

TWELVE READINGS ON THE LICHEN THALLUS

VIII. Theoretical

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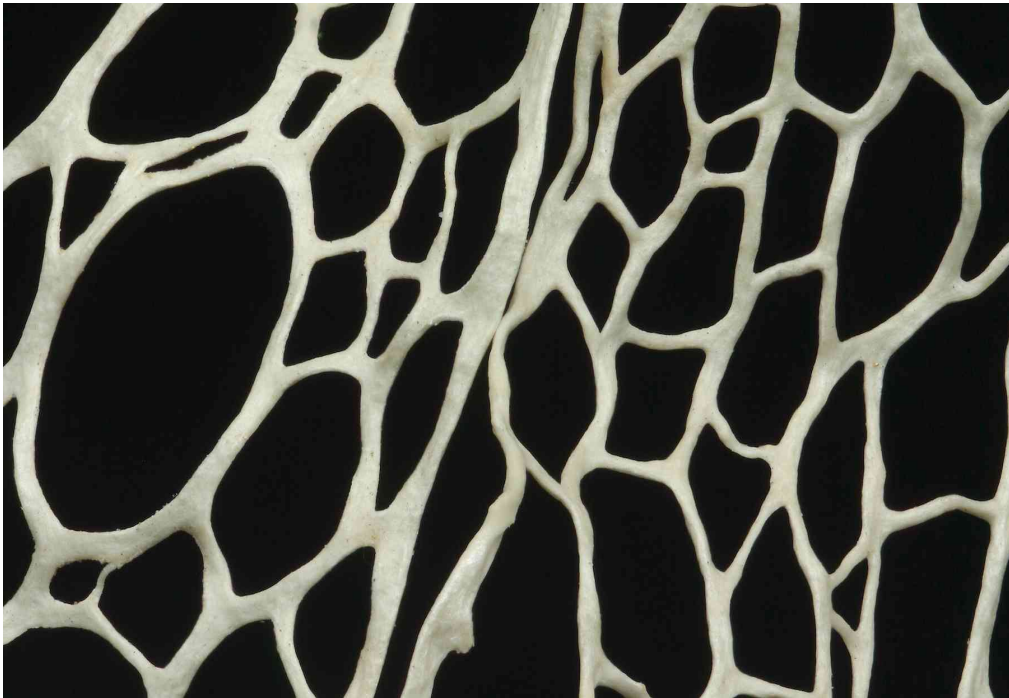


Figure 1. This Fishnet Lichen (fungal partner: *Ramalina menziesii*) is not only a network of networks of networks, it is also cells within a “metacell.” Photomontage by Tim Wheeler.

Systems biology is about putting together rather than taking apart, integration rather than reduction.

Dennis Noble, *The Music of Life*

I DON'T KNOW ABOUT YOU, but eight essays into a twelve-part series feels, to me, like a good time finally to execute a certain intention that has been building within these pages ever since the first line of Essay I: a theory of the lichen lifestyle.

And why not? Much of the groundwork has already been laid. Lichens, I've been heard to say, make sense above all when viewed as independent organisms, separate from their member parts. Thinking of lichens this way is a boon not only to lichens but also to lichenologists, finally equipt to give a sensible definition of the organisms they study

(Essay v). Still, lichens aren't *only* organisms. In Essay VI, I argue we get better conceptual traction when we learn to think of lichens also as systems. The dual status of lichens as organisms *and* ecosystems has precedent in the fundamentally dual nature of the eukaryotic cell (Essay VII).

I might as well place my cards face up. To posit a theory of lichens seems to me a particularly canny way to call attention to the proposition that lichens exist – especially if the theory in question happens to be a grand unifying one. I don't claim this will be easy. What I need is some way in. Instead of conceiving

lichens in the usual modern reductionist tradition – as a hodgepodge-of-seemingly-unrelated-attributes – I need to see them the way a good naturalist would. Lichens as pattern, as context, and perhaps also as a kind of unity.

