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ORIGINAL PAPER

Relational Biology of Symbiosis

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Abstract I formulate in relational terms the ubiquitous biological interaction of symbiosis. I explicate the topology of the different modes of relational interactions of (M, R)-networks, the entailment diagrams that model the host and the symbiont. These modes all have biological realizations as various categories of symbiotic relationships, ranging from mutualism to parasitism to infection.

Keywords Relational biology · Symbiosis · (M, R)-systems · Infection · Interaction

1 Definitions and Examples

Symbiosis (Greek *σύν* with, *βίωσις* living; literally 'living together') is the close and often long-term biological interaction between different species, thence called *symbionts*.

A symbiotic relationship between individuals of two different species may be categorized by effect as mutualistic, commensal, or parasitic: *mutualism* is a relationship where both derive a benefit; *commensalism* is a relationship where one benefits and the other is neither significantly harmed nor helped; and *parasitism* is a relationship in which one benefits while the other is harmed. The relationship is often not symmetric, even in mutualism. It is usually obvious that one of the two symbionts is the *host*, in the sense that it harbours the other, and provides substrate, shelter, or nourishment. With the usage of 'host', 'symbiont' whence refers to the 'non-host partner' in the symbiosis. Thus in context one may write, for example,

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"two symbionts" in a symbiotic relationship, as well as the conjunction "host–symbiont" (especially "host–parasite").

A stereotypical example of mutualism is the relationship between the clownfish and the sea anemone. The clownfish feeds on small invertebrates which may otherwise harm the sea anemone; excrement from the clownfish provides nutrients to the sea anemone; and the territorial clownfish fends off anemone-eating predators. Reciprocally, in addition to providing ambient food for the clownfish, the sea anemone also offers a protective dwelling armed with its stinging tentacles, the clownfish being immune to the nematocysts and potent toxins of its host. Barnacles are sedentary crustaceans that as habitat attach themselves permanently to a substrate, including another organism (e.g., shellfish, whale), with the commensalism leaving the substrate organism unharmed. Almost all organisms have internal and external parasites; examples: louse, hookworm, dodder, mould. *Infection* is a detrimental form of parasitism, in which the host is colonized by a foreign (usually microscopic) species.

Symbiosis may alternatively be categorized by topology. *Endosymbiosis* is a symbiotic relationship in which one symbiont lives *within* the tissues of the other. An example is the nitrogen-fixing bacteria that live in nodules on legume roots. Lichen is an endosymbiotic union between a fungus and a photosynthetic alga. The endosymbiotic theory of cell evolution—that certain organelles (such as mitochondria and chloroplasts) of eukaryotic cells are originally separate prokaryotic organisms taken inside as endosymbionts—has been generally accepted. Contrastively, *ectosymbiosis* is a symbiotic relationship in which the symbiont lives on the *surface* (which includes the outer body surface as well as the inner surface such as that of the digestive tract or the ducts of exocrine glands) of the host. Many herbivores, for example, have gut fauna that help them digest plant matter.

Symbiosis may also be categorized by necessity as either obligate or facultative: an *obligate* relationship is necessary for the survival of at least one of the organisms involved, while a *facultative* relationship may be beneficial but not essential for survival of the organisms. An extreme example of obligate mutualism is between the tube worms and symbiotic bacteria that live at hydrothermal vents and cold seeps: the worm has no digestive tract and is completely dependent on its internal symbionts for nutrition. Most myrmecophilous associations between ants and a variety of other organisms (plants, arthropods, and fungi) are facultative mutualisms.

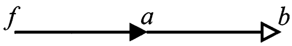
Viruses are obligate intracellular parasites—viral genomes only function after they replicate in a cell. Viruses are not alive: they are collections of chemicals and by themselves do not reproduce; a cellular host is needed. While symbiosis (hence its subcategory parasitism) almost always concerns *organisms* (i.e., living systems), the definition in general terms of "interacting *species*" allows the inclusion of viruses.

