1

Self-integration – an emerging concept from the fungal mycelium

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Introduction

For so long neglected in the development and promulgation of evolutionary theory, there are increasing signs that mycelial fungi can bring new insights into the origins of phenotypic diversity and change. They challenge some of our most fundamental assumptions about natural selection and its significance relative to other processes in determining the direction of evolutionary pathways. This is because of the way mycelia are physically organized as versatile systems of interconnected tubes that can span heterogeneous environments in which energy is often in very variable supply (Rayner 1994; Rayner, Griffith & Ainsworth, 1995*a*).

Current models of evolutionary change effectively treat the boundaries of living systems and their components as fixed (that is, determinate). Consequently, the dynamic processes underlying change are assumed to be driven by purely external forces acting on discrete objects – genes and individuals (see Dawkins, 1995). However, such discretist models of evolutionary and ecological dynamics are potentially very misleading because all known life forms, from single cells to communities, are dynamic systems which assimilate supplies of free energy from their surroundings and distribute this energy into growth, development, reproduction and movement. They achieve this by possessing boundaries through which they regulate energy exchange with their surroundings and other life forms (Rayner, 1997*a*). For life forms to thrive and survive as energy supplies wax and wane, these boundaries have to be capable of enhancing gains through the proliferation of assimilative free surface in energy-rich environments whilst minimizing losses by various means of containment in inhospitable environments. This requires the configuration and properties of boundaries to change according to circumstances.

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More information

Living system boundaries cannot therefore be absolutely fixed any more than they can be absolutely sealed: rather they are dynamic, reactive interfaces, forever in some degree of flux. Their properties both define and are defined by the properties of the interactive arenas – the 'dynamic contexts' – incorporated by living systems. (Please note that in this sense 'context' does not equate with external environment as such, but is rather the 'domain', 'territory' or 'field' occupied by and including a life form as it develops through space and time.) Many of these properties derive from materials or energy sources – for example, water, air, minerals and light – that are not encoded in DNA, and are overlooked in much evolutionary theory, but are nevertheless salient in moulding the dynamic interplay between genetic information and environment into diverse phenotypic forms and behaviours. The dynamic boundaries of living systems therefore define both the sites and mode of action of natural selection as an interactive, channelling process rather than a mechanical sifting of particle-like units. They enable living systems to respond to the environmental heterogeneity that these systems both interact with and help to generate.

This chapter aims to show how the interconnectedness and versatility of mycelial organization uphold a 'systemic' evolutionary approach which explains phenotypic diversity in terms of how the properties of dynamic contextual boundaries regulate processes of input, throughput and output of energy. Special emphasis will be given to the way mycelia epitomize the integrational processes of boundary-sealing, boundary-redistribution and boundary-fusion. These much neglected processes counteract the tendency for living systems to subdivide into discrete, competitive, energy-dissipating units.

Order, organization and chaos – the mycelial example

Recent decades have witnessed significant developments in the way that pattern-generating processes in dynamic physical systems can be understood and modelled mathematically. These developments are encompassed within an array of interrelated concepts, variously described as non-linearity, chaos, complexity, fractal geometry and self-organization. Using fungal mycelia for cross-reference, we will try here to clarify the biological relevance of these developments. We hope to show how the concepts extend beyond rather than negate discretist paradigms, and so open up new prospects for future understanding.

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'Self-differentiation' – the route to 'incoherence'

Many of the developments just referred to arise from consideration of the effects of two kinds of feedback and their counteraction. Positive feedback – autocatalysis – arises from the ability of a system to amplify itself using energy input from its local environment. This ability generates an expansive drive which, if unconstrained, causes the system to increase exponentially. Negative feedback damps down expansive drive by directly or indirectly increasing resistance or dissipation as input increases.

The counteraction between positive and negative feedback causes systems to be non-linear (non-additive) and to become unstable if the rate of input exceeds a critical threshold or 'throughput capacity'. Below this threshold, the counteraction causes a smooth build-up to a dynamic equilibrium at which there is no net increase in the system's expansion: the system then remains, in effect, self-contained. Above this threshold, the system becomes 'forced' and hence prone to subdivide, by means of a series of bifurcations, into increasing numbers of subdomains or states. These subdomains may be manifest as increasingly complex, but nonetheless recurrent and predictable, oscillations, countercurrents or branches. Above a yet higher threshold, the subdivisions cease to occur recurrently. Instead, the system traverses what approaches an infinite variety of states in a manner which is apparently erratic and extremely sensitive to initial conditions, and therefore unpredictable in the long term. This is deterministic chaos.