To get things started, here are ten characteristics that taken together seem to me to capture the salient features – at least the most pertinent ones – of the lichen lifestyle. Most, but not quite all, pertain to all lichen groups, regardless of origin or stripe or creed:

- ♦ The lichen lifestyle has evolved on several different occasions, each origin giving rise to an independent lineage.
- ♦ Lichens have no phylogenies, only their bionts do.
- ♦ Lichen bionts retain their independent identities.
- ♦ Nearly all lichens have a cortex.
- ♦ Lichens, like most plants, are autotrophic.
- ♦ Lichens span a tremendous range of form.
- ♦ Most lichens either resynthesize or reassemble at each generation.
- ♦ The resynthesis/reassembly process begins in a prethallus.
- ♦ Lichens are conspicuously more robust than their member parts.
- ♦ Some lichens are capable, over evolutionary timescales, of becoming delichenized, that is, of disbanding into their constituent parts.

Let these, then, be the attributes I'd most like to accommodate in a unifying theory of lichens. I'll tell you one thing, though. I'm likely to succeed at this, or have a running chance of doing so, only to the extent I first succeed in developing two major themes these essays have been circling around more or less since the beginning, but have not, until now, ever quite taken hold of. The first theme is biological networks. The second theme is emergence.

BIOLOGICAL NETWORKS

My dictionary defines *network* as (among other things) "a group, system, etc. of interconnected or cooperating individuals." This will do. Taken down to basics, all networks have two components: nodes and links. In practice, a node is any entity within a network that participates in decisions relevant to its operation. Biological networks exist across a vast range of spatial scales from the level of the molecule (or below) to that of the biosphere conceived as an overarching biophysical system, almost an organism, as in Lovelock's "Gaia

Hypothesis." Examples of nodes might therefore include: a molecule, a peptide, a protein, a cell, you, us, and so on up. Now links. Links are the lines of communication by which the nodes keep in touch with one another. Effectively they take the form of feedback circuits, continuously transmitting information between pairs of nodes. Depending on environmental input, these feedback circuits either tend to maintain the network (or systems, etc. within it) at a steady level of operation (= negative feedback) or else they promote adaptational change (= positive feedback) (Figure 3).

We should probably refrain from thinking of lichen networks as consisting, for example, of thousands of fungal hyphae (links) interconnecting thousands of algal cells (nodes). Certainly something of the kind is at work within the lichen thallus, but expressing it this way doesn't really capture what is meant by biological network. Instead, consider Figure 2, where the lines (links) and circles (nodes) are meant to form a kind of circuitry map with little if any resemblance to a real organism. What Figure 2B illustrates is not the network itself, but what the network would look like if we could strip away the details – the parts, the positions, the parrying – and focus only on the lines of communication.

Scarcely a decade ago it would have been difficult, perhaps impossible, to arrive at a unifying theory of anything – much less lichens – down the poorly lit byways of network theory. Today things are different. The breakthrough came in 1999, when the World Wide Web – the most tractable of all complex networks – was found to have a highly distinctive structure referred to as scale-free (Figure 2).

Figure 2 describes the basic operation of scale-free networks. Here I'll confine myself to calling attention to their two most noteworthy characteristics. The first characteristic is an extraordinary robustness. Whereas random networks have a loose, tattered structure, scale-free networks are compact, cohesive, and able to absorb considerable perturbation without suffering adverse effects. The second characteristic is their seeming ubiquity. Since first being reported, little more than a decade ago, scale-free networks have turned up across an astonishing array of remarkably dissimilar networks, many shaped by evolution, others by unwitting human intention. There seems to be growing consensus that scale-free topology is, in effect, a byproduct of the underlying order of things; that it presses up hard against the basic organizing tendencies of the universe itself; and that it is less likely to be

