Studying only negative feedback was not initially debilitating because most applications of feedback pertained to the control of fabricated systems, where negative feedback is desirable. For example, the common governor was built into steam and internal combustion engines to control the speed of their operation. The governor was usually some form of centrifugal weights that were spun by the engine. As the engine accelerated, the weights moved further from the center of rotation and were levered to a valve that decreased the supply of steam or fuel to the engine, thereby slowing the increase. If the rotating weights had been levered so as to supply *additional* fuel as speed increased (positive feedback), the engine would have raced out of control and destroyed itself. In a linear world, positive feedback is always destructive.

Once the study of feedback moved beyond artificial contrivances and into the nonlinear, highly dissipative realm of living systems, it became necessary to reconsider the role of positive feedback. Living systems dissipate a large fraction of what they ingest, so that some sort of stimulation is required to keep them operating. Because organisms are largely self-entailing (Rosen 2000), the most reasonable place to search for such stimulation was within the system itself. Thus it was that any number of biologists came to investigate the role that positive feedback (autostimulation) plays in the life process (e.g., Eigen 1971; Haken 1988; Maturana and Varela 1980; Kauffman 1995; DeAngelis, Post, and Travis 1986; Ulanowicz 1986; and Deacon 2006). Much of that focus has come to dwell on autocatalysis as the genesis of both form and stability in evolving systems (Ulanowicz 1997, Kauffman 1995).[2]

Autocatalysis as Dynamical Agency

Autocatalysis is a particular form of positive feedback wherein the effect of every consecutive link in the feedback loop is positive. Such facilitation need not be assumed obligate and rigid, as with mechanical systems. There simply needs be present the *propensity* for each participant to facilitate its downstream member. As inferred above, whenever autocatalysis acts in tandem with atomism (as is legitimate when applied to most simple chemical systems), it may be regarded as wholly mechanical in nature. However, in more complex situations, as concern us here, and especially in conjunction with complex chance events, several distinctly nonmechanical attributes suddenly appear.

The nonmechanical attributes of autocatalysis become more apparent once they are illustrated in terms of a particular but generic example. Without loss of generality, I direct the reader's attention to the simple three-component interaction depicted in Figure 4.1. We assume that the action of process A has a propensity to augment a second process B. (To repeat for emphasis: A and B are not tightly and mechanically linked. Rather, when process A increases in magnitude, most [but not all] of the time, B also will increase). B in its turn tends to accelerate C in similar fashion, and C has the same effect upon A.

My favorite ecological example of autocatalysis is the community that builds upon the aquatic macrophyte, *Utricularia* (common name "Bladderwort." See Ulanowicz 1995b). All members of the genus *Utricularia* are carnivorous plants that trap and ingest animals, like the familiar Venus Fly Trap, except *Utricularia* traps its prey using small utricles or bladders scattered along its feather-like stems and leaves (Figure 4.2a). Each utricle

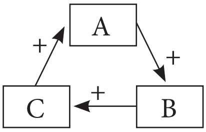


Figure 4.1. Schematic of a hypothetical three-component autocatalytic cycle.

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 that the plant had maintained inside the bladder. In the field the surface of *Utricularia* plants always supports a film of algal growth known as periphyton (Figure 4.2b). This periphyton serves in turn as food for any number of species of small zooplankton. The autocatalytic cycle is completed when the *Utricularia* captures and absorbs many of the zooplankton. To summarize, the growth of *Utricularia* provides an expanding platform upon which more periphyton can grow. More

