” (Sterelny 1999)—of the organism increases. As we shall describe later, when organisms do this, the result is an increase in number of levels of nestedness of individuals within individuals, organisms within organisms. The transitions from prokaryotic cell to eukaryotic cell, from solitary eukaryotic cell to multicellular eukaryote, and from multicellulars to colonies are all transitions of this sort (Maynard Smith and Szathmáry 1995; Pettersson 1996; McShea 2001).^{††}

In dissipative systems generally, the driving force for these increases, when they occur, is the increased capacity for dissipation conferred by each additional level. For one thing, an increase in nestedness is also an increase in size, and a larger system—along with the complexity of the nestedness itself—has more dissipative capacity than a small one. Judson (2017) shows that throughout history the dissipative capacity of organisms tends to grow, even accelerate. They take in ever more free energy and dissipate it faster. Also, the additional level increases the number of possible states and therefore tends to increase the possible routes for gradient dissipation. And, if the diversity of possible routes of dissipation increases, then the potential for entropy production increases as well (in accordance with the so-called maximum entropy production [MEP] principle). Nevertheless, many

^{††}Importantly, “hierarchy” is used here only in its structural sense to refer to the nesting of systems within systems, such as nerve cells within a brain or individuals within a society. It is not hierarchy in the sense of causal hierarchies, like military chains of command, where there is no physical nesting of lower levels within higher, nor in the sense of specification hierarchies, like postal addresses.

^{††}Reid writes (p. 306) that higher levels generate a “downward directional effect” on the lower levels. He cites, for instance, Koestler: “‘Holon’ means simply a subunit or module of a hierarchical level”; Rollo: “Not only does hierarchical organization provide reliability and stability but modularized structure also allows modification of subcomponents without global disruption”; Vrba and Eldredge: “Hierarchy is a central phenomenon of life ... Causation ... may be upward from lower levels, downward from higher levels or lodged at the focal level”; and Polanyi, who “wrote about how emergent levels in hierarchies imposed boundary conditions on the lower levels (in Life’s irreducible structure)” (Reid 2007: pp. 301–307).

dissipative systems will not be able to make these transitions. Hurricanes, chemical clocks, or fluid vortices of various kinds, all of these physical systems have hierarchical structure, but that structure has limits. These systems evolve through well-defined stages but do not tend to increase in hierarchical structure once those limits are reached. One limitation for many dissipative systems is the local thermodynamic constraints that are imposed by the environment at their boundaries (Kleidon 2012, 2021). The constraints are surmountable for some dissipative systems, in particular those like biological, psychological, and social systems that can modify that environment. Another limitation is that, compared with biological systems, many physical systems have a limited number of degrees of freedom (a small number of independent coordinates or variables that specify the system), and therefore a limited range of behavior. In the more complex biological and social systems, the range of possible behaviors is quite large, to the point that it significantly raises the probability of the system discovering configurations with greater hierarchical structure. This has been argued to occur in the fractal networks of parts within large multicellular organisms (West et al. 1997). In these, a consequence is that the frictional dissipation is reduced, and the internal system becomes more efficient. Eventually a new local physical limit is reached, one that might again be overcome as the system explores further. We return to this in the discussion of the MTE.

The association between increasing degrees of freedom and higher-level emergence is known in some physical systems (Perunov et al. 2016). As Kachman et al. (2017: p. 5) put it: “The self-organized resonance we have characterized provides a clean, idealized *in silico* illustration of a potentially more general thermodynamic mechanism for emergent energy-seeking behavior in a many-body mixture with a diverse space of chemical combinations.” The application to biology is straightforward. Emergent energy-seeking behavior—feeding—is commonplace in biological systems. More generally, as Prigogine and Nicolis (1971: p. 109) put it, evolution in biology and sociology is associated with an increase in hierarchy, in that it gives “rise to the creation of more and

more complex structures.” These systems are actually a “superposition of co-ordinated structures and functions of increasing complexity. This hierarchy in structure ... [is a] ... feature” of the system (p. 114).

Thus, in certain systems, the trinomial of Figure 1 comes to have nested structure, multiple levels of [function ↔ fluctuation ↔ structure] nested within one another, with newer and higher levels emerging sequentially at the top. Prigogine’s (1982) scheme explains and predicts hierarchy.

Prigogine Trinomials: The “Matryoshka Dolls” in Biology

Prigogine’s trinomial helps us understand how a nested hierarchical structure can arise in organisms. Consider a symbiotic organism described by Lynn Margulis and Dorion Sagan in *Acquiring Genomes* (Margulis and Sagan 2003). A single termite individual is, in Prigogine’s terms, a complex dissipative structure with a diversity of internal functions in mutual feedback with one another. That is to say, in biological terms, it is an organism, with lower-level parts that interact with and regulate one another. One such function within the termite is the set of parts that are involved in the digestion of wood, a set that includes in some species a variety of gut microbes or in other species the fungi that grow in termite-colony nests and are ingested. These microbes and fungi, along with other digestion-related parts, perform a function for the larger structure, the termite as a whole. At lower levels, for example, within the microbes in the termite’s gut, other parts constitute functions that operate on behalf the microbes, for example, their cellular organelles (mitochondria, nucleus, etc.). Some of the eukaryotic microbes also have bacteria in symbiosis within them. In effect, we have a case here of endo-endosymbiosis, functions within functions within a whole, in other words, a hierarchical organization.