Remember Humpty Dumpty: this broad definition of symbiosis that I am using—simply as "the living together of closely interacting species"—is, however, not universal. Its usage is often more narrow, and describes only those relationships from which both organisms benefit, i.e., synonymous with mutualism. See Wilkinson (2001) for a succinct discussion on this very topic.

2 Relational Diagram

This paper is a sequel to a continuing sequence of papers on relational biology published in this journal: Louie (2006), Louie and Kercel (2007), and Louie (2008). I shall draw upon notation and results from these earlier papers. For a more detailed exposition, the enthused reader may find a comprehensive introduction on relational biology in general, and on *relational diagram in graph-theoretic form* in particular, in my book *More Than Life Itself* (Louie 2009).

Let $f \in H(A,B)$ be a mapping from set A to set B (i.e., $f : A \to B$). When f is represented in the element-chasing version $f : a \mapsto b$ (where $a \in A$ and $b \in B$), its relational diagram may be drawn as a network with three *nodes* and two *directed edges*, i.e., a directed graph (or *digraph* for short):



(1)

The *hollow-headed arrow* denotes the *flow* from input (material cause) $a \in A$ to output (final cause) $b \in B$, whence the final cause of the mapping may be identified also as the hollow-headed arrow that terminates on the output

(2)

The *solid-headed arrow* denotes the induction of or constraint upon the flow by the *processor* (efficient cause) *f*, whence the efficient cause of the mapping may be identified also as the solid-headed arrow that originates from the processor

(3)

The formal cause of the mapping may be identified as the *ordered pair* ⟨processor, flow⟩ of the two kinds of arrows:

(4)

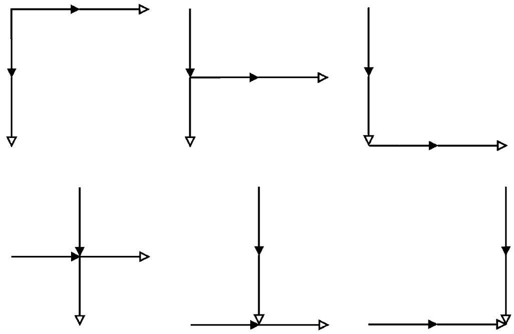
The processor and output relationship may be characterized '*f entails b*', denoted by

$$f \vdash b \tag{5}$$

where $\vdash$ is called the *entailment symbol*. A relational diagram is also called an *entailment network*.

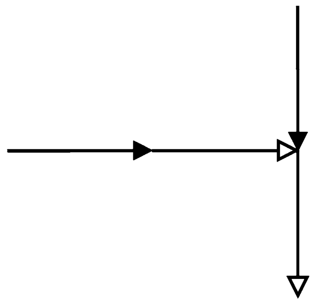
3 Relational Interactions as Compositions

The relational diagrams of mappings may *interact*: two mappings, with the appropriate domains and codomains, may be connected at different common nodes. Since there are three nodes in the relational diagram of each mapping, on account of symmetry there are six possible modes of nodal connection:



(6)

As a first example, consider

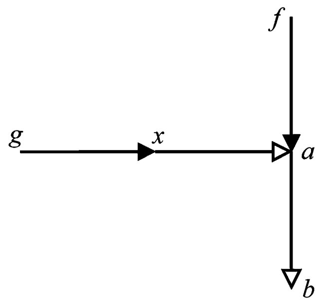


(7)

Such a relational interaction arises when one has two mappings $f \in H(A, B)$ and $g \in H(X, A)$, whence *the codomain of g is the domain of f*. Thus

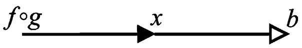
$$X \xrightarrow{g} A \xrightarrow{f} B\,. \tag{8}$$

Let the element chases be $f : a \mapsto b$ (thus $f \vdash b$) and $g : x \mapsto a$ (thus $g \vdash a$), whence *the final cause of g is the material cause of f*. The relational diagrams of the two mappings connect at the common node a as



(9)

This *sequential composition* of relational diagrams represents the composite mapping $f \circ g \in H(X, B)$ with $f \circ g : x \mapsto b$, and has the abbreviated relational diagram