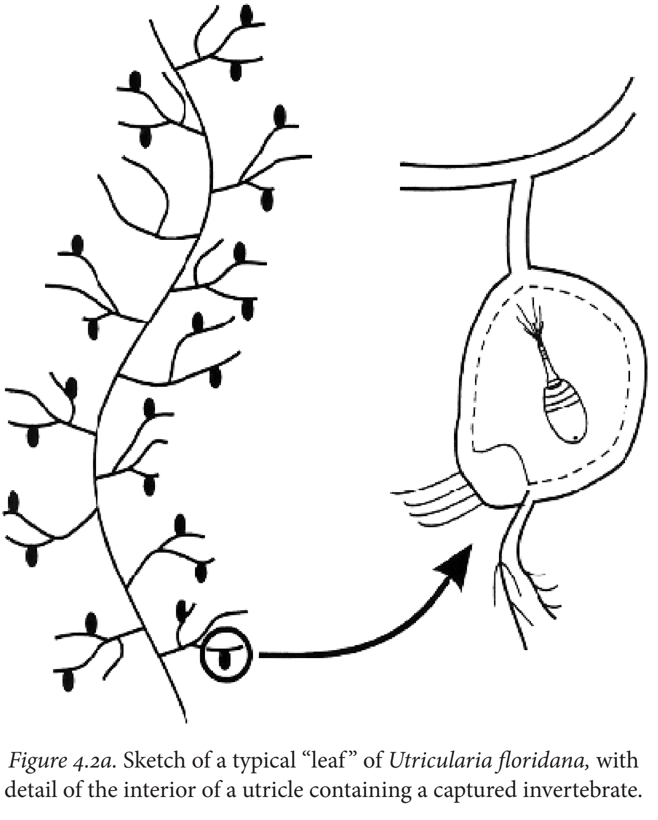


Figure 4.2a. Sketch of a typical "leaf" of *Utricularia floridana,* with detail of the interior of a utricle containing a captured invertebrate.

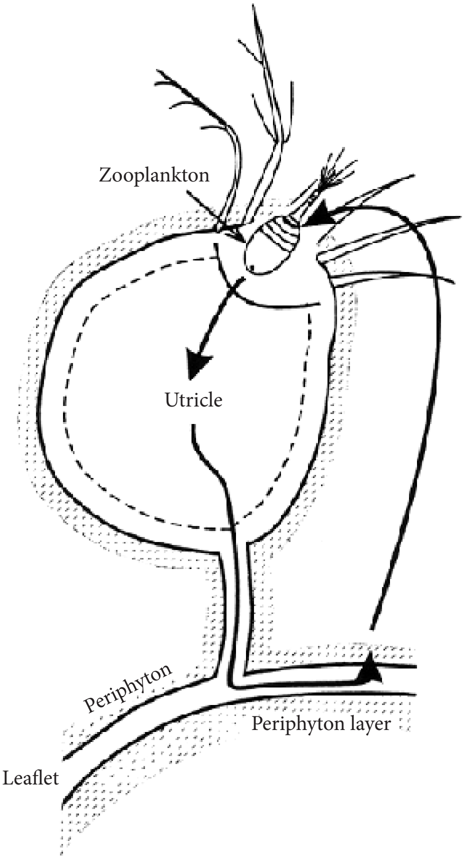


Figure 4.2b. Schematic of the autocatalytic loop in the Utricularia system. Macrophyte provides necessary surface upon which periphyton (speckled area) can grow. Zooplankton consumes periphyton, and is itself trapped in bladder and absorbed in turn by the *Utricularia.*

periphyton means more food for zooplankton, and more zooplankton result in more captures by *Utricularia*, which facilitates the latter's growth.

Generally, autocatalysis among propensities gives rise to at least eight system attributes, which, taken as a whole, comprise a decidedly nonmechanical dynamic (Ulanowicz 1997). For one, autocatalysis is explicitly *growth-enhancing* (by definition). Growth anywhere engenders growth everywhere else along the loop. Furthermore, autocatalysis exists as a *formal* structure or configuration of processes. Most germane to the discussion of evolution is the fact that autocatalysis is capable of exerting *selection* pressure upon its own ever-changing constituents. To see this, let us suppose that some small change occurs spontaneously in process B. If that change either makes B more sensitive to A or a more effective catalyst of C, then the change will receive enhanced stimulus from A. Conversely, if the change in B either makes it less sensitive to the effects of A or a weaker catalyst of C, then that change will likely receive diminished support from A. For example, if some change in the periphyton community were to make it more digestible or a better food to the zooplankton, one would expect the zooplankton to increase and yield more support for the growth of *Utricularia*, which, in turn, would provide more surface area for that type of periphyton to colonize. Conversely, a change in periphyton that renders it less digestible might benefit the attached algae in the short term but would decrease the growth of *Utricularia* over the long haul, and that periphyton would be faced with less available habitat. In this system, autocatalysis would select for more digestible periphyton.