But the single termite is also a function inside a larger structure, the termite mound, which considered as a whole is a superorganism, with division of labor and specialization among its parts (castes), including reproductive division of labor. One could say that the fungi

are *domesticated* by the termite colony (Margulis and Sagan 2003), maintained by a kind of agricultural practice and technology by the termite collective. This arrangement is a symbiotic collaboration or coordination, in that it serves the interests of the fungi as well as the termites, just as the operation of a cell within a multicellular organism serves the interests of the cell itself, to some degree, as well as those of the body. In this arrangement, the fungi are not merely ancillary parts, they are central components. Most of the flow of metabolic energy in the mound passes through the fungi rather than the termites (Turner 2002).

So again, as Margulis and Sagan put it, this is a domestication, but who has domesticated whom? Our use of the term is hierarchical, and therefore it is the top level, the termite mound, the superorganism, that has *domesticated* both termites and fungi, which in turn have domesticated their internal microbes.^{SS} What is the top level? In some cases, it is not perfectly clear. In South Africa, *Macrotermes natalensis* termite mounds are up to 3-m-high “skyscrapers,” which as the colony reproduces seed adjacent colonies, in the end generating termite mound “city” ecosystems—a yet-higher level of hierarchy.

Notice that, in this view, the superorganism is not only the product of the interaction of the termites, it is—in the case of the *Macrotermes* termite mound—a *holobiont* (Margulis and Fester 1991) made up of a symbiosis of nested living units consisting of termites, fungi, protists, and bacteria, plus a variety of nonliving ones (such as the exoskeletons of the termites and the dirt of the termite mound). The superorganism is all of these together, the whole termite mound. Notice too that there is an upward transfer of function that has taken place in the evolution of this superorganism. Termite cells can be understood to have transferred some of their functions to termites, and the termites themselves have transferred some of their functions to the termite mound. The termites work

by and for the superorganism in the same way that termite cells work by and for the termite.

In sum, we have a nesting of trinomials where structures can become functions of a larger structure, as in a nested set of “matryoshka dolls” (see Fig. 2).

The Historical Trajectory of Trinomials.—The jump in hierarchy from bacteria to the first eukaryotic cells appears to have been made when mitochondria were definitively and irreversibly incorporated into other cells (Lane and Martin 2010). In our trinomial, the mitochondria that were once free-living bacteria were transformed from independent structures into parts, or functions—in this case parts that function in cellular respiration—within the eukaryotic cell. Then, in the origin of multicellularity such as we see in plants and animals, the cells that were once free-living protists were transformed from independent structures into parts, becoming functions within a multicellular organism, a new structure at a higher level. As the trinomial flowchart illustrates (Fig. 2), the causal arrow points both up and down in these entities. On the one hand, the eukaryotic cell directs its organelles, including its mitochondria, and the animal directs its component eukaryotic cells. On the other hand, both eukaryotic cells and animals are structures that emerge from their parts or functions.

Our hypothesis is that it is precisely this nesting of the Prigogine trinomial that allows an increase in hierarchical complexity in the history of life, that includes the MTE in organisms but also extends the trend in hierarchy into the realm of ecology, up to the level of the whole Earth, Gaia. As each new level arises and then explores the various biophysical possibilities at that level, it eventually exhausts them, and new possibilities become available only with the addition of newer and higher levels yet. Further, as we discuss in the next section, nestedness allows an acceleration of the addition of new levels, an increase in rate beyond what would be expected from a purely passive process.

For the transition to the eukaryotic cell, Lane and Martin (2010) have argued that endosymbiosis allowed for an enormous increase in the energy available to the nascent eukaryotic cell, energy that could be used for protein

^{SS}J. Scott Turner, who writes brilliantly about extended organisms, however, does not go beyond the standard focus on the termites themselves. According to him, termites are the protagonists, and as a whole they have been able to form an extended organism whose digestion (and respiration) is outside themselves (Turner 2002).