An implicit feature of physical systems that exhibit non-linear dynamics is the presence of one or more dynamic boundaries. The very term 'feedback' implies a reactive interface that mediates this influence. Without a boundary, whether of attraction or constraint, that allows assimilation but prevents instantaneous dispersion, there can be no autocatalysis and no containment. The fact that the importance of dynamic boundaries is often overlooked, has led consciously or unconsciously to discretist interpretations of non-linear systems. These interpretations arise because attention is focused on the behaviour of individual components of the systems rather than the boundaries which shape and are shaped by these behaviours. An example occurs in what has been termed 'self-organization theory' and its attendant metaphor of 'order out of chaos' (Prigogine & Stengers, 1984). The most generally accepted idea of self-organization is that it involves the production of potentially complex patterns or structures through the operation of simple calculational

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procedures (algorithms) in a many-bodied system. Since the algorithms do not themselves directly encode the patterns or structures, generation of the latter is described as an 'emergent property' of the system (see Bonabeau *et al.*, 1997).

For self-organization to occur, it has been considered necessary for the systems to be thermodynamically open and far from equilibrium, so that they can be sustained by high rates of input and dissipation of energy. Consequently, the emergent structures or patterns they produce are described as 'dissipative', maximizing the conversion of free energy input to entropy (Prigogine & Stengers, 1984). Since emergence of dissipative structures occurs in what appears to be a previously patternless or structureless domain, it is assumed to originate from chaos or even randomness. Examples commonly used to illustrate this idea include 'random' mixtures of autocatalytic ('activator') and constraining ('inhibitor') chemicals, and 'random' arrays of social organisms (for example, slime mould amoebae, ants). These systems generate annular and spiral patterns if suitably prompted by local perturbations (e.g. Goodwin, 1994).

The assumption of a chaotic or random origin for self-organizing patterns may, however, be inappropriate. In fact, it is thought more apt to describe chaos as an extreme form of order which emerges as a consequence of high rates of input of free energy into an initially coherent (self-contained) system (Rayner, 1997*b*). Here, it is important to understand what is implied systemically by coherence, randomness, homogeneity and heterogeneity, and how these terms relate to concepts of order, organization, chaos and entropy. The systemic application of all these terms and concepts depends on the way that systems both define and are defined by their dynamic boundaries, and so differs in some important respects from conventional analytical usage. To begin with, it is vital to realize that randomness is the converse of homogeneity. This fact is often overlooked because for purposes of calculation, random assemblies are assumed analytically to be sets of independent (discrete) data points whose density can be treated on average as homogeneous – the same in different samples – provided that sufficient numbers are accounted for. When sample sizes are small, however, random distributions exhibit extreme heterogeneity. Furthermore, although the distribution of data between set intervals does not imply that these data are interdependent and so non-random from an analytical perspective, in which boundaries are absolute, the same cannot be said from a systemic viewpoint. What randomness,

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that is, total 'incoherence', implies systemically is the lack of a containing boundary, so the components of a system can be anywhere, anytime and incapable of concerted action. Such absolute disorder is equatable with entropy. By contrast, homogeneity implies being the same everywhere, at all scales, that is, absolute order. Whilst a fully random system is incapable of concerted action, a fully coherent system is incapable of change. Dynamic systems therefore operate between these extremes – that is, with increasing degrees of freedom from relative coherence to relative incoherence. The boundaries of these systems represent sites of relative order which, when in disordered surroundings, tend to lose coherence.

These considerations focus attention, at any particular scale of reference, on the boundary of a system as the expression of its relative order and dynamic state. The effect of introducing free energy into a dynamically bounded system is, directly or indirectly, to cause an expansion of the system's boundary. If the rate of input to the system is below the 'throughput capacity' defined by the resistances imposed by the system's boundary (see above), the boundary expands smoothly, retaining its symmetry and minimizing its surface area and consequent dissipation to its surroundings. A germinating fungal spore exhibiting initial spherical growth exemplifies this. However, if the rate of input exceeds the throughput capacity, the system begins to lose coherence by 'breaking its symmetry' and generating emergent structure. It first polarizes and then subdivides to produce more and more dissipative (and assimilative) free surface – as epitomized by the emergence and subsequent branching of a germ tube (see Fig. 1.1). All this emergent, increasingly complex structure, the most extreme form of which is chaotically distributed, represents proliferated boundary – and hence as presently defined, increased order. However, the origin of this order is not disorder, but a highly integrated, coherent initial state. We view this initial state as more highly organized.