Once more we reiterate that all linkages are contingent in nature, not deterministic. We further note that such selection works not only on the component objects but on the processes and propensities as well. Hence, any effort to explain the development of an autocatalytic configuration in terms of a fixed set of elements or processes (i.e., via causal reductionism) is doomed ultimately to fail. These features should help to make clear how atomism and closure could preclude from our vision the full range of autocatalytic behavior.

It is also important to note that the selection pressure exerted by autocatalysis arises from within the system. This is in stark contrast to Darwin's conscious effort to preserve the Newtonian framework by externalizing the agency of selection. The action of autocatalytic feedback tends to *import* the environment into the system or, alternatively, *embeds* the system into its environment.[3]

Here it becomes necessary to interrupt the discussion of the properties of autocatalysis to interject the third and final postulate upon which our narrative about developing systems will rest: because there are differences between the forms on which selection is acting, there must be some way for those forms to substantiate and retain their history throughout the course of that selection. Accordingly, we recognize as fundamental what Darwin brought into scientific discourse:

> III. Systems differ from one another according to their history, some of which is recorded in their material configurations.

In these days of molecular biology, the last statement immediately conjures up images of DNA or similar polymers, and these indeed play a major role in how systems convey form and dynamics from one generation to the next. But "material configuration" is by no means limited to static modes of retention. It is necessary to think more broadly because there most assuredly were proto-organisms before DNA and their like ever evolved. Furthermore, the mode of recording doesn't even have to imprint upon a persistent object. History can endure as well through time as a very stable configuration of processes, which reestablishes itself whenever the system is disturbed. In many ways, the structure of activities within a society embodies the history of that society every bit as much or more than the aggregate DNA of the individuals that make up the community (cf. Wilson 1980).

Implicit in axiom III is the notion of information, or what Gregory Bateson (1972, 475) called "the difference that makes a difference." Because biological entities are heterogeneous, they possess more information than their nonliving counterparts, such as mass, energy, or atoms of simple molecules, which cannot be distinguished one from another. Furthermore, the laws of matter and energy are all reversible and, therefore, conservative (Noether 1983). The dynamics of information, however, resemble and complement the irreversible and nonconservative production of thermodynamic entropy. Although these dynamics of information do not violate the reversible laws of nature, neither are they fully restrained by them (e.g., chapter 6., Jørgensen et al. 2007) As Elsasser concluded, given sufficient complexity, the combinatorics of structures that contain information overwhelm physical laws. Bateson, for his part, implicitly recognized such extralawful behavior by distinguishing between two fundamental categories of existence—the "creatura" and "pleroma" mentioned earlier. Critically aligned with Bateson's distinction is the notion that history can serve as a criterion for identity.[4] In other words, the trajectory of a system through time conceivably could be used in lieu of a set of its existing properties.

Now knowledgeable about ways that systems can retain their histories, we can return to our catalogue of the assets of autocatalysis. In doing so, we immediately recognize a corollary feature of selection—namely, that it exhibits an extremely important behavior called *centripetality*. The centripetal nature of autocatalysis becomes evident as soon as we realize that any change in B is also likely to involve a change in the amounts of material and energy that flow to sustain B. In our *Utricularia* example, for instance, if the periphyton is starved for phosphorus and any change (or immigrant species) enables the film of algae to increase its activity by taking in more phosphorus, that change will be rewarded by the loop. From this, we perceive a tendency to reward and support those changes that bring ever more resources into B. As this circumstance pertains to all the other members of the feedback loop as well, any autocatalytic cycle becomes the center of a centripetal vortex, pulling as many resources as possible into its domain (Figure 4.3). Even in the absence of any spatial integument, the autocatalytic loop itself defines the locus of this organic trait. That is, centripetality becomes a core element of a system's identity.