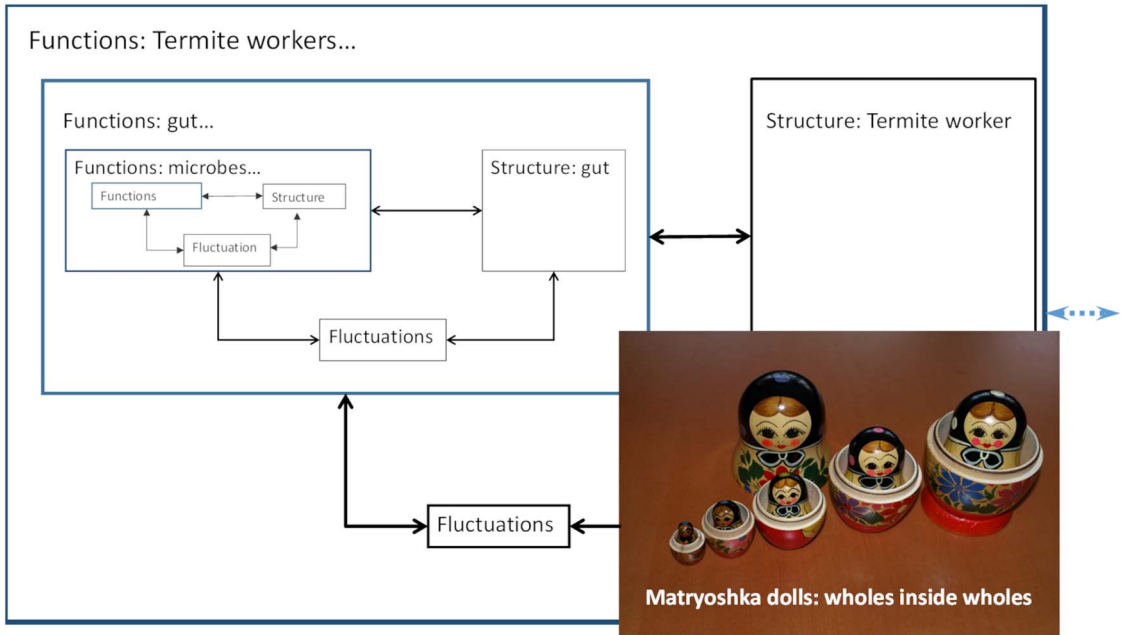


FIGURE 2. Succession of Prigogine trinomial structures, nested within one another. By analogy, a set of parts within a bacterium perform a function for the bacterium. The bacterium in turn is one of a set of parts within a cell of the intestine that is performing various functions for the cell. The cells of the intestine are a set of parts that perform digestion for an individual termite. And a set of termites plus associated nest fungi are a set of parts that perform functions for a termite mound.

synthesis and the expansion of the DNA complement in the cell. This expansion, they argue, extends orders of magnitude beyond what would have been possible by other routes, such as polyploidy. And it is this expansion in DNA that allowed eukaryotes to explore new areas of protein space, new pathways to innovation. In Prigogine's terms, it is the transfer of capability to the hierarchically superior entity, the structure (here, the eukaryotic cell), by its parts (former prokaryotes), now transformed into Prigogine functions, that allowed the evolutionary jump to be made and allowed the biophysical (in this case, energetic) barriers to innovation present in prokaryotes to be overcome. As Lane and Martin (2010) conclude, the jump would not have been possible by the standard neo-Darwinian route, natural selection acting on gradually accumulated mutations in isolated prokaryotic individuals.

Free-living eukaryotic cells in turn have biophysical limits that could be transcended when they formed multicellular organisms. For example, Bonner (1988) has pointed out that body size in single-cell organisms is

limited by the rate at which oxygen can be delivered to the interior by diffusion. West et al. (1997) show that fractal networks accessible to multicellular life resolve the limit and also have better relative efficiency. Also, the relatively free flow of materials inside a single cell may limit the degree to which it can differentiate, and therefore limits the degree to which it can divide labor among its parts. Cellular organelles provide some division of labor but nowhere near the enormous opportunities offered by multicellularity—organisms some with hundreds of different specialized cell types, each type either alone or in combination potentially a Prigogine function. With the transformation of former free-living structures (solitary eukaryotic cells) into functions, a new higher-level structure emerged (differentiated multicellularity), with macroscopic properties unavailable—even unimaginable—at a lower level. Obvious examples include homeothermy and the advent of complicated neural and hormonal regulatory systems, made possible by the differentiation of cells into types. An even simpler innovation is the origin of

circulatory systems, again made possible by cell-type differentiation, allowing a dramatic increase in body size (Bonner 1988). The size step from prokaryotic cell to eukaryotic cell was large. But the step from eukaryotic cell to multicellular behemoths—from protist to hulking redwood tree and blue whale—was many orders of magnitude larger (Heim et al. 2017).

The next hierarchical level in the history of life was the transformation of multicellular organisms into colonies, in some of which coloniality is developed to a degree that makes the term “superorganism” appropriate. The best-known examples are the social insects, such as the termites discussed earlier, arising some 200 Ma (Bordy et al. 2004). Less well known is that this degree of coloniality was achieved much earlier by the bryozoans, about 480 Ma (Taylor and Wilson 1999). These colonial animals are built of repeated modular units, each a multicellular individual. In many species, there is significant division of labor, with certain modules (zooids) specialized for feeding, others for reproduction, and still others for defense. In these zooids, the commitment to a particular phenotype and function is often irreversible. Further, in some species, individual modules combine to form intermediate-scale structures, such as excurrent chimneys that direct the flow of nutrient-depleted water away from the colony, the equivalent of an “organ” at the colony level (McShea 2001). It is unclear how far this transition to the colony level has proceeded or can proceed. The extent of the division of labor is quite modest, in that even the most colonial species have only a few castes or zooid types. On the other hand, the increase in body size permitted by these transitions is fairly impressive. Army-ant colonies have hundreds of thousands of individuals and sprawling fire ant supercolonies have millions, spread in some cases over hundreds of miles.

What all three of these transitions mark is the advent of a new level of what Volk (2003) called “holarchy,” or what Lenton and Latour (2018) called “heterarchy.” In our terms (McShea 2001, 2015; McShea and Changizi 2003), it is a rise in hierarchy.