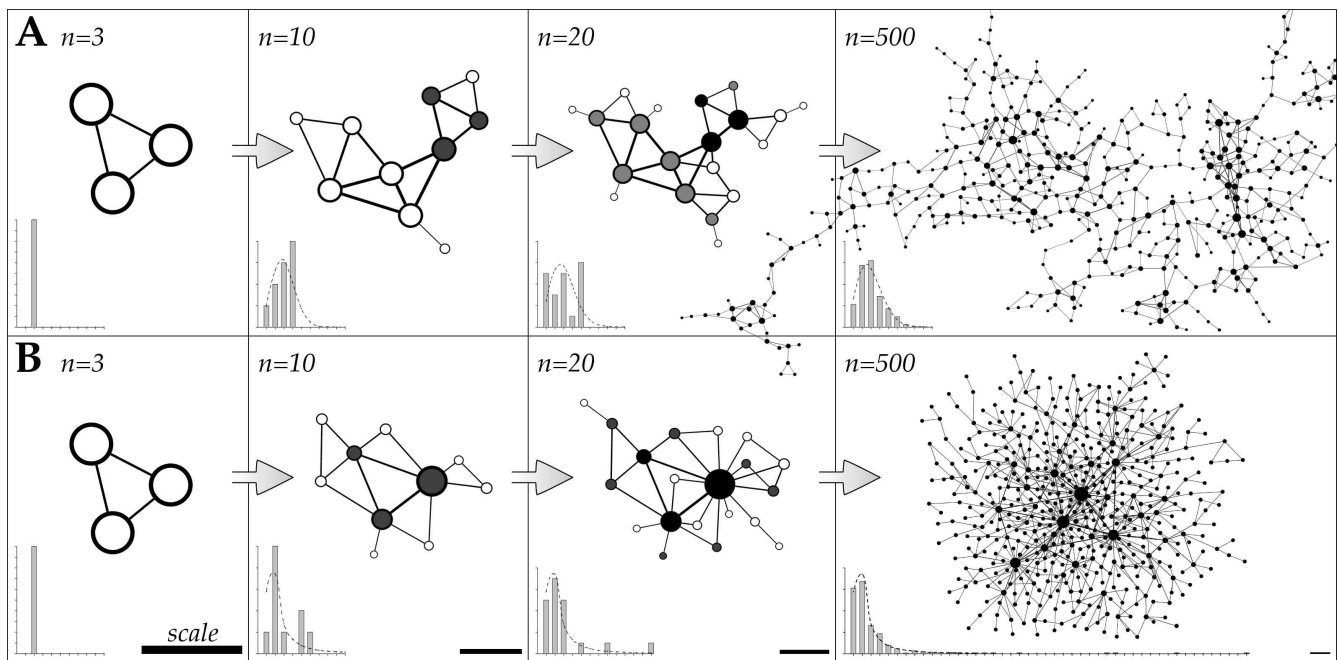


Figure 2. A = random network (Erdős-Rényi model); B = scale-free network (Barabási-Albert model). Networks consist of nodes (circles) and links (lines). In the story above, you can follow the growth of two kinds of networks from their identical humble beginnings as three interlinked nodes. In the so-called “random” network (A), nodes are linked randomly with no preference to any other nodes. In the “scale-free” network (B), nodes are added one at a time, linking preferentially with nodes already having many links. In fact the probability of linking with a node is linearly proportional to the number of links it already has. A well linked node is referred to as a hub.

By the time they are fully developed (fourth column), the two networks could hardly be more different. The random network clearly shows a Poisson distribution centered around three links per node. It sprawls out haphazardly without any clear hubs. Communication between the two ends might require scores of links. Such networks readily disintegrate upon removal of even a small number of randomly-chosen nodes. By contrast, the scale-free network exhibits a strong power-law distribution to the right of the peak at one and two links per node. The exponent in this particular network is about -2.6. Almost all networks so far measured in nature fall somewhere between -2.0 and -3.0: a magic range promoting strong hubs and hence rapid communication between all nodes. At the same time the nodes and the hubs can't be divided into two distinct classes, rather they form a continuum of sizes. Thus the network as a whole has no one “characteristic” scale; it is *scale-free*.