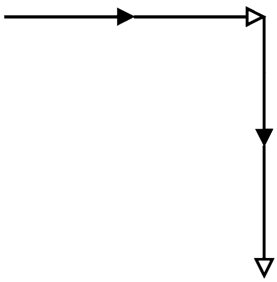
(10)

whence the corresponding entailment diagram is

$$f \circ g \vdash b \tag{11}$$

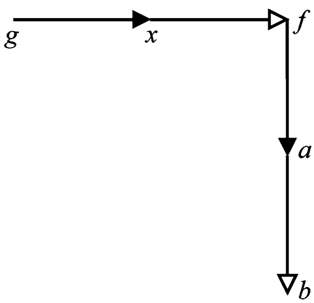
($f \circ g$ *entails* b). Note that in these diagrams (10) and (11) for the single efficient cause $f \circ g$, both efficient causes f and g, as well as the (final) final cause b, are accounted for.

Next, consider the relational interaction



(12)

This happens when one has two mappings $f \in H(A, B)$ and $g \in H(X, H(A, B))$, whence *the codomain of g contains f*. Because of this 'containment', the mapping g may be considered to occupy a higher 'hierarchical level' than the mapping f. Let the element chases be $f : a \mapsto b$ and $g : x \mapsto f$, whence *the final cause of g is the efficient cause of f*. Then one has the *hierarchical composition* of relational diagrams



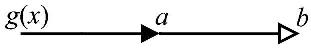
(13)

with the corresponding composition of entailment diagrams

$$g \vdash f \vdash b. \tag{14}$$

A comparison of (11) and (14) reinforces the graphical differences of diagrams (7) and (12), and shows that sequential composition and hierarchical composition are different in kind: they are *formally* different.

While the diagram (13) *may* contract into something similar in form to (10), namely

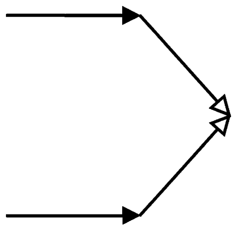


(15)

in this abbreviated form the entailed efficient cause *f* becomes ‘hidden’. Since the accounting (and tracking) of *all* efficient causes in an entailment system is crucial in our synthesis in relational biology, one needs to preserve every solid-headed arrow. So there will not be any abbreviation of hierarchical compositions.

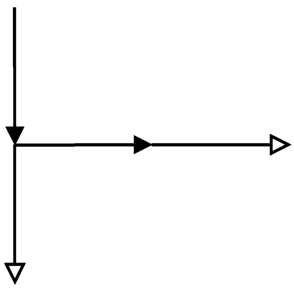
4 Other Modes of Relational Interaction

For an interaction to be a composition, the hollow-headed arrow of one mapping must terminate on a node of the other mapping: the first mapping must *entail* something in the second. So, the only remaining *possibility* of composition is the interaction


(16)

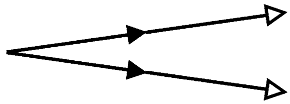
But this configuration simply shows two mappings with a common codomain, and the mappings do not compose. The two interactions (7) and (12) are, therefore, the only *compositions* of two mappings.

The connection


(17)

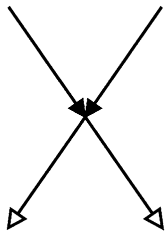
shows that the *domain* of one mapping consists of mappings; i.e., the material cause of one is the efficient cause of the other.

The final two connections



(18)

and

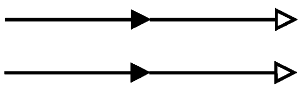


(19)

were disallowed in Louie (2009). These restrictions turned out to be unnecessary (and are hereby lifted).

Diagram (18) shows the efficient causes of two mappings coincide, which implies that so must their domains and codomains (since a mapping uniquely determines its domain and codomain). This apparent degeneracy need not, however, be abandoned. Indeed, the geometry of (18), with two solid-headed arrows originating from the same vertex, can be useful in entailment networks when one wants to distinguish two element-chasing paths $f : a_1 \mapsto b_1$ and $f : a_2 \mapsto b_2$.