Like the packaging that is used to enclose all kinds of commodities, the order invested in boundaries is energetically costly, for two reasons. Firstly, a high rate of energy input is required to cause systems to become unstable and break symmetry. Secondly, proliferating boundaries present an increased dissipative free surface which renders the system more susceptible to random environmental influences and counteracts the input of free energy, so that more erratic but less labile structures emerge.

Given that boundary-proliferation can only be sustained by continuing energy input, an important question is what happens to dissipative struc-

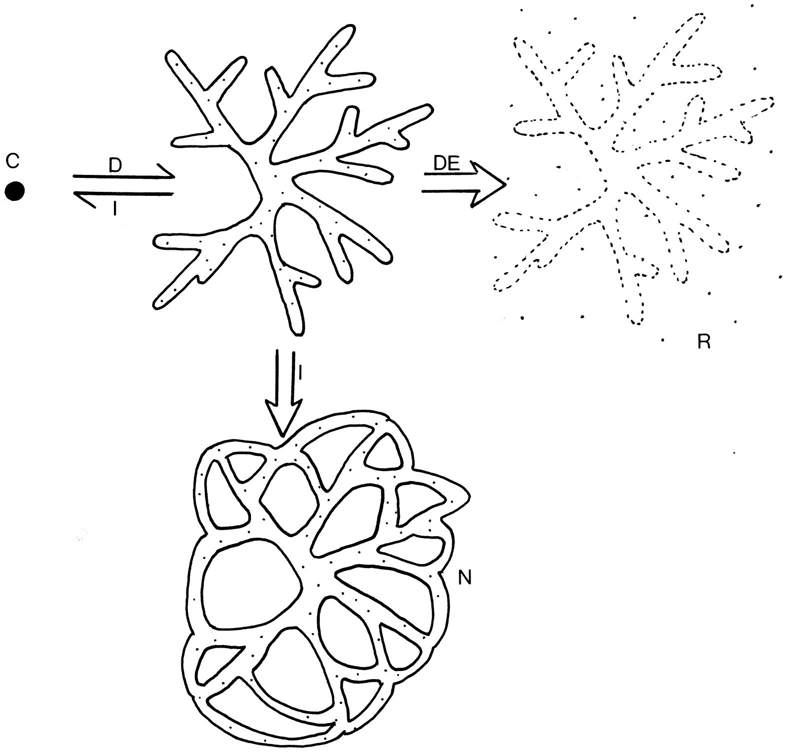

Fig. 1.1. The role of dynamic boundaries in the production of dissipative structure ('order') and coherent 'organization'. Assimilation of free energy into a coherent initial state (C) results in the proliferation and subdivision of boundary (dissipative structure) by 'self-differentiation' (D). Irreversible decay or degeneration (DE) of this structure in the absence of energy replenishment leads to random disorder (R). 'Self-integration' of this structure by boundary-fusion, boundary-sealing and boundary-redistribution minimizes its dissipative free surface, enabling it to reconfigure into coherent initial states or persistent networks (N). (From Rayner, 1997*b*.)

tures when external supplies of free energy are restricted? A related, fundamentally important, question is what is the origin of the initial coherent state from which dissipative structures emerge in energetically unrestricted environments? Essentially, if external energy supplies are withdrawn from a dissipatively structured system, the long-term survival of the system (or part of it) rests on a stark alternative (Fig. 1.1). The system may continue to dissipate, or it undergoes processes that minimize exposure of free surface. The first option leads to dissolution, an irreversible decay into an entropic state. The second option results in a reduction of order and an increase in organization. The sustainability and persistence of life forms in energetically variable environments depends on this second option, which involves three dissipation-minimizing processes: boundary-fusion, boundary-sealing and boundary-redistribution. We term this second option 'self-integration', as distinct from the emergence of dissipative structures, which we term 'self-differentiation'.