To describe scale-free networks as “robust” is an understatement; in fact they have no critical threshold for disintegration. Even should most of the nodes fail, chances are good that the remaining ones will remain connected. Having numerous small nodes and few, scattered hubs means it's mostly the nodes that are affected by random perturbation. What's more, no single hub is essential to network function. On the other hand, the loss of a few central hubs can cause the entire network to splinter into isolated clusters of nodes.

Biological systems based on scale-free networks exhibit a high degree of clustering, that is, the nodes tend to form local, tightly interlinked groups, or modules. These modules are themselves linked together in larger networks, which in turn link with other networks, and so on up. Cellular functions, for example, are likely to be carried out in a highly modular fashion. At the same time the cells themselves to some extent operate as individuals, as do the organs and organisms they comprise.

Scale-free networks have now been observed in all three domains of life – Eukarya, Bacteria, Archaea (A-L. Barabási & Z.N. Oltvai: 2004: *Nature Reviews/Genetics*: 5:101-114). They are in fact a more or less universal feature of natural systems. It now seems clear that the flexibility and robustness of scale-free networks – certainly including lichens – does not arise from a constant fine-tuning of the individual components. Instead it is inherent in the very nature of network topology itself: a law, so to speak, of nature.

Graphics by Jason Hollinger.

a consequence of evolutionary process than a precondition for it.

So far I've spoken about scale-free networks as though they could be represented on the page, as in Figure 2B. As far as their circuitry diagram is concerned, this is in fact true; but only because scale-free networks are, after all, *scale-free*, meaning that no one scale can be taken as representative of the network as a whole. Practically speaking, though, being scale-free also means that no matter how you look at its circuitry map, it's still got the same *formal* topology. This is true horizontally, across a single spatial scale; but it's also true vertically, at quite different spatial scales. Enlarge any one of the 500 nodes in Figure 2B to the size of the original network, and what you'll see is simply Figure 2B staring back at you. Or again, scale Figure 2B up or down as much as you like, from the molecule to the organism, and still what you get is Figure 2B.

What's hardest to grasp in all of this, at least for me, is that this scale-free network, this multi-dimensional *system of systems of systems*, is fully interlinked. Every node within it is capable, almost instantaneously, of communicating with every other node: both horizontally and vertically. It's the hubs, of course, that make this possible. Also, the modules make it possible (Figure 2). By their good work, even the most far-flung nodes are at most only five or six removes from one another.

EMERGENCE

Emergence is inherent in all biological systems and (since life itself is an emergent property of non-life) in at least some inanimate matter as well. It's a tricky concept, hard to think about, harder still to write about. As defined by systems theory, emergence is the elaboration of novelty in complex systems during the process of self-organization; or more briefly, as $1 + 1 \neq 2$. Of course there are other definitions, since emergence is a familiar concept in physics, mathematics, chemistry, sociology, and theology – each bringing its own unique perspective to bear.

Here of course my focus is on network theory, particularly scale-free networks. If it's true that scale-free networks are universal, then surely we ought to see evidence of emergence lurking about somewhere inside of them. I think we do: in the clustering of nodes. Though not shown in Figure 2 – which is only a circuitry map, after all – most nodes in a scale-free

network sooner or later cluster into modules, and the modules, in turn, eventually aggregate into subsystems and, finally, into namable systems. In total there are hundreds of systems in operation within any biological network at any one time.

What causes the nodes to cluster as they do, and then hierarchically, again and again? In living systems, it's obviously some sort of intersection with the genes; but beyond that – at a deeper level – nobody knows. Still here's something: while the underlying topology of scale-free networks is everywhere the same, yet the laws of the physical universe operate very differently at different spatial scales (Essay IV). Squirrels dash with ease up and down the trunks of trees. Houseflies stroll across the ceiling. Flatworms breathe deep without benefit of lungs or gills. Scale down to the size of a molecule and you've entered still another *very* different physical relation to the universe. Such seeming incommensurability takes on special significance when you consider how all biological networks are in vertical communication with themselves across a vast array of spatial scales.