Most readers are familiar with the propensity of living systems to sequester materials and energy. Anyone who has had to remove a beehive built within the wall of a dwelling has doubtless marveled at the sheer mass of honey and wax that had been accumulated. But such aggregations reflect the action of a particular part of an ecosystem, rather than the community as a whole. More to the point are tropical coral reefs, which, via their considerable synergetic activities, draw a richness of nutrients out of a desert-like and relatively inactive surround-

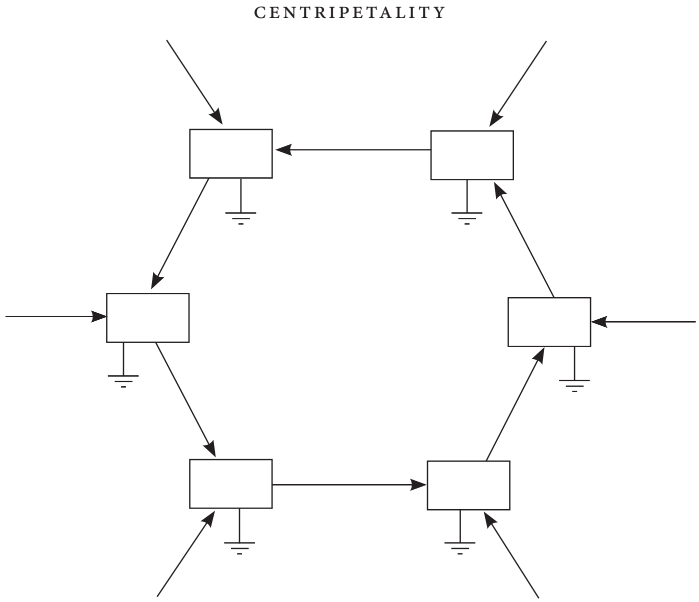


Figure 4.3. Centripetal action as engendered by autocatalysis.

ing sea. Then there are the soils that cover the floors of most terrestrial biomes. That this soil accumulates through the action of the entire community is best demonstrated by examples of the process in reverse. That is, when a community is sufficiently disturbed, it no longer is able to retain its soil. There are numerous examples of such atrophy—perhaps the most startling is the disappearance of the deep soils that once covered the island of Iceland.[5] Only centuries ago, before the advent of humans, the island was covered with heavy forest and lush soils (Hallsdottir 1995). The wood of the forest was soon exhausted building housing and ships, while the settlers let loose sheep they brought from Europe to graze upon the landscape (Kristinsson 1995). Today much of Iceland resembles a moonscape. In fact, parts of Iceland were used by NASA during the 1960s to practice for their moon missions. Loss of centripetality accompanied the disruption of community functioning, and with it went the system's legacy of soil.

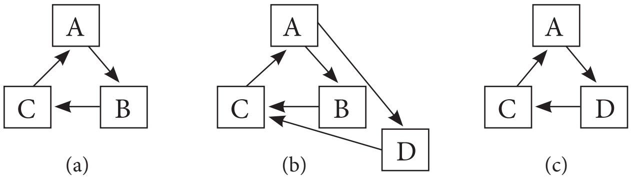
It is very difficult to overstate the importance of centripetality. It is a largely neglected, but absolutely essential attribute of living systems. Furthermore, centripetality is an agency proper to the loop as a whole. Although the accumulation of resources is accomplished at the compartmental level, the drive to increase such activity is strictly a consequence of the relational structure of the whole. As mentioned in chapter 2 in connection with Darwin's theory, a very important but unstated premise of his scenario is that participants strive to capture and accumulate resources. The conventional Darwinian narrative does not mention the origins of this drive, but we now see it as the deductive consequence of autocatalytic action.

The renowned philosopher Bertrand Russell (1993, 22) was among the first to appreciate the central importance of centripetality to evolution, although he referred to it under the guise of "chemical imperialism":

> 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 mine)

Unfortunately, he did not offer to explain the etiology of such "imperialism," but it was obvious in the way Russell phrased his comment that he was *not* referring to the disembodied, external action of "natural selection." Rather, he considered the striving, so conveniently ignored in almost all discussions on evolution, to be both innate and constitutional. Hence, although the origins of Russell's drive remain a tacit mystery under conventional Darwinism, here it becomes an explicit consequence of the second postulate of process ecology.

To underscore the fundamental and essential status that Russell accorded centripetality, we now assert that competition is derivative by comparison. That is, whenever two or more autocatalyic loops draw from the same pool of resources, it is their autocatalytic centripetality that *induces competition* between them. By way of example, we notice that, whenever two loops partially overlap, the outcome could be the exclusion of one of the loops. In Figure 4.4b, for example, element D is assumed to appear spontaneously in conjunction with A and



(a) (b) (c)

Figure 4.4a. Original configuration. *Figure 4.4b.* Competition between component B and a new component D, which is either more sensitive to catalysis by A or a better catalyst of C. *Figure 4.4c.* B is replaced by D, and the loop section A-B-C by that of A-D-C.