*The “Machinification,” “Domestication,” and “De-Darwinization” of Lower-Level Structures.—*Natural selection as conventionally understood

acts directly on organisms, and only indirectly on their parts. The reproductive success of a mitochondrion, or of a worker in a termite mound, is a function of the reproductive success of the larger individuals that contain them. There is obviously some reciprocity here, in that the reproductive success of the whole depends on the proper function of the parts, but selection “sees” only the net effect of the parts’ interaction with one another, and thus to a large extent individual parts are screened off from selection at the level of the whole (Brandon 1990). To the extent that this occurs, the expectation is that selection acting at the level of the whole will modify the parts to accommodate the needs of the whole. Thus, in the emergence of a new hierarchical level, as free-living entities combine to form a new higher-level whole, the functional capabilities present in the entities are transferred to the whole and in the process are stripped of much of their autonomy and individuality. In Michod and Herron’s (2006) terms, the parts lose their ability to adapt. Margulis (1990) describes them as “depoietized”; Margulis and Sagan (2003) describe them as “domesticated” by the whole, as discussed; and Szathmáry (2015) calls this the “de-Darwinization” of the parts. Finally, McShea (2015) calls it the “machinification” of parts, in that they are to large degree rendered passive, transformed into machines serving the needs of the whole. In terms of Prigogine’s trinomial, the entities that correspond to structures are—when combined to form a new higher-level structure—transformed into functions within the higher-level structure. And in the subsequent transfer of capabilities from the entities to the new higher-level structure, these new functions become modified for their new roles. In other words, as discussed in the previous section, the causal arrow runs both ways: higher-level structure arises from lower-level functions, and higher-level functions act downwardly modifying those same functions.

This machinification of the lower-level parts has an important role in irreversibility (McShea 2015). It goes partway toward explaining why the buildup of hierarchy is to some extent ratcheted. Machinification provides a kind of floor under each new level, reducing the

likelihood that the functions will regain their autonomy and that the gain in hierarchy will be lost. In other words, it contributes to the ongoing rise in hierarchy over the history of life. As will be seen, however, there is more to that trend.

Prigogine Trinomials and the Causes underlying Hierarchical Change

The rise in hierarchy is widely acknowledged, but most of the discussion in the evolutionary literature has focused on the problem of how and under what circumstances selection can favor stable collaborations of lower-level organisms (Maynard Smith and Szathmary 1995; Michod and Herron 2006)—in other words, the cheater problem and group selection. There has also been some attention to the conditions that favor specialization of lower-level individuals and the origin of division of labor (e.g., Simpson 2012). And certain transitions have drawn a fair amount of interest, notably the origin of eusociality and superorganisms in the ants, bees, wasps, and termites. But the overall trend itself has attracted very little attention (although see Pettersson 1996; McShea 2001; McShea and Changizi 2003; Heim et al. 2017), and little has been said about its possible causes at the scale of life as a whole. The presumption has been that it can be explained by the benefits of cooperation (Corning and Szathmary 2015), or by selection for large body size (Bonner 1988; Heim et al. 2017). Here we present the trend trajectory, argue that it cannot be explained by either of the two standard mechanisms of macroevolution trends. We then show that Prigogine’s conceptual scheme offers an explanation that is at once unifying of these other proposals and consistent with the trajectory of the trend.

The Trend Trajectory.—Figure 3 shows the rise in hierarchy, the repeated nesting of Prigogine trinomials, over the history of life (McShea 2001, 2015). There are four data points, corresponding to the origin of prokaryotes on Earth, the first eukaryotic cell, the first multicellular eukaryotic individual, and the first eukaryotic colonial individual.

Based on the fossil record and genetic and chemical evidence, the first (irreversible)

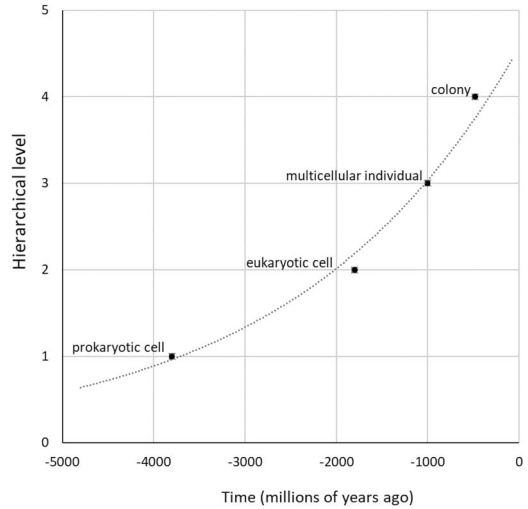


FIGURE 3. First appearance of organisms according to their hierarchical level in Earth history. See text and Supplementary Table material for explanations.

occurrences of each level are as follows (see Supplementary Table for references and justification):

1. LUCA (last universal common ancestor): first bacteria on Earth about 3.8 Ga;
2. LECA (last eukaryotic common ancestor): first eukaryotic cell (with mitochondria incorporated) about 1.8 Ga;
3. first multicellular organism about 1 Ga; and
4. first colonial organism (bryozoans) about 0.48 Ga.

What these transitions have in common, beyond the end result, the near-irreversible emergence of a higher-level whole, is a shared evolutionary pathway. Okasha (2005) studied these transitions in detail and pointed out three characteristic phases. The first is cooperation between “particles” (or lower-level entities). The second is the emergence of community. And the third is the transfer of fitness to the upper level (Michod and Herron 2006). In the course of this, the “particles” become specialized and—in Prigogine’s terms—transformed into functions within and for the larger structure. At the higher level, a new individual arises. In other words, these four represent what have been called the major transitions in *individuality*. Thus, with respect to the MTE, we adopt the position advocated by

Herron (2021), limiting the list to transitions in individuality. This corresponds to what McShea (2001) called hierarchy, the nestedness of individuals within individuals (sensu Lewontin 1970; Clarke 2016; and many others), and maps nicely onto Prigogine's view, captured by the matryoshka-doll analogy.