I say emergence is what happens when tensions generated within these vertical conversations reach a critical level beyond which some functional unit within the conversation abruptly reconfigures. Phase transition is another way of looking at this reconfiguration from a lower to a higher level of order. Water into ice say, or, more profoundly, hydrogen and oxygen atoms into water. In this view, emergence is the outward manifestation of internal realignment. What results is a brand new system, some or all of the properties of which could not have been predicted ahead of the upgrade. To me it seems likely that emergence, far from being a biological anomaly, is in fact life's most ubiquitous outward property, popping up all over the place, manifest in the physicality of every organic molecule and so on up. That we happen not to see emergence this way is likely, in my view, to tell us more about human perception than about the underlying order of the universe.

LICHEN METACELL THEORY

Based on the preceding discussion, the multiple independent origins of the lichen lifestyle can now perhaps be regarded as an expected consequence of certain structural and emergent properties inherent in all naturally occurring networks.

The Metacell Theory of Lichens postulates that in all cases the lichen thallus dates from the first appearance of a cortex. Originally it will have provided a kind of "cell membrane" that through the creation of a biosphere-like "metacell" facilitated the evolution of complex relational systems among the fungal, algal, bacterial "organelles" within. It is specifically the underlying scale-free topology of these internal systems that taken together has conferred upon the lichen – as earlier upon the eukaryotic cell – a level of robustness far exceeding that of the bionts, and that in particular has stimulated efficiencies in the assimilation, transport, storage, conversion and reallocation of carbon. The lichen thallus can thus be seen as an emergent property of these efficiencies; it is in effect an autotrophic organism characterized by a level of internal homeostasis sufficient to promote, for each lichen species, a characteristic architecture, chemistry and outward form. Finally, Metacell Theory interprets the ecosystem-like properties of the lichen – retention of biont identity, reassembly at each generation, lack of an independent phylogeny – as a byproduct, first, of the presence of a fungal partner able to assimilate carbon externally, and second, of its evolution in terrestrial settings. By contrast, the eukaryotic cell surely owes its higher level of integration at least in part to its evolution in water.

SOME HYPOTHESES

Explanation and theory have much in common. They differ, however, insofar as explanation allows a certain understanding, but does not necessarily enable prediction, whereas theory by definition necessarily accomplishes both. The proper measure of the Lichen Metacell Theory is therefore to be found in its predictive value: in the number of testable hypotheses it shakes loose, so to speak, from the mangrove of possibility.

INDEPENDENT ORIGIN

Preamble: Metacell theory assumes that the cortex is itself an emergent property of a highly evolved fungal-algal relationship. Working backwards, it postulates that such a relationship would be unlikely to arise except within the context of some pre-existing cortex-like structure. Might this cortical function have been performed, at least in some cases, endolithically, that is, through prolonged existence beneath a semi-transparent mineral surface, e.g., schist? Derived endolithic lichens are well known to occur in Antarctica.

Hypothesis: It is unknown whether precorticate "protolichens" exist at the present time; but in any event they are to be looked for in the context of

exfoliating schistose rocks, especially in cool, humid localities not subject to prolonged snow cover. The single most salient hallmark of the protolichen lifestyle should be the elaboration of secondary chemistry (Essay x).

PRETHALLUS

Preamble: All lichens have arisen from corticate crustose forebears, the earliest of which are unlikely to have produced soredia or other specialized vegetative reproductive propagules. Hence even the first lichens – across all independent origins of the lichen lifestyle – must have had the capacity to resynthesize at each generation. This strongly suggests that the prethallus (Essay VII) is not a derived feature, but may in fact predate the lichen cortex – and hence strictly speaking the lichen itself. At the same time, it is possible that the prethallus is a highly conserved feature, owing to the exacting conditions of thallus initiation.