'Self-integration' – retaining and regaining coherence

Since dissipative free surface is energetically costly, any process that minimizes this surface is energy-saving and even energy-yielding. The three self-integrational processes depicted in Figs. 1.1 and 1.2 all have these effects. Operating separately or in concert, these processes enable living systems to conserve, explore for and recycle resources by means of fundamentally simple adjustments in their boundary properties that accord with local circumstances. They are well illustrated by fungal mycelia.

Boundary-fusion both lessens the amount of dissipative surface and releases energy that was previously contained in this surface through its dissolution. It is most obvious amongst mycelial fungi in the process of anastomosis. Anastomosis can occur both between individual hyphae, and between hyphal aggregates such as mycelial cords (Thompson & Rayner, 1983; Dowson, Rayner & Boddy, 1988*a*). It converts a dendritic branching system with resistances in series, to a more coherent network with resistances at least partially in parallel. It thereby makes the system more retentive and less prone to proliferate branches. At the same time it enables the system to amplify its organizational scale, through enhanced delivery to sites of emergence of distributive or reproductive structures, for example rhizomorphs and fruit bodies, on its boundary.

Boundary-sealing involves various ways of reducing permeability and hence increasing the 'insulation' of a system. Sealing a fixed boundary results in the production of survival structures, as in various kinds of constitutively dormant spores, sclerotia and pseudosclerotia by fungal mycelia. Sealing a deformable boundary results in the emergence of distributive structures that serve reproductive or explorative/migratory functions. Since the sites of input to these structures are distal to their sites of proliferation, their branching pattern will be distributary- or fountain-like, contrasting with the tributary-like branching pattern of

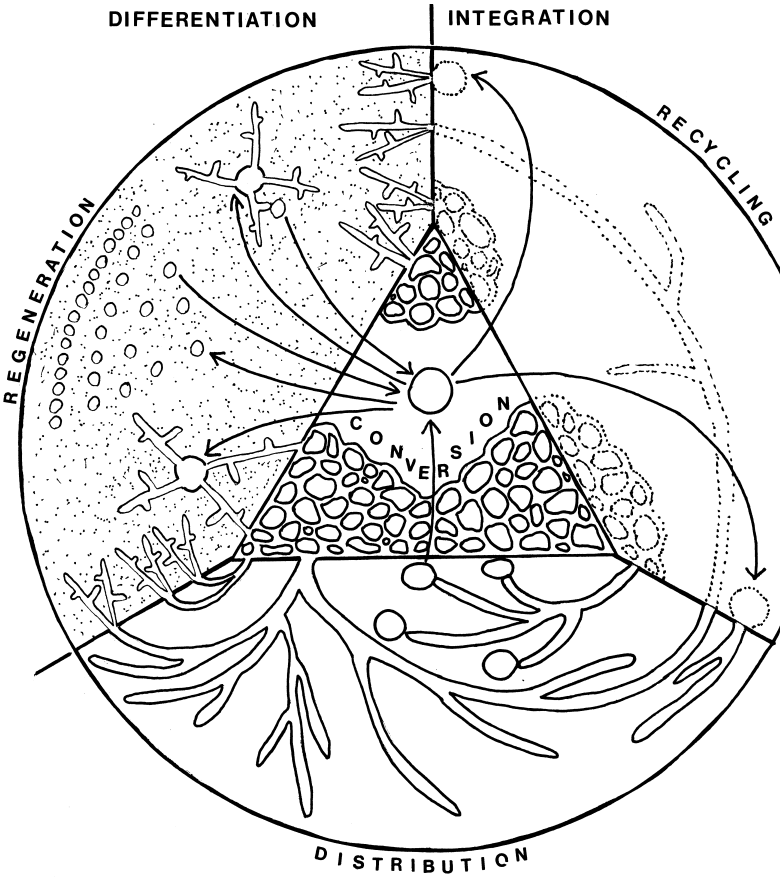

Fig. 1.2. The interplay between self-integration and self-differentiation to produce distinctive organizational states in resource-rich (stippled) and resource-restricted environments. The interplay enables energy to be assimilated (allowing regeneration of boundaries), conserved (by conversion of boundaries into impermeable form), explored for (through internal distribution of energy sources) or recycled (via redistribution of boundaries) according to circumstances. Fine lines indicate permeable contextual boundaries, bold lines impermeable boundaries and dotted lines degenerating boundaries. (From Rayner, 1997*a*.)

assimilative structures. Moreover, sealing the lateral boundary of a tube or channel whilst maintaining its apical boundary in a deformable, responsive state enables a much more focused response to a directional stimulus – much like blinkering a horse! This correlates with the observation that migratory structures in fungal mycelia are more prone to exhibit tropic responses than assimilative structures (Rayner & Boddy, 1988).