C. If D is more sensitive to A and/or a better catalyst of C, then there is a likelihood that the ensuing dynamics will so favor D over B, that B will either fade into the background or disappear altogether. Innate selection pressure and centripetality can actually guide the replacement of elements.

Ecology and evolutionary theory hew tightly to Darwin's example by separating factors of selection from the organisms on which they act. As a result, these fields have, to the best of my knowledge, produced no explicit example of autocatalytic replacement. Economists, however, being less constrained by Darwinian orthodoxy, seem more open to autocatalysis. Igor Matutinović (2005, 12), for example, writes:

> Firms with the strongest autocatalytic loop experience the fastest growth and, consequently, considerably outgrow other competitors. Some of these firms—usually the early entrants—that choose to position themselves in the center of the market where they serve the widest range of needs are most likely to become the new industry hubs.

Returning to Figure 4.4, if B can be replaced by D, there remains no reason that C cannot be replaced by E and A by F, so that the cycle A, B, C could eventually transform into F, D, E, (Figure 4.4c). One concludes that the characteristic lifetime of the autocatalytic form usually exceeds that of most of its constituents. This longevity is exceptional only in that it is sustained in absence of any external agency of repair or development. That is, dynamics remain wholly entailed within the system (Rosen 2000). By way of example, virtually none of the cells that composed our bodies seven years ago (with the exception of our neurons) remains as parts of us today. A very small fraction of the atoms in our body were in us eighteen months ago. Yet, if your mother were to see you for the first time in ten years, she would recognize you immediately.

So, we see how a configuration of processes can, as a whole, strongly affect which objects remain in a system and which pass from the scene. This observation inverts, to a degree, the conventional wisdom that it is objects that direct processes. The processes, as a union, make a palpable contribution toward the creation of their constituent elements. This reversal of causal influence lies at the crux of process ecology, and it extirpates the Newtonian stricture of closure (Ulanowicz 2001).

One should never lose sight of the fact that the autocatalytic scheme is predicated upon mutual beneficence or, more simply put, upon mutuality. Although facilitation in autocatalysis proceeds in only one direction (sense), its outcome is, nevertheless, mutual in the sense that an advantage anywhere in the autocatalytic circuit propagates so as to share that advantage with all other participants. That competition derives from mutuality and not vice-versa represents an important inversion in the ontology of actions. The new ordination helps to clear up some matters. For example, competition has been absolutely central to Darwinian evolution, and that heavy emphasis has rendered the origins of cooperation and altruism obscure, at best. Of course, scenarios have been scripted that attempt to situate cooperative actions within the framework of competitions (e.g., Smith 1982). But these efforts at reconciliation invariably misplace mutuality in the scheme of things. Properly seen, it is the platform from which competition can launch: without mutuality at some lower level, competition at higher levels simply cannot occur. The reason one rodent is able to strive against its competitors is that any individual animal is a walking "orgy of mutual benefaction" (May 1981, 95) within itself. Alternatively, mutuality manifested at higher levels fosters competition at levels below, as we saw with the competition between B and D in Figure 4.4b.[6]

Brian Fath and Bernard Patten (1998) have suggested that, even if we remain entirely at the focal level (where competition is most apparent), there is reason to expect that matters will propagate through the network and evolve over time so that mutuality will gradually displace or overcome predatory and competitive interactions. This will happen whenever positive indirect effects grow to be more influential than direct negative effects. For example, during the wet season in the forested regions of the Everglades, alligators account for 10 percent of total predation on crawfish, and turtles account for double that amount. The alligator, however, preys on turtles as well. The effect of alligators eating turtles is beneficial to the crawfish because it reduces the amount of crawfish lost to turtles. In quantitative terms (Ulanowicz and Puccia 1990), the cumulative indirect effect that alligators have on crawfish is positive because alligators consume enough of the crawfish's other predators to more than compensate for the negative impact of their direct predation (Bondavalli and Ulanowicz 1999). Whether indirect effects between any two compartments are positive or negative is a function of the relative magnitudes of trophic exchanges along all pathways linking the two species (Ulanowicz and Puccia 1990). Fath and Patten maintain that these magnitudes are constantly adjusting in such a way that the positive indirect effects of the type just mentioned gradually become more prevalent.