Hypothesis: In cases where the photopartner in the prethallus and the photopartner in the lichen thallus belong to different species, it is likely that the former has been associated with the lichen system much longer than the latter.

Preamble: During the early stages of thallus resynthesis, thallus initiation is necessarily delayed until such time as the requisite systems are fully activated to complex behaviour. It is within the prethallus that these systems come up to speed. The prethallus is thus to be viewed primarily as an "incubation chamber" for systems start-up. Provision of carbon to the newly germinated lichen fungus (as it awaits an appropriate photopartner) is of only secondary importance.

Hypothesis: The photopartner in the prethallus and the photopartner in the lichen thallus need not always belong to different species. In some cases they will be found to be identical.

CORTEX, AUTOTROPHISM

Preamble: All lichens across all independent origins of the lichen lifestyle have evolved from corticate precursors. Noncorticate lichens are necessarily derived from corticate precursors. Such lichens could never have evolved without first passing through a prolonged period of incubation within the "cell" created by the cortex.

Hypothesis: The absence of a cortex will always be a derived character.

Preamble: The cortex was an early emergent property of the evolving lichen, and thus provided the “incubation chamber” within which the bionts achieved network-wide autotrophism – the ability to establish, elaborate and reproduce solely from carbon assimilated within its own systems. Hence the cortex is far more than a protective cover.

Hypothesis: At least in meso- and macrolichens, the cortex will eventually be found to play a significant and perhaps dominant role in the elaboration of thallus morphology, e.g., by controlling differential gas exchange in different portions of the thallus.

THALLUS MORPHOLOGY

Preamble: The tremendous morphological diversity observed among the macrolichens is in no way an attribute of the lichen partners, rather it is entirely an emergent property of the lichen meta-network itself. This observation will be discussed at greater length in Essays IX and X.

Hypothesis: The phylogeny of the lichen bionts does not correlate with morphological variation at the level of the lichen species. Even certain taxa currently regarded as “subspecies” and “varieties” will eventually be found, by molecular means, to represent ecotypes, not genotypes. Of course many other subspecies and varieties warrant recognition as distinct species.

ROBUSTNESS, OBLIGATORY REASSEMBLY

Preamble: The lichen thallus is a ready symbol for durability. Nothing of the kind could be said of the organisms that make up the lichen thallus – least of all the fungus. The astonishing robustness of the lichen thallus is at least in part a byproduct of its underlying scale-free topology; see Figure 2.

Hypothesis: Stress-induced modification to a previously healthy lichen thallus is likely to appear only after a prolonged and repeated perturbation to the lichen system. Thus it is theoretically possible that two thalli virtually identical in outward appearance could differ greatly in physiological condition. If true, then this has obvious ramifications for transplant and other manipulative experiments conducted on the lichen thallus.

Preamble: The widespread requirement of the lichen thallus to reassemble at each generation, usually under less than optimum environmental conditions, points to the robustness of even the initial stages of thallus development. This assertion is further

supported by the observation that most lichens establish external to the supporting substrate, where they are more or less fully exposed to environmental fluctuation.

Hypothesis: It will eventually be shown that even early on in the process of lichen resynthesis / reassembly, the lichen bionts give up their species-specific characteristics – and hence also their individual identities – into the overarching lichen network.

LOSS OF LICHENIZATION

Preamble: It is now known that some lichens are capable, over evolutionary timescales, to delichenize, that is, to disband into their component parts. Such species effectively transition from a higher (lichenized) to a lower (unlichenized) level of organization, i.e., in response to the acquisition and relinquishing of scale-free systems. Only lichens in which the internal operating systems have an especially low level of complexity are likely to cross the phase transition between the lichenized and the unlichenized state.

Hypothesis: Loss of lichenization will be found to occur exclusively in crustose lichens, and to be especially characteristic of independently evolved lichen groups in which meso- and macrolichens are either absent or in low diversity.