Given this view, the question arises whether to include ecological units as higher-level individuals, above the level of the colony. Consistent with other treatments of hierarchy (e.g., McShea 2001), our focus was on individuals in the organismal sense, but we will have more to say later about Gaia, the ecological individual at the largest scale.

The Acceleration.—The curve in Figure 3 is a trend in the maximum, that is, the first occurrences in the level of hierarchy achieved by the hierarchically deepest organism on Earth at a given time. One of the most striking features of the trend in Figure 3 is the strong acceleration, a curve that seems well approximated by an exponential function. Although LUCA (hierarchical level 1) appeared early in the Earth history, shortly after Earth became habitable,*** the waiting time from the first prokaryote to the first eukaryotic cell is about 2000 Myr, longer if prokaryotic life predates the first microfossils, as seems likely. The next step, to the first eukaryotic multicellular individual, took less time, about 800 Myr, and the following step to the first individuated colony required even less, about 500 Myr.

Caution is needed here on account of the uncertainties in reading the rock record: the gaps in the record, error in dating, and the sensitivity of the data points to alternative interpretations of the fossils. But several factors suggest that the trend and the shape of the curve is probably quite robust. First, we experimented with alternative readings of the fossil record (see

Supplementary Table), but the curve survived all manipulations. Second, McShea and Changizi (2003; also McShea 2001) found a smooth exponential-looking trend using a hierarchy scale that recognized intermediate degrees of individuality. For example, colonies of bacteria with division of labor fall on the McShea and Changizi hierarchy scale at a level above a solitary prokaryote but below the eukaryotic cell. Using this scale, the trend had nine data points rather than just four, and the shape of the curve was the same. Third, these are first occurrences in the level of hierarchy achieved by the hierarchically deepest organism on Earth at a given time, but there were many other later (independent or not) hierarchical transitions in the same time range. For instance, the transitions to multicellularity and to coloniality occurred multiple times, all of them more quickly than the prokaryote to eukaryote transition, suggesting that the curve is accelerated, irrespective of whether the first occurrence has been correctly identified. (See McShea [2001] for more discussion of possible sources of error and of the likely robustness of the shape of the curve.) In sum, the exponential-like acceleration is quite robust, unlikely to be altered by new findings, better dating, or changes in interpretation.

The Trend Mechanism: Neither Passive nor Selection Driven.—What explains the trend in Figure 3? To investigate this, we need to first look at what in macroevolutionary studies is called the “trend mechanism,” the pattern of change among lineages that underlies a trend. Two broad categories of the trend mechanism have been described, passive and driven (Gould 1988, 1996; McShea 1994). A driven trend is one that occurs when a group diversifies under the influence of some force, usually understood to be natural selection. In a driven trend, increases occur more often than decreases, producing an increase in the mean for the group. A passive trend occurs when forces are absent, but the group diversifies in the presence of a lower limit or boundary. In a passive trend, increases and decreases occur equally often, on average, but the mean for the group increases as the group diffuses upward, away from the lower bound.

There are good reasons, both empirical and theoretical, to reject the passive mechanism

***An interesting speculation follows: if we consider bacteria as extremely complex dissipative structures that emerged from a chemical “soup,” that transition too must be added to the trajectory of the maximum. Then, if the shape of curve has been roughly constant, the jump in level from the chemical soup to the first bacterium would have taken longer than the time it took for bacteria to produce the first eukaryote cell. This reasoning has an obvious implication: the origin of life in the universe would be very ancient and extraterrestrial, and LUCA would have to have come from outside the Earth.

for hierarchy. First, the empirical. In a passive trend, increases and decreases are equally probable, but this seems very unlikely for a trend like this. It would require that the reverse transitions—prokaryotic cells arising from eukaryotic cells, free-living eukaryotic cells arising from multicellular eukaryotes, and solitary multicellulars arising from colonial species—occur as often as the forward transitions. And this we do not see. The origins of new higher levels from organisms at lower levels is typically accompanied by a reduction in complexity—a loss of parts—at the lower level, a loss that makes reversal especially difficult. Mitochondria have lost much of their genome, and similarly, in fully individuated multicellular organisms, the cells have been drained of many of their parts—including major organelles—relative to the single-celled eukaryotes from which they evolved (McShea 2002). Presumably, the removal of cell parts occurs because they have become redundant, performing functions now performed by the whole. A similar process is at work in the formation of colonies. Workers in some social insect colonies have lost their ovaries. In bryozoan colonies, certain zooids with a purely defensive function—avicularia—have lost virtually all of their physiologically active tissues. As discussed, this complexity drain that accompanies the origin of fully individuated higher levels has the effect of “de-Darwinizing” or “machinifying” (McShea 2015) the lower-level individuals, transforming them into parts within a larger whole. And these machinified parts will be, generally speaking, incapable of a return to solitary living.^{†††}

^{†††}At the genetic level, this process could be quite general, producing gene reduction whenever embeddedness in an ecological unit (the local “environment”) provides an organism with essential nutrients or functions, enabling it to lose the gene sequences involved in the production of those nutrients or functions (Ellers et al. 2012). This might partly explain the recently observed genetic reduction within each level of phylogeny (Albalat and Cañestro 2016; Guijarro-Clarke et al. 2020). This gene loss and transfer of functional capability to the ecological unit amounts to a partial machinification of the organism, an increase in its dependence on the ecological unit and reduction in its autonomy. But in turn, the nestedness that implies, as we reasoned earlier, increases the probability of finding new dissipation routes and is therefore selected and stabilized by Prigogine thermodynamics.