The 'crossed-path' connection (19) may cause confusion, since it is not immediately clear which solid-headed arrow is paired with which hollow-headed arrow. But the resolution required is simply that one must be careful in tracing paths. When circumstances warrant, the crossed-path may be unfolded into two disjoint paths thus

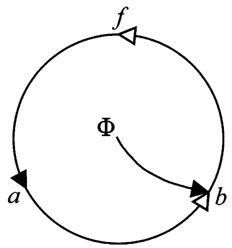


(20)

Note that the interactions (17) and (18) may also be similarly resolved without loss of entailment structure into two disjoint paths (20).

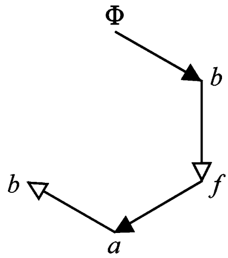
5 Multiple Connections and Unfolding

It is possible that the relational interaction of two mappings consists of connections at more than one common node. The relational diagram may be resolved by unfolding into single connections for analysis. For example, the relational diagram



(21)

may be unfolded into the hierarchical composition

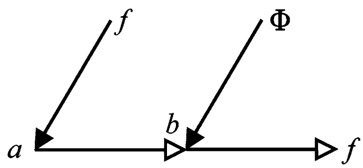


(22)

while preserving the entailment

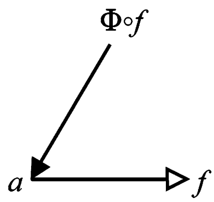
$$\Phi \vdash f \vdash b. \tag{23}$$

Note that the phrase *while preserving the entailment* is important here. This is because diagram (21) may also be unfolded into the sequential composition



(24)

which abbreviates to the relational diagram



(25)

whence the corresponding entailment diagram is

$$\Phi \circ f \vdash f. \tag{26}$$

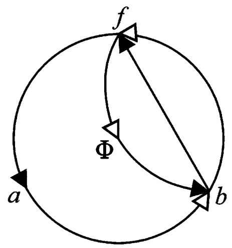
Comparing (23) with (26), one sees that the latter loses one entailment in the process. Thus one must be careful in a resolution analysis to preserve hierarchical compositions.

6 (M, R)-Network

Recall that (M, R)-systems are a class of relational models that define organisms. The reader is referred to our earlier papers and Louie (2009) for a review. In particular, I define an *(M, R)-network* as an entailment network of a finite collection of metabolism and repair components, and an *(M, R)-system* as an (M, R)-network that is closed to efficient causation. Recall that a natural system is *closed to efficient causation* if its every efficient cause is entailed within the system.

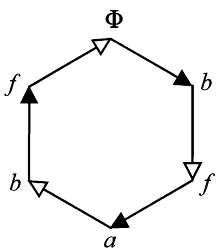
In terms of relational diagrams, an (M, R)-network is an entailment network of ⟨solid-headed arrow, hollow-headed arrow⟩ ordered pairs in which there is at least one cycle containing two or more solid-headed arrows. (This makes an (M, R)-network a *complex system* in our lexicon.) An (M, R)-system is an entailment network of ⟨solid-headed arrow, hollow-headed arrow⟩ ordered pairs in which there is a cycle that contains all the solid-headed arrows. (This makes an (M, R)-system a *living system*, i.e., an *organism*, in our lexicon.)

The relational diagram of the simplest (M, R)-system is



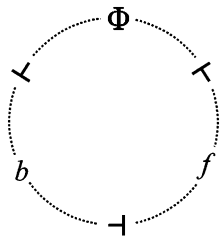
(27)

It may be unfolded into the *hierarchical cycle* (i.e., cycle with hierarchical compositions)



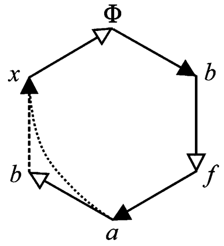
(28)

with the cyclic entailment



(29)

For each of the other two alternate encodings of the replication component, the (M, R)-system also unfolds into a similar hierarchical cycle

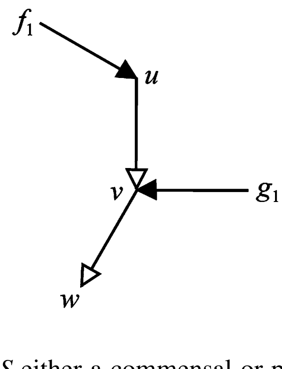


(30)

with an appropriate choice of x, the material cause of replication.

