Provided for non-commercial research and educational use. Not for reproduction, distribution or commercial use.

This article was originally published in the *Encyclopedia of Ecology*, Volumes 1-5 published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues who you know, and providing a copy to your institution's administrator.



All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

http://www.elsevier.com/locate/permissionusematerial

R E Ulanowicz. Autocatalysis. In Sven Erik Jørgensen and Brian D. Fath (Editor-in-Chief), Systems Ecology. Vol. [1] of Encyclopedia of Ecology, 5 vols. pp. [288-290] Oxford: Elsevier.

Autocatalysis

R E Ulanowicz, University of Maryland Center for Environmental Science, Solomons, MD, USA

© 2008 Elsevier B.V. All rights reserved.

Introduction	Centripetality and Agency
Autocatalysis in Ecology	Further Reading

Introduction

In chemistry the term catalysis means the speeding up of a chemical reaction. It follows that autocatalysis then means "the catalysis of a chemical reaction by one of the products of the reaction." For example, oxalic acid oxidizes purple permanganate. When a few crystals of $MnSO_4$ are added to a mixture of the chemicals, the conversion to Mn(II) is sped up. If no $MnSO_4$ is added, then the reaction will gradually speed up of itself, because Mn(II) is gradually being created by the reaction, and this product autocatalyzes the reaction itself. Autocatalysis in chemistry is usually considered to occur among relatively simple, fixed, and inflexible reactants. As such it is commonly regarded as a subclass of general mechanisms.

Autocatalysis in Ecology

In systems ecology, autocatalysis is regarded as a generalized form of mutualism, that is, an association between organisms of two different species in which each member benefits. In systems ecology focus remains more on processes and less on objects. Hence, an autocatalytic configuration of two or more ecological processes is one in which the processes can be arrayed in a closed cycle, wherein each process in the cycle facilitates the next. Without loss of generality, one may focus on a serial, circular conjunction of three processes – A, B, and C (**Figure 1**). Thus, any increase in the rate of process A is likely to induce a corresponding increase in process B, which in turn elicits an increase in process C, and whence back to A.

A didactic example of autocatalysis in ecology is the community that builds around the aquatic macrophyte,



Figure 1 Schematic of a hypothetical three-component autocatalytic cycle.

Utricularia (commonly called Bladderwort). All members of the genus *Utricularia* are carnivorous plants. Scattered along its feather-like stems and leaves are small bladders, called utricles (**Figure 2a**). Each utricle has a few





hair- like triggers at its terminal end, which, when touched by a feeding microheterotroph, 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. This feeding upon microheterotrophs helps the Utricularia to grow and increase its surface area (process A). In nature the surface of Utricularia plants is always host to a film of diatomaceous algal growth known as periphyton, so that more surface area encourages the growth of more periphyton (process B). More periphyton in its turn means more food to support the growth of any number of species of small microheterotrophs (process C). The autocatalytic cycle is closed when it is noted that a greater density of microheterotrophs provides more resources for the Utricularia to grow (process A again) by capturing and absorbing more abundant zooplankton (Figure 2b).

Unlike in chemistry, the actors in ecology are more complex, malleable entities with capabilities to undergo small, incremental alterations. Such malleability substantially enhances the repertoires of autocatalysis and enables it to exhibit some very nonmechanical behaviors. This is especially the case when autocatalysis involves processes that can change in stochastic and nonpredictable ways. An important characteristic of causal cycles (e.g., autocatalysis) is that when random events impinge upon them, they usually yield nonrandom results. This is the consequence of the first and foremost attribute of autocatalysis – its generation of selection pressure.

To see how autocatalysis generates selection, one begins by considering a small spontaneous change in process B. If that change either makes B more sensitive to A or a more effective catalyst of C, then the transition will receive enhanced stimulus from A. In the Utricularia example, diatoms that have a higher P/B ratio and are more palatable to microheterotrophs would be favored as members of the periphyton community. Conversely, if the change in B makes it either less sensitive to the effects of A or a weaker catalyst of C, then that perturbation will likely receive diminished support from A. Hence, the response of this causal circuit is decidedly not symmetric, and out of this asymmetry emerges a direction. This direction is not imparted or cued by any externality; its action resides wholly within the system. As one might expect from a causal circuit, the resulting directionality is in part tautologous, that is, autocatalytic systems respond to random events over time in such a way as to increase their degree of autocatalysis. It should be emphasized that this directionality, by virtue of its internal and transient nature, should not be conflated with teleology. There is no externally determined or preexisting goal toward which the system strives. Direction arises purely out of the immediate response by the internal system to a novel, random event impacting one of the autocatalytic members.