In theory, there are also reasons to reject a passive mechanism, namely, it does not predict the accelerating rise in the maximum evident in Figure 3. In simulations, the expected trajectory for the first occurrence of a hierarchical increase (or some measure of complexity) for a passive mechanism or diffusive process is a square-root function of the time from the separation from the initial level (here, bacteria). Thus, the expected trajectory is concave down. However, the trajectory in Figure 3 is concave up.

The same reasoning forces us to reject a driven trend mechanism, at least as conventionally understood. A driven trend is generally assumed to be driven by a constant upward selection pressure, producing a greater probability of increases than decreases. In the modeling of these trends in the current literature, the bias in favor of increase is assumed to be constant, as are other trend parameters, such as the rates of speciation and extinction. (And these are generally assumed to be roughly equal, because even small differences result in either unrealistic explosive rises in diversity or rapid extinction of the whole clade of life.) In any case, with constant parameters, a driven trend does produce a rise in the maximum that is faster than in a passive trend, but it is still concave down (McShea 1994).

Two further points need to be made. One is that rejection of a driven mechanism does not rule out a selective advantage for higher levels. What it rules out is a consistent advantage, a constant selection pressure pushing upward. It also rules out the stochastically constant selection pressure assumed in the standard models of a driven system. It does not rule out a series of dramatic changes in parameters at the interfaces between levels, a trend powered by a very different sort of mechanism, which we discuss shortly.

Also, there are two global factors that makes the trend all the more difficult to explain. We call them “friction” and “barriers.” What we call “friction” refers to the biophysical limitations intrinsic to organisms at successively greater hierarchical levels. At higher levels, organisms are larger and therefore tend to reproduce more slowly, with smaller population sizes. Both of these reduce the rate, compared with, say, prokaryotes, at which

lineages are able to explore alternative phenotypes, which in turn reduces the rate at which even higher levels will be discovered. It is worth pointing out that between prokaryotes and termite mounds or vertebrates, there are four or five orders of magnitude difference in generation time and about nine orders of magnitude difference in population size (although the total biomass of plants exceeds that of prokaryotes by one order of magnitude) (Bar-On et al. 2018). In other words, these frictional considerations are expected to be fairly severe, making concave down the expectation for the curve in Figure 3. Further, for prokaryotes, the expectation would be that the diversity of their metabolism and their ability to adapt to extreme environments would give them an advantage over higher-level organisms in finding ways to overcome physical environmental limitations. Again, higher-level organisms experience these limitations more severely, decreasing—relative to prokaryotes—the rate at which they should be able to explore new phenotypes, and therefore the rate of discovery of even higher levels. This too suggests the curve should be concave down. And the fact that it is not suggests that these limits can be overcome.

Barriers refers to the physical environment limits on the resources and free energy available to organisms and their ability to dissipate (Kleidon 2012, 2021). What this means is that for a “neutral” environment, there will be constraints that fix how far hierarchy can evolve. The environment fixes the material and energetic resources available to life, and the thermodynamics at the scale of the whole Earth places absolute limits on all biological processes. This topic deserves a longer treatment than is possible to give here. For present purposes, we will just say that it is clear from the concave-up shape of the curve that these limits can be overcome, or perhaps more likely, that the biosphere itself has evolved in a way that has raised these limits overall.

Finally, one might imagine that the concave-up trend can be accounted for by the rise in diversity, in particular the immense rise in number of species in the fossil record near the time of the origin of multicellularity. More diversity means more rolls of the dice, more opportunities to discover new phenotypes,

and therefore new higher levels, perhaps accounting for the relatively rapid discovery of coloniality. On the other hand, our picture of early prokaryotic and even single-celled eukaryotic diversity is likely hugely biased by the incompleteness of the fossil record. It is possible, even likely, that Archean and Proterozoic diversity was significantly greater than that produced in the multicellular revolution, again giving an advantage to organisms at lower hierarchical levels.

Thus, to explain an accelerating concave-up curve, we need to look outside the box, beyond the usual trend mechanisms.

Before making that move, we need to address an “elephant in the room”: chance. The entire effort here might seem misguided, because we have only four data points, and therefore the trend might have been entirely the result of stand-alone, contingent events. For example, the transition to eukaryotic cells might have been driven by the rise in oxygen in the atmosphere at that time (Heim et al. 2017), while the origin of multicellularity could have been produced by some other environmental shift or perhaps of the chance origin of some new gene regulatory mechanism. We cannot rule this out, but there is evidence to suggest a single causal regime. As mentioned earlier, McShea and Changizi (2003; also McShea 2001) found a smooth, exponential-looking trend using a hierarchy scale that recognized intermediate degrees of individuality, a trend with nine data points rather than just four. In any case, even if a series of unrelated contingent events, unrepeatably in reruns of the history of life, cannot now be ruled out, the search for a consistent cause is a worthwhile first step.