7 Relational Symbiosis

Consider two types of cells, denoted by H and S. Suppose S requires a metabolite v as input in a metabolic process $g_1 : v \mapsto w$, but it cannot produce v for itself. If H produces v in one of its own metabolic process $f_1 : u \mapsto v$, then it is clear that an interaction between H and S will be beneficial to S:

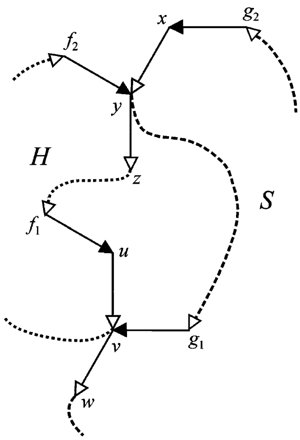


(31)

This arrangement makes S either a commensal or parasitic symbiont, depending on the effect of sharing metabolite v for the host H. (Remember the processes f_1

and g_2 are but single components of large entailment networks that are the cells *H* and *S*, respectively. Diagram (31) simply isolates them to show their interaction.)

If, in addition, *H* requires a metabolite *y* that it itself cannot produce but *S* can, then their interaction may be a mutualism, a reciprocal sharing of the metabolites *v* and *y*:



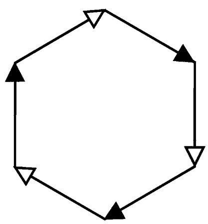
(32)

With this simple example as illustration, I can define symbiosis in relational biological terms thus:

Definition *Symbiosis* is the close and often long-term relational interaction between different (M, R)-networks.

8 Modes of Relational Interaction

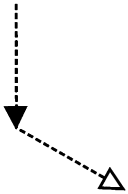
Henceforth, I shall use the generic hierarchical cycle



(33)

to symbolically represent a living system. But one must keep in mind, however, that the entailment network of an organism is in general a far more complicated relational diagram consisting of a large number of interconnected arrows. In particular, let diagram (33) denote the host *H* of a symbiosis.

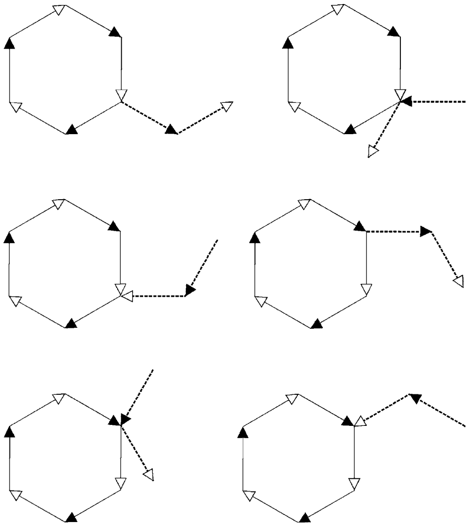
And I shall use



(34)

to denote a relational process in a symbiont *S*. Of course, just like that of the host, the entailment network of the symbiont is a complex relational diagram. But the interactions between diagrams (33) and (34) are sufficient to show all the modes of symbiotic relationships.

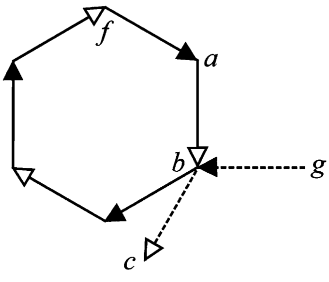
There are six possible modes of nodal connection between host and symbiont:



(35)

9 Metabolic Symbiosis