FALSIFICATION

The final test of any theory is that it should be capable of invalidation. For the Lichen Metacell Theory, this poses a slight difficulty, in that neither of its two main conceptual cornerstones – network theory and emergence – has yet been taken up by mainstream lichenology. Even so, the Lichen Metacell Theory does offer at least two obvious openings for falsification: one involving the prethallus, and the other the relation of thallus morphology to lichen biont phylogeny.

First the prethallus. The theory predicts that the prethallus will be found to function in much the same way as the computer BIOS during systems start-up, that is, it provides a platform on which the computer’s functions and programs can be initiated. Should my assertions concerning this start-up function of the prethallus prove invalid, then the fabric of the Lichen Metacell Theory will have received a major tear.

Now thallus morphology. Here the theory predicts that biont phylogeny on the one hand and within-species morphological variation, on the other hand, are

unlikely to be correlated. This concept appears to be counterintuitive to many lichenologists, presumably on analogy with the considerable role of genetics on plant and animal morphology. Testing it could therefore prove particularly helpful – both with regard to the Lichen Metacell Theory in particular, and as concerns our understanding of thallus morphology in general. All such studies known to me to date appear to support the theory, though more work is clearly needed.

Metacell Theory aside, my main objective in this essay has been to import into lichenology – by which I mean the study of *whole* lichens – an approach at once out of date and, who can say, possibly up and coming. What's attractive about network thinking is that networks occupy a kind of middle ground between the

atomistic impulses of reductionism and the sometimes empty promise of holism – including, by the way, computer generated ordination. Like reductionism, network thinking invites a focus on the parts of things. But at the same time it requires that the parts be referred to the whole – the systems to the network – rather than the other way around. In my next essay, I'll have much more to say on this topic as applied to lichens. For now, let me leave you with nine tenets from the writings of Gregory Bateson (1904-1980) – apparently the only modern thinker seriously to tackle the logical relationship of network structure to network function. His tenets invite many fascinating thought experiments around complex networks of every kind, lichens among them. "Do come in," they seem to say.

Tenet 1: A biological system perceived at any one level can be thought of as an emergent property of systems or systems of systems (modules) interacting at one or more levels below.

Tenet 2: All enduring biological systems – DNA, organelles, cells, organs, organisms, ecosystems, Gaia – possess the ability to self-correct.

Tenet 3: Self-correction within biological systems operates at the level of hierarchically organized subsystems via the perception of "difference" during the completion of feedback circuits. It thus requires a continual exchange of information, both horizontally across subsystems, and vertically from one hierarchic level to the level immediately above or below.

Tenet 4: Feedback circuits tend either to minimize error (negative feedback) or else to accentuate it (positive feedback). Negative feedback permits biological systems to absorb small external perturbations without disruption to the system as a whole.

Tenet 5: Positive feedback circuits will be permanently integrated into biological systems only to the extent that the affected subsystem default settings – also termed "bias" – are susceptible of readjustment. In the absence of adaptive change, the system may lose the ability to self-correct.

Tenet 6: When biological systems or subsystems permanently lose the ability to self-correct, they will spiral into terminal, but always systematic distortions.

Tenet 7: Flexibility within a biological system or subsystem can be defined as unused potential for change. It is conferred in proportion as it operates near the centers of their range of tolerance. Operation near the limits of tolerance introduces inflexibility into the system.

Tenet 8: Unused potentiality within a biological system or subsystem often permits expansion into the available areas of unused freedom, with corresponding loss of flexibility. Thus healthy systems over time tend to alternate between periods of flexibility and periods of inflexibility.

Tenet 9: Biological systems are to some extent sensitively dependent on initial conditions, such that small variations in input can promote large discrepancies in outcome. The magnitude of such discrepancies will be dependent on bias amplitude in each of the successively affected subsystems.

Figure 3. Nine tenets of cybernetics, with special reference to systems function within the thalli of macrolichens. Adapted in part from *Steps to an Ecology of Mind*, by Gregory Bateson. For an example of how these tenets might intersect with real lichen systems, see Essay VI in this series.