Opportunities and Forces: The Prigogine Trinomial as Likely Cause.—For the trend in hierarchy, several factors may be at work. The most obvious is a ratchet, hinted at earlier. The origin of each new level is irreversible and sets a floor under future change. The descendants of the pioneering lineage that discovers each new level must either stay at that level or—occasionally—move higher. Knoll and Bambach (2000) appear to have had something like this mechanism in mind in proposing a series of “megatrajectories” in the history of

life, each a breakthrough that led to an expansion of ecospace utilization and laid a foundation for the next megatrajectory. They describe the process as diffusion away from a left wall and a repeated scaling of a right wall. Here the suggestion is that each new Prigogine trinomial diversifies adjacent to a left wall—a eukaryotic cell cannot reverse to the prokaryotic condition—and lays a foundation for the later scaling of the right—the move to multicellularity. Still, a ratchet, however strong and irreversible, cannot by itself account for an accelerating maximum, even putting aside considerations of friction and barriers.

Beyond the ratchet, there is a source of new opportunities, one that is specific to hierarchy and lies at the heart of the Prigogine conceptual scheme. In an organism consisting of nested entities within entities, each new level dramatically raises the possible number of combinations of lower-level entities that could serve as the source of innovation. Imagine a multicellular organism with 4 possible cell types that combine in tissues and organs in combinations of 3 cells. Such an organism would have a space of 64 different combinations of cell types, 64 different tissue or organ types, available to explore in its search for adaptive innovation. In hierarchical evolution, innovation is doubtless encouraged by genomic and taxic diversity but it could also be supercharged by the combinatoric power of nested components (McShea and Changizi 2003).

In Prigogine's thinking, this extends to combinations of entities multiple levels down in the hierarchy. A termite colony can farm by making use of fungal cells, two levels down. An animal can improve its digestion by making use of bacteria, also two levels down. In these cases, the higher-level individual is taking advantage not only of the diversity and resulting combinatorics of lower-level entities, but the fact that these entities come preloaded with functional capabilities acquired over millions or in some cases billions of years. And this applies to the cooperators drafted into symbiotic associations of organisms, of course, but also to genes and gene combinations that are routinely incorporated into organisms via transposable elements and other routes. Further, these lower-level entities—whether organisms or molecules—

are preadapted for the kind of cooperation that makes cross-level combinations workable. The bacteria that support our gut are already adapted to play well with others.

The point is that in this combinatoric process, individuals at higher levels (e.g., multicellulars and colonies) have a decided advantage over lower-level ones (e.g., protists and bacteria) in that they have more levels below themselves from which to draw. Bacteria, for example, have only the pool of genes and other molecules in their environment to draw upon for innovation. A colonial organism, three levels up, has those *plus* entities drawn from all three supramolecular levels—bacteria, eukaryotic cells, and multicellular individuals—and therefore has orders of magnitude more opportunities to find successful combinations in explorations leading to the next new level. Further, as emphasized by Margulis and Sagan (2003), gene transfer and symbiogenesis at the lower levels were and remain important factors in this higher-level advantage, giving higher-level organisms access to the full space of genetic combinations. This access was likely critical in the acceleration.

It is not hard to see a similar principle at work in the evolution of technology. In the design of a new can opener, an engineer has a fair variety of different metals, plastics, and shapes to work with. But in the design of a novel electronic device, he or she has all of that plus a wide range of electronic components (jacks, capacitors, chips, etc.) at the next level up, plus a wide range of complex devices (fans, transformers, circuit boards, etc.) at a level above that, and so on.

Thus, there is a positive feedback loop. An increase in hierarchy leads to a dramatic increase in combinatoric possibilities for cooperation, which in turn leads to dramatic increases in the probability of discovering a route to the next higher level. Credit for this insight perhaps belongs to Piotr Kropotkin (1902), who observed a progressive trend toward “mutual aid,” which here translates as a trend in hierarchy, noting that the trend is enhanced by the complexity of the entities that participate in it.

We will add that there is another upward tendency that magnifies the effect of the positive

feedback described. Each new hierarchical level is a point of stability, a structure arrived at through fluctuations from below and stabilized by the flow of energy through it and, as we have described (see “The Historical Trajectory of Trinomials” discussion), could be well positioned to overcome any barriers imposed by the local environment (West et al. 1997; Lane and Martin 2010). In Prigogine’s terms, variations at the level of organisms (fluctuations) that increase the energy dissipation are amplified and, in the process of being amplified, in turn raise the probability of the formation of higher-level organisms, which again are stabilized by the greater flow of energy that a higher level permits. What is critical here is that the rate of dissipation rises nonlinearly with size. Larger systems dissipate gradients disproportionately more rapidly than smaller systems.

We acknowledge that this formulation uses language that is unfamiliar in biology, but the underlying principles are not unfamiliar. Still, why make this move? Why turn to the language of physics? For one thing, this approach adds to a growing body of literature that takes seriously the role of dissipative-system principles in biology (e.g., Jorgensen and Fath 2004; Chaisson 2010; England 2015). But more importantly, this approach adds a new dimension to the study of large-scale evolutionary trends, one that ought to be especially welcome for a trend in which standard models and explanations have so far failed, and one that brings along with it a new top-down way of thinking about causality. Importantly, the Prigogine approach does not deny selection. Indeed, it could be construed to exemplify an alternative way that selection can be cashed out, in terms of energy flows and stability (Van Valen 1976, 1989), rather than the usual reproductive terms (but that is a project for another occasion). Finally, a key virtue of the Prigogine formulation is that it makes a direct connection between the trend in organismal hierarchy and a broader set of entities and processes, many of which are purely physical. That is, it places the rise in biological hierarchy in a larger context, revealing it to be a trend that is probably not unique to life on Earth, nor even special to biological systems, but rather a generic feature of dissipative structures generally.