That mutualistic configurations would grow and persist is no great mystery—autocatalytic mutualism is the only combination of interactions that *uniformly* supports the growth and continued existence of all members. Once a negative interaction enters at any point, that effect may propagate in ways that work to the detriment of at least some members. As we have seen, finite resources inevitably will lead to negative interactions at other levels, but their appearance is accidental (in the philosophical sense that they arise for extrinsic reasons). Mutuality, by contrast, is ontologically primal. It is an essential condition that merits foundational status.

A further feature of centripetality is that the drive it generates imparts an inherent direction to the system, namely, that of ever-more effective autocatalysis. In the terminology of physics, the unidirectional sense of autocatalysis is *symmetry-breaking*. I should hasten to add, however, that one should not confuse this rudimentary directionality with full-blown teleology. For example, it is not necessary that the system strive toward some preordained endpoint. The direction of the system at any one instant is defined by its state at that time, and that state changes as the system develops. This situation can perhaps best be envisioned as "localized hill-climbing,"[7] where the direction the system takes is set by its local neighborhood and remains insensitive to conditions farther away. I have used the term *telos* to denote this weaker form of directionality and to distinguish it from the rarer and more complex behavior known as teleology—Darwin's predilection for the latter notwithstanding.

Yet another important aspect of the asymmetry in autocatalysis is that, whenever such a system is perturbed, autocatalysis acts in homeostatic fashion to restore its own intensity. Sometimes this occurs so as to restore the system to how it appeared before disturbance. The system "heals" itself, so to speak. We might imagine, for example, element B in Figure 4.4 becoming defective and being replaced by a functioning homolog, B' (instead of D). In this manner, systems can be stabilized with respect to encounters with radical chance events of small magnitude. This same homeostasis, when viewed in hierarchical perspective, implies that the radius of disturbance of any chance event will remain circumscribed by autocatalytic selection at higher levels. In other words, the larger system is insulated, to a degree, from much of the disturbance acting at lower levels. Unlike the rigidity and brittleness of Newtonian systems, chance need not destroy an ecological system.

The combined actions of selection and asymmetry serve to fortify those propensities that contribute most to the autocatalytic action within the system. This answers the question posed toward the end of the last chapter as to how propensities grow in strength. If left unperturbed, autocatalysis would reinforce propensities to a degree that they begin to act in mechanical, law-like fashion. The effect of autocatalysis is to strengthen the "fabric of causality" and make it less flexible in the process. The overall trend is for the constraints in processes to start out weak and arbitrary, yielding outcomes that differ only marginally from the stochastic (see Figure 2.1). Gradually (or abruptly in rare cases), the constraints will continue to strengthen each other in the absence of major perturbations until their behavior becomes almost law-like (as in Figure 2.3). Such transition has been referred to as *canalization* (Waddington 1942), and we shall pursue such directionality further in the next section.

Taken together, selection pressure, centripetality, and a longer characteristic lifetime all give evidence that the larger organic structure begins to exhibit a degree of *autonomy* from its constituents. This should come as no big surprise, however, because we have discussed how such autonomy becomes implicit in the second axiom just as soon as one dispenses with atomism. One conclusion worth repeating, however, is that attempts at reducing the workings of an organic system exclusively to the properties of its composite elements always prove futile over the long run.

The organic dynamics just described can be considered *emergent* in the epistemic sense (i.e., virtual). Organic behavior all too often remains cryptic, however, due to a common predilection to view matters narrowly. In Figure 4.5, for example, if one were to consider only those elements in the lower right-hand corner (as enclosed by the solid line), one could readily identify an initial cause and a final effect. If, however, one were to expand the scope of observation to include a full autocatalyic cycle of processes (as enclosed by the dotted line), then the ensemble of system properties we have enumerated would become immediately evident. For example, if an ecologist were to concentrate on studying the consumption by zooplankton of periphyton attached to *Utricularia* in limestone lakes in Florida,