Centripetality and Agency

A second important and related directionality emerges out of autocatalysis - that of centripetality. To see this one notes in particular that any change in B is likely to involve a change in the amounts of material and energy that are required to sustain process B. As a corollary to selection pressure one immediately recognizes the tendency to reward and support any changes that serve to bring ever more resources into B. Because this condition pertains to any and all members of the causal circuit, any autocatalytic cycle becomes the epicenter of a centripetal flow of resources toward which as many resources as possible will converge (Figure 3). That is, an autocatalytic loop defines itself as the focus of centripetal flows. A didactic example of such centripetality is coral reef communities, which by their considerable synergistic activities draw a richness of nutrients out of a desertlike and relatively inactive surrounding sea.

The centripetality generated by autocatalysis is a much-neglected and essential attribute of the life process. For example, evolutionary narratives are replete with explicit or implicit references to such actions as striving or struggling, but the origin of such directional behaviors almost always remains unmentioned. Such actions are simply postulated. Centripetality, however, appears to be at the very roots of such behaviors. To see this, one only needs to recognize that it is centripetality that gives rise to the much vaunted competition, which is the crux of evolutionary theory. For centripetality guarantees that, whenever two or more autocatalytic loops exist in the same system and draw from the same pool of finite resources, competition among the foci necessarily ensues. In particular, whenever two loops share pathway segments in common, the result of this competition is likely to be the exclusion or radical diminution of one of the nonoverlapping sections. For example, should a new element D happen to appear and to connect with A and C in parallel to their connections with B (Figure 4), then



Figure 3 Centripetal action as engendered by autocatalysis.



Figure 4 (a) Original configuration. (b) Competition between component B and a new component D, which is either more sensitive to catalysis by A or a better catalyst of C. (c) B is replaced by D, and the loop section A–B–C by that of A–D–C.

if D is more sensitive to A and/or a better catalyst of C, the ensuing dynamics should favor D over B to the extent that B will either fade into the background or disappear altogether. That is, the selection pressure and centripetality generated by complex autocatalysis (a macroscopic ensemble) is capable of shaping and replacing its own elements. Perhaps the instances that spring most quickly to mind here involve the evolution of obligately mutualistic pollinators, such as yuccas and yucca moths, which coevolve with the yucca so as to displace other pollinators.

One notes in passing that the same tendency to replace B with D could as readily replace a defective or destroyed B with another similar component B', that is, autocatalysis lies behind the ability of living systems to repair themselves.

It becomes obvious that the autocatalytic system is no longer acting merely at the behest of externalities, but it is actively drawing ever more resources unto itself. In fact, the tendency of centripetality to transform as much as possible into itself lies at the very crux of evolutionary drive; for absent such striving, there would be no competition at the next level up.

Furthermore, one perceives autocatalytic action as the agency behind one of a pair of agonistic tendencies that together account for the patterns of life-forms and functions. On the one hand is the stochastic, entropic tendency to fall apart, which at the same time generates new diversities of form and behavior. Arrayed against the inevitable centrifugal drift toward disorder is the autocatalytic selection and centripetal pull toward greater activity and tighter organization. Opposing thrusts though they are, the continued development of life would be impossible without the actions of both.

Finally, the focal position that autocatalytic configurations of processes occupy in the phenomenon of life is aptly illustrated by considering what differs between a living organism (say a deer) and the same entity immediately upon death. The mass of the deer remains the same, as does its overall form, chemical constitution, embodied energy, and genomic configuration. What the live deer had that the dead deer no longer possesses is simply its configuration of autocatalytic processes.

See also: Ecological Network Analysis, Ascendency; Ecological Network Analysis, Energy Analysis.

Further Reading

- Eigen M and Schuster P (1979) The Hypercycle: A Principle of Natural Self-Organization. Berlin: Springer.
- Kauffman SA (1995) At Home in the Universe: The Search for Laws of Self-Organization and Complexity. New York: Oxford University Press.
- Ulanowicz RE (1995) *Utricularia's* secret: The advantages of positive feedback in oligotrophic environments. *Ecological Modelling* 79: 49–57.
- Ulanowicz RE (1997) *Ecology, the Ascendent Perspective*. New York: Columbia University Press.