Summing up this section, it seems clear that conventional macroevolutionary mechanisms cannot account for the accelerating trend in hierarchy. Something more is needed, especially because friction and barriers are expected to hinder by many orders of magnitude the rate of increase. And the Prigogine view offers a good candidate for the “something more,” a positive feedback between hierarchy and the combinatorics governing the rate of exploration for new levels, plus the nonlinear increase in dissipative power (Judson 2017) and efficiency (West et al. 1997) of higher-level entities. In addition, there is—as will be seen in the next section—the parallel top-down help from macrostructures like ecosystems and Gaia. Of course, it remains to be seen whether these together would be sufficient to explain the accelerating curve. A quantitative approach—beyond the scope of this paper—is needed.

A Final Note: The Prigogine Conjecture, from Bacteria to Gaia

Earth’s biosphere and ecosystems disperse solar photons, increasing the entropy of the universe quickly relative to a lifeless Earth-like planet (Kleidon and Lorenz 2005; de Castro 2020: annex 1). This fact opens the door to the existence of a complex dissipative structure at regional and global scales mediated by ecosystems above them and living organisms below them, forming nested “matryoshka doll” trinomials. In fact, we can choose to think about the whole nested series as ecological (Eldredge and Salthe 1984). After all, organisms themselves are symbiotic ecological communities (holobionts: Margulis and Fester 1991), living within ecosystems, which in turn can be understood as termite mound-style organic superstructures. And therefore, we expect “domestication” to occur, just as in the earlier discussion of organisms, meaning that we expect a transfer of functions upward toward ever-higher ecological levels. And we also expect causal arrows running downward from structure (e.g., ecosystem) to its functions (e.g., organisms), modifying and organizing them.

According to the Prigogine trinomial, the same logic and physics that lead to the rise of hierarchical levels will tend to lead to the

formation of the largest of all ecological structures, Gaia. At the planetary level, living organisms are connected by the global cycling of elements, in a manner that is at least analogous to the way the circulatory system connects cells and organs in a multicellular organism. This integrated global entity, Gaia, is a dissipative structure, of course, an ecological structure in which small ecological units—and below them, organisms—constitute functional parts, participating in the generation of entropy by the whole. As for all dissipative structures, the dissipation stabilizes it. Further, inasmuch as Gaia is a complex dissipative structure, it acts downwardly on its component functions. In Prigogine's words, it will "organize its own functional space." In effect, the biosphere itself becomes a powerful selective force, acting downwardly on its component ecological units, including the organisms within them (Margulis and Sagan 2003: chap. 4).

Thus at greater-than-organism scales, Prigogine's conjecture says that ecosystems would tend to integrate organisms, Gaia would tend to integrate ecosystems, and both in turn would tend to organize life forms and processes to perform functions for her. In effect, the selfishness of organisms is offset, to some degree, by a thermodynamic tendency for them to symbiotically coordinate with one another and to participate in the dissipative mission of the whole. The "cheaters" that undermine "altruists" and create such difficulty in cybernetic models of Gaia, such as Daisyworld and others (de Castro and Rubin 2021), are tamed, so to speak, because to evolve a more powerful system with greater dissipative capacity requires coordination and cooperation. Thus, in the terms we use earlier, just as a termite individual domesticates its gut flora, and a termite mound domesticates the termites, Gaia is expected to domesticate the ecological units and organisms that constitute it.

Importantly, the Prigogine view is consistent with much of the recent discussion of "sequential selection" (Lenton et al. 2018), "metacommunity" (Leibold et al. 2004), "whole system selection" (Lansing et al. 1998), "niche construction" (Laland et al. 2016), "Gaia selection" (Margulis and Sagan 2003), "drive of higher cycling rations by biogeochemical guilds" (Volk 2004),

"symbiotic coordination" (de Castro and Rubin 2021), "selection of processes and patterns" (Doolittle and Inkpen 2018), and the "holistic integration of processes of the Biosphere" (Kleidon 2012). But in addition, the Prigogine view adds something to this theoretical work: a double positive-feedback loop. Thermodynamic dissipation increases the probability of an Okasha (2005) hierarchical transformation. That is, the increase in complexity with each step offers more opportunities to discover more and better ways to dissipate energy, which in turn increases the probability of further transformations that, once attained, eliminate local biophysical limits to further evolution. Also, the Prigogine trinomial places this discussion in a larger theoretical framework: the emergence of Gaia as the structure that shapes organisms (helping to reduce what we have called friction) and modulate and transform the relationship with the external environment (reducing what we have called barriers). The critical element in all of these dissipative structures, from Bénard cells to organisms to ecological units to Gaia, is the downward-pointing causal arrow, the feedback from upper level to lower, closing the trinomial.

Finally, it is worth pointing out that the Prigogine formulation problematizes the long-standing question of whether Gaia is an organism, transforming that question from an either-or to one of degree. The extent to which a structure is an organism could be said to depend on its complexity, on the degree to which fluctuations increasing dissipation are stabilized and favored, and on the degree to which the component functions are domesticated and transformed into parts in service to the whole. The Prigogine trinomial gives us a new way to think about the "organicity" of Gaia (de Castro 2013, 2019).

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Data Availability Statement

The Supplementary Table is publicly available via: https://geeds.es/wp-content/uploads/2022/01/Supplementary-material_Prigogine-and-MTE.xlsx.

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