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Such responses greatly enhance the energetic efficiency of any distributive system.

Boundary-redistribution involves the transfer of resources from degenerative to generative sites. In mycelia, it is evident in various examples of ‘autolysis’ and ‘self-parasitism’ (e.g. Rayner, 1977*a*; Rayner & Boddy, 1988).

Boundary properties and life history patterns

From a discretist standpoint, life cycles are commonly thought of as reproductive cycles – the means by which genes make more of themselves. The ability of a particular genotype, given a particular set of niche parameters, to make use of these cycles in delivering as many as possible of its own offspring into succeeding generations defines its adaptive fitness.

Even from this standpoint, however, it has long been appreciated that reproduction is subject to biotic or abiotic environmental constraints. Recognition of the effects of these constraints on population dynamics has given rise to classical theories of *r*- and K-selection, based on the reproductive rate (r) and equilibrium or carrying capacity ($K = 1 - 1/r$) terms of the non-linear logistic equation (see, for example, Andrews, 1992). Correspondingly, high rates of reproduction are associated with *r*-selection in unrestrictive environments, whilst lower rates of reproduction occur as a result of K-selection in restrictive environments.

Whilst *r*–K-selection theories explain why, in an adaptational sense, reproductive rates in unrestrictive and restrictive environments differ, how, in an organizational sense, life forms and life cycle stages are attuned physically to their surroundings has attracted less attention. Consequently, important insights into the origins and versatility of phenotypic form in response to inconstant environmental circumstances may have been missed.

From the systemic perspective illustrated in Figs. 1.1 and 1.2, far from defining the beginnings and endings of discontinuous generations of discrete individuals within finite niches, life cycles represent a means of generating and maintaining a continuous dynamic context in changeable surroundings. This is the answer to the riddle of the chicken and the egg (or the spore and the sporophore): neither came first – rather they represent distinctive boundary configurations of the same dynamic system!

The continuity of context that is ensured by life cycles is an expression of the fundamental indeterminacy of living systems, that is, their capacity for ongoing production and reconfiguration of boundaries, and obscures the discretist distinction between growth and reproduction. Examples of this indeterminacy can be found from molecular to social scales of biological organization, with boundaries being defined anywhere from intracellular to extra-organism locations (Rayner, 1997*a*). Correspondingly, the dynamic contexts of motile organisms – such as many animals – are not defined by where the body boundaries of these organisms are at a particular instant. Rather, they are defined topographically by the trajectories that these organisms map out as they use their powers of locomotion to follow and create paths of least resistance, and regionally by the territories within which the trajectories are confined. By contrast, the topographical and regional contexts of organisms, such as many plants and mycelial fungi, that grow rather than move bodily from place to place, coincide directly with the proliferation and overall extent of their body boundaries.

The concept that life forms inhabit and generate indeterminate contexts introduces the need to develop a more dynamic view of niches not as fixed but as fluid and variably interconnected space–time–energy domains. This in turn has important implications for the way *r*–K-selection theory can be used to understand the relationship between life form and life cycle in the generation of exploitative and/or persistent organizations.

When supplies of readily accessible resources are temporarily plentiful – that is, under *r*-selective conditions – following destructive or enrichment disturbance of natural habitats, the self-differentiation or regenerative processes depicted in Figs. 1.1 and 1.2 are promoted. These processes result in rapid proliferation, associated with high metabolic rates, but produce highly dissipative structures that are only sustainable as long as there is continual enrichment. In the absence of replenishment, conditions in any habitat are prone to become more restrictive – that is, to change from *r*- to *K*-selective – due to increasing competition or abiotic stress (including resource depletion). This necessitates self-integration into a more coherent organization if total dissipation is to be avoided.

Systems in which boundary-redistribution into relatively discrete dispersal and survival units predominates are characteristically strongly exploitative and somatically non-persistent – for example, many mitosporic (asexual) fungi. By contrast, boundary-sealing, accompanied by fusion and redistribution, produces a more retentive, coherent organization that allows resources to be conserved or distributed within a protective or explorative context, for example within sclerotia or rhizomorphs.