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Formal agency in ecosystem development

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2.1 Introduction

Perhaps the greatest reservation that most scientists and philosophers have against the concept of holistic or 'top-down' causality is the apparent absence of a robust exposition of just how such influence might arise. True, those interested in hierarchy theory have made great strides of late in clarifying the role of higher-level constraints in generating order at the finer scales (Allen & Starr, 1982). But the idea of a constraint usually conjures up a mental image of a wall or a boundary – rather passive elements in the scheme of things. How can a wall ever hope to compete as an agent of cause against the exciting imagery evoked by the story of magical dancing molecular genes at work *directing* the assembly of the mature phenome?

If top-down causality is to achieve any credibility, it is necessary that its proponents point to a plausible *agent* behind such influence. As I have done elsewhere (Ulanowicz, 1986), I wish to focus here upon the role of positive feedback as an agent that helps to order events at the micro levels. What I wish to achieve in this narrative is to enhance the case for positive feedback by more accurately mapping its domain in the Aristotelian scheme of causality, by better enumerating its attributes, and by demonstrating that it affects both the extensive and intensive properties of flow networks.

2.2 Aristotelian causality

One of the unfortunate aspects about much of biological discourse is that the concept of causality is often used in generic fashion without any mention of the truly intricate nature of causal linkage. Aristotle was quite aware that cause was not a simple notion and defined

four categories to describe the phenomenon: (1) material, (2) efficient, (3) formal and (4) final. Moreover, a single event can have more than one type of cause. The familiar example is the building of a house. The material cause lies in the bricks, mortar and wood used in the construction; the efficient cause is embodied in the laborers who assembled the materials; the formal cause is usually considered to derive from the architectural principles or blueprints according to which the house was put together; and the final cause was the desire for a house on the part of those who ordered the building, or more generally, the need for housing in the area where the residence was built.

For most of its prosperous existence, science has been confined to the quantification of material and the elucidation of efficient causes. However, in order to fully apprehend the nature of biological order, it appears necessary to entertain the possibility of and to attempt to quantify formal, final and non-proximate causes (Rosen, 1985; Patten *et al.*, 1976).

Recently, Salthe (unpubl. ms) has offered the very provocative insight that the appearance of efficient, formal and final causes appears to be correlated to the hierarchical context in which they are being observed. Thus, those agents of cause observed at finer scales are more likely to be classified as efficient, whereas final cause (if it is considered at all) usually derives from outside the system in question, i.e. at some higher level. Formal cause, as its name implies, is intimately tied up with the structure of the system itself and thus is a feature of the focal level. One should not attempt to draw the trichotomy too strictly, but the distinctions will prove useful in the discussion of agency presented in the following sections.

2.3 Material and efficient causality

Networks of material and energy flows are particularly well-suited to the exploration of causality in ecology (Platt *et al.*, 1981). Each arc is the palpable result of temporal sequences of similar arcs in the past, and it contributes to the material cause of like arcs at future times. Whence, the flow network portrays the aggregate of material causes in its underlying ecosystem. Furthermore, the topology of the network permits the quantitative exploration of non-proximate material causes. When Hannon (1973), Patten *et al.* (1976) and others employ linear algebra to assess the indirect or non-proximate causes for ecological events, they are pioneering a long-overdue form of scientific inquiry.

Unfortunately, flow networks are often ill-suited to the elaboration of efficient causality. As mentioned earlier, efficient causes lie predominantly at finer scales, i.e. within the nodes of the flow graph. Thus, genetic and

behavioral mechanisms, and adaptive 'strategies' do not always lend themselves to depiction in terms of networks – at least as networks cast at the ecosystems level. However, environmental perturbations constitute one class of efficient causality that can be represented in the network format. In any event, the description of these efficient causes is the crux of most conventional biology and ecology. There is no dearth of activity nor paucity of discoveries in this realm. The chief goal here is to demonstrate how the study of flow networks constitutes a complementary endeavor that allows one to incorporate less familiar aspects of causality into ecology and biology.

2.4 Positive feedback as a formal agent

Of the four causes cited in the familiar example of constructing a house, perhaps the least explicit is the formal cause. Whereas one is content with the other three kinds, one is impulsively driven to look beyond the blueprint toward the architect. Why? It appears the blueprint alone does not possess sufficient *agency*. It does not generate any action on its own. Its power is entirely derivative of the architect. A true agent should be autonomous to some degree of the causes which engender it.

That the blueprint is a weak excuse for the formal cause of a house is more an inadequacy of the example (house building) than it is a flaw in the underlying concept (formal cause). Formal cause is an essential element of practically all biological phenomena. It often happens in biology that the present *form* of a system mediates what will subsequently appear and transpire. Hence, Weiss (1969) cites the intriguing example of early blastular formation. During the first few cellular divisions, when the diameter of the cell is not greatly exceeded by the blastular diameter, practically all the component cells communicate equally with the external environment. Not too long into the process of growth, however, geometrical relations dictate that a fundamental dichotomy appears between 'internal' and 'external' cell members, which distinction may induce corresponding differences in cell morphology and function.

A situation that is more pertinent to ecology occurs during succession, where the juxtaposition of the component processes and their rates may result in a change in the environment (the build up of detritus or waste products, a change in light regime, etc.) that sets the stage for the next system configuration.

The difficulty with these two examples is that the source of agency is not very explicit. In the example by Weiss, the emerging geometrical constraint appears almost as a passive element of the system.

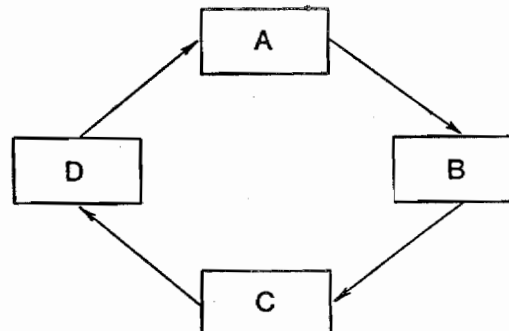
Positive feedback is an example of a formal cause whose agency is much more apparent. In its simplest form positive feedback occurs when the activity of a given element increases the activity of one or more other elements that in turn increase the activity of the original element still more. Positive feedback is usually represented graphically in the form of a unidirectional closed cycle of influence as in Fig. 2.1. Biogeochemical cycles of material or energy in ecosystems are examples of positive feedback configurations of material causality (Ulanowicz, 1983). Hence, positive feedback is explicitly formal in character.

Positive feedback is imbued with at least five attributes, all of which contribute toward its inherent agency. It is (a) semi-autonomous, (b) emergent, (c) growth enhancing, (d) selective and (e) competitive.

The autonomous element in positive feedback is evident in the example shown in Fig. 2.1. At the focal level the cycle has no external cause. All causality, direct or indirect, originates within the system. Of course, no real system can correspond exactly to Fig. 2.1, for then it would violate logical (Goedel's hypothesis) and thermodynamic (second law) constraints. Real cycles communicate with the external world as in Fig. 2.2. But it likewise would be a mistake to label the system in Fig. 2.2 as entirely non-autonomous. A measurable fraction of each component's material causality is seen to originate in itself. Real systems with feedback are partially autonomous.

The appearance of cyclical causality in a system is contingent upon the position of the focal level in the hierarchical scheme. Suppose, for example, that at a given level of observation one sees only a subset of the elements in a particular cycle, as illustrated by the solid boundary in Fig. 2.3. The pathway of causality connecting this subset is strictly non-

Fig. 2.1. A closed, autonomous cycle of influence.



autonomous. However, if one expands the domain of observation (the dotted boundary in Fig. 2.3), then one might become aware of a degree of system autonomy associated with the newly perceived cycle that has *emerged* from increasing the scale of observation. Autonomous behavior becomes more apparent as one increases the field of observation.

That positive feedback is growth-enhancing is virtually tautological. In the absence of overwhelming constraints, an increase in activity anywhere in the cycle serves to engender greater activity everywhere else in the loop.

Fig. 2.2. A semi-autonomous cycle of influence. (Units are arbitrary.)

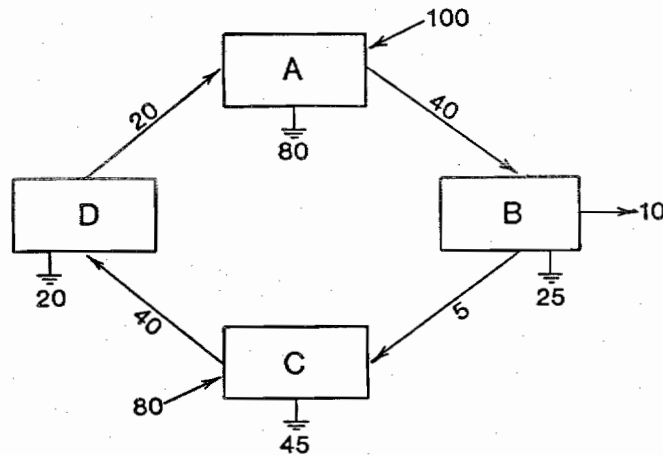
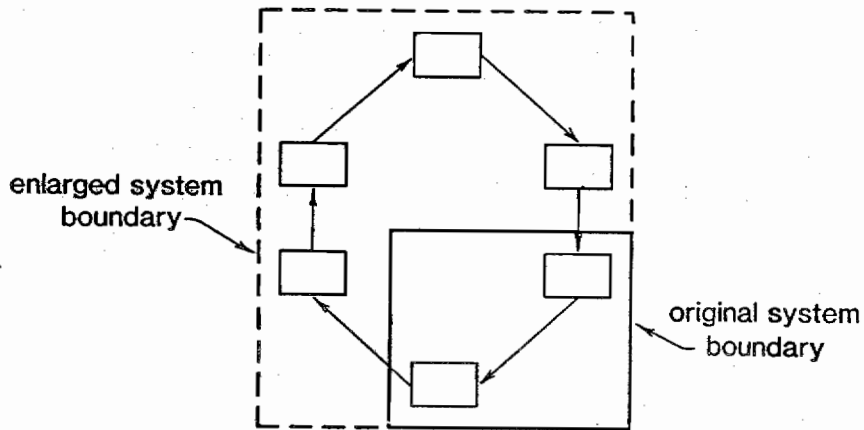


Fig. 2.3. An autonomous cycle emerges from an enlargement of the scope of observation from the solid square to the dotted.

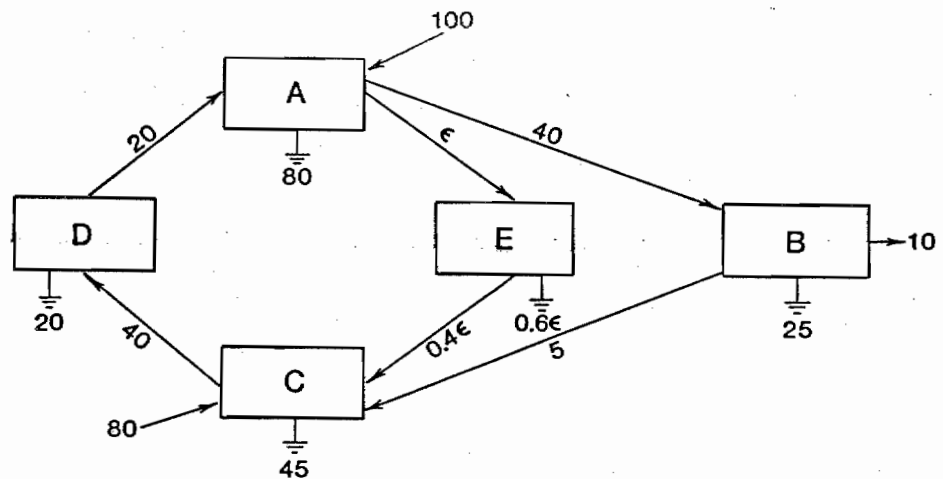


The activity level of the cycle is progressively elevated until it is restrained in some way from further increase.

Most important as regards network development is the possibility that positive feedback can serve as an agent of selection. To see how selection might arise one only needs to observe what happens when a perturbation changes the activity of any compartment in a cycle. If the change diminishes the outputs of the given node, then the negative result will propagate around the cycle upon itself. Conversely, if the change is incremental, it will be reflected positively upon itself (rewarded). Hence, by its very nature, positive feedback discriminates among the perturbations occurring in its cycle. The persistence of the characteristics of component elements are directly influenced by the feedback structure in which they occur.

The selection pressure engendered by feedback acts not only to change the features of the components, but also may help to alter the list of participating components. To better grasp this possibility, one may imagine that through some mechanism, stochastic or otherwise, a new element enters the system in Fig. 2.2 giving rise to the new configuration in Fig. 2.4. The new species, E, is seen to be more efficient at conveying a small amount, ϵ , of material cause from A to C. The pathway through E is progressively rewarded, and, if the whole system is acting near its limits (as it eventually must), the continued growth of the pathway A-E-C will occur at the expense of the activity of B. After a while B is displaced

Fig. 2.4. The cycle in Fig. 2 acquires a new element, E, that is more efficient than B at transporting medium from A to C.

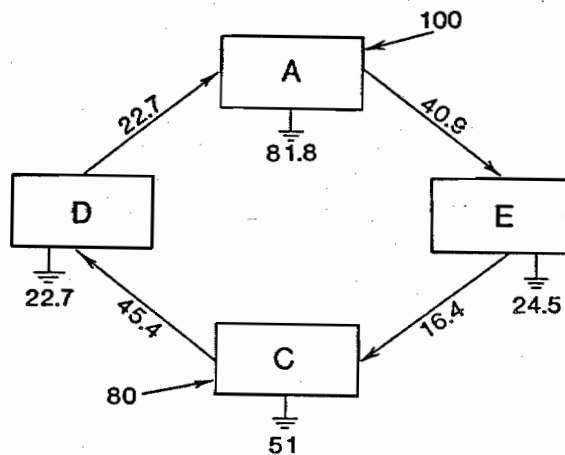


by E in the cycle, as shown in Fig. 2.5. It is possible to imagine that ultimately all of the original components are replaced by more efficient members, so that an identifiable structure may persist beyond the lifetimes of its constituents, all the while playing an active role in guiding its eventual make-up.

Selection in the face of limitations inevitably results in competition, such as occurred between B and E in Fig. 2.4. One also can expect competition between feedback loops whenever common elements appear in both circuits. But direct overlap of the cycles is not absolutely necessary. For example, a single resource can (directly or indirectly) contribute to more than one positive feedback loop, setting the stage for competition between non-overlapping cycles. Thus, each of the various feedback loops is seen to take on its separate agency and appears as a center into which material or energy is inexorably drawn, much in the fashion of Denbigh's 'chemical imperialism'.

The emerging picture of positive feedback as a formal agent is both a dynamic and an intriguing one. This single formal process has both extensive and intensive consequences. Its growth enhancing characteristics ~~impel the system toward ever greater levels of flow activity~~, and the aggregate level of flow in a system is a common measure of a system's 'size' or extent (e.g. the GNP, or Gross National Product in economics). But flow is not being enhanced uniformly in the network. Rather, a greater proportion is being more narrowly channeled along those feedback pathways of higher transfer efficiencies. In the absence of any mechanisms

Fig. 2.5. Element E has displaced B in the cycle of positive feedback.



generating new components and/or pathways (which are always present in non-senescing systems), the evolving network topology would appear increasingly more simplified, or better articulated. This progressive articulation depends only on the ratios of the various flows and is an intensive feature of the development of the system.

Thus, the growth and development of a system network are seen to be separate outward manifestations of an underlying unitary process.

2.5 Quantifying the effects of formal agency

The foregoing examples serve as heuristic tools for understanding formal agency. But in order to make such agency more amenable to objective scrutiny, it becomes necessary to outline how one might measure the effects of positive feedback in ecological and other living systems. The network format serves this purpose admirably. As remarked earlier, Patten (1982) has used network representations of ecosystem kinetics to assay non-proximate causality in ecosystems. This same format allows one to trace quantitatively the effects of formal and (as will be discussed in the next section) final agencies.

To demonstrate how to calculate measures of size and organization in ecological networks, I will employ the structure of the oyster reef community shown in Fig. 1.8. However, it should be stressed that this configuration is only an instantaneous snapshot of the ecosystem, so that one is limited to calculating the static attributes of size and organization. Growth and development, on the other hand, are temporal increases in these static measures, and to quantify these dynamic processes requires that the network be fully described at two or more distinct times.

Earlier, system size was assumed to be the total amount of flow activity in the system. Most simply put, the total system throughput of the oyster reef community is the sum of the magnitudes of all the arrows depicted in Fig. 1.8. This amounts to $125.05 \text{ kcal m}^{-2} \text{ day}^{-1}$.

The organization of the oyster community is not as simply determined. As a prelude, it is helpful to redefine slightly the flows as labeled in Fig. 1.8, such that $f_{i0} = Z_i$ and $f_{n+1,i} = Y_i$. Then the total systems throughput, T , may be written more conveniently as

$$T = \sum_{i=0}^n \sum_{j=1}^{n+1} f_{ji}$$

All other things being equal, a strongly organized community is highly articulated in the sense discussed in the last section. Knowing where a quantum of energy or mass is located at any time in a highly articulated

system yields a great amount of information as to where the same quantum will be after its next transition. When averaged over all the components in the system, the amount of such information, A , may be quantified as

$$A = K \sum_{i=1}^{n+1} \sum_{j=0}^n (f_{ij}/T) \log \left[\frac{f_{ij} T}{\left(\sum_{k=1}^{n+1} f_{kj} \right) \left(\sum_{m=0}^n f_{im} \right)} \right].$$

This complicated looking formula is a version of the well-known average mutual information adapted for network theory by Rutledge *et al.* (1976) and Hirata & Ulanowicz (1984). The quantity K is the arbitrary scalar factor which is inherent in all information variables.

The interested reader should verify for him/herself that A is largest when the network for which it is being calculated is maximally articulated, as in Fig. 2.1. Conversely, A is identically zero when no articulation is evident, i.e. when each compartment exchanges equal amounts of medium with all compartments (and with itself). All real networks have values of A intermediate to these extremes.

Growth and development are purported to be separate manifestations of a single underlying agent, positive feedback. Consonant with this observation is the assumption that size and organization are co-factors in a single system attribute. Now, the scalar factor, K , in the formula for mutual information may be chosen at the discretion of the observer. Its dimensions are usually set by the base of the logarithmic operator. Tribus & McIrvine (1971), however, urge that K be chosen so as to impart actual physical dimensions to the information being measured. What better choice is there than to set $K = T$, making size and organization literal and numeric co-factors in a single network attribute, called the ascendancy? A rise in ascendancy, therefore, represents an increase in system size or organization (or both), i.e. growth and development. As positive feedback is a formal cause of growth and development, the results of its agency will be reflected in the changes in network ascendancy.

The ascendancy of the oyster reef network is calculated by substituting the various flows into the formula for A , setting $K = T$ and the logarithmic base to 2. The result is that $A = 166.35 \text{ kcal-bits m}^{-2} \text{ day}^{-1}$.

2.6 Quantifying final cause

Previously, it had been difficult to conceive of an example of final cause in physical or biological terms, much less to hope to quantify its agency. However, if one accepts the suggestion that the notion of final cause is a consequence of the hierarchical view of nature, assigning a

Table 2.1. Components of the ascendancy of the oyster reef community (Fig. 1.8).

	0	1	2	3	4	5	6	7
0	.0	.0	.0	.0	.0	.0	.0	.0
1	66.0368	.0	.0	.0	.0	.0	.0	.0
2	.0	17.3193	.0	.0	6.3166	3.9940	0.4626	.0
3	.0	.0	20.3457	.0	.0	.0	.0	.0
4	.0	.0	16.5011	1.3529	.0	.0	.0	.0
5	.0	.0	0.3377	3.4712	1.2934	.0	.0	.0
6	.0	0.6036	.0	.0	.0	0.6272	.0	.0
7	.0	21.9374	-1.5914	6.2657	1.2455	-0.4096	0.2374	.0

Values in kcal-bits $\text{m}^{-2} \text{day}^{-1}$. Component in row i and column j was generated by the flow from j to i . The 0 represents external inputs; the 7, the combined exports and respirations.

number to such top-down influence might not be an impossible task. Toward this end, it is noted that one may rewrite the formula for ascendancy as the double sum of $(n+2)^2$ terms,

$$A = \sum_{i=1}^{n+1} \sum_{j=0}^n f_{ij} \log \left[\frac{f_{ij} T}{\left(\sum_{k=1}^{n+1} f_{kj} \right) \left(\sum_{m=0}^n f_{im} \right)} \right].$$

The 49 terms generated by the oyster reef network are arrayed in Table 2.1. One sees that corresponding to each non-zero f_{ij} is a logarithmic term that is a function of the configuration of the *entire* network. When the medium in circulation is energy (as it is in the oyster reef network) and the base of the logarithms is 2, then A has the dimensions of power-bits. Traditionally, power functions in irreversible thermodynamics are written as the sums of products of conjugate pairs of fluxes and forces (Onsager, 1931). If this analogy is applied to the terms in the last formula, one sees that the logarithmic terms correspond to the forces. That is, the logarithmic terms might be said to express the whole-system level pressure (formal cause at the level of the system, final cause at the level of the flow) upon their corresponding flows. These 'factors' may be positive or negative (although A is always non-negative, the particular components of A may be negative) and the degree to which the flows do *not* respond to their conjugate forces is an indication of the severity of the constraints to which the system is subject.

As an example, the contribution to A from f_{54} is read from Table 2.1 to be 1.2934 kcal-bits $\text{m}^{-2} \text{day}^{-1}$. Dividing this value by $f_{54} = 0.6609 \text{ kcal m}^{-2} \text{day}^{-1}$, assigns a value to the conjugate 'force' of 1.957 bits. Because the

system is in steady state, the tendency of this system-level pressure to further increase f_{54} is being balanced by unwritten constraints, such as energy limitations, mass balance, environmental limits, perturbations, etc.

This analogy of a system-level force apparent in the network is highly speculative and tenuous at best. However, it was drawn to illustrate how it might be possible to measure the effect of formal cause operating at the system level when manifested as a final cause of events (flows) at a finer scale. Elsewhere (Ulanowicz, 1986), I show how influence from even higher level configurations upon the given system is quantified via another network information variable called the 'tribute'.

2.7 Conclusions

Practically all the progress associated with the last 300 years of the scientific age has been made by elucidating material, efficient and proximate causes. Formal, final and non-proximate causes have not figured much in the body of scientific narrative. The idea that such causes exist has been considered fanciful by many; that they might be measured has, to the best of my knowledge, not received serious consideration.

Portraying complex evolving systems in terms of their constitutive networks is thereby seen as an enormous aid to viewing new perspectives on reality. With some input from hierarchy and information theories, network analysis now allows one to quantitatively track the effects of formal, final and non-proximate causal agencies that, for all practical purposes, have been heretofore neglected.

What progress has been made thus far in elucidating these non-Newtonian forms of causality has been largely phenomenological in nature. But such has been the case with most beginnings in the history of science. There is every reason to hope that further research into the network analysis of living systems will lead to radically clearer insights into the life process.

2.8 Summary

- 1 Formal cause is associated with the structure of ecological systems.
- 2 Positive feedback, represented as closed cycles in ecological networks, helps order events at the hierarchical level below. Positive feedback is an agent of formal causality.
- 3 Positive feedback is imbued with at least five attributes, all of which contribute to its inherent agency; it is semi-autonomous, emergent, growth enhancing, selective and competitive.

- 4 Growth and development are separate manifestations of a single underlying agent, positive feedback.
- 5 Flow networks serve for the measurement of formal cause operating at the system level and manifested as a final cause of events at a lower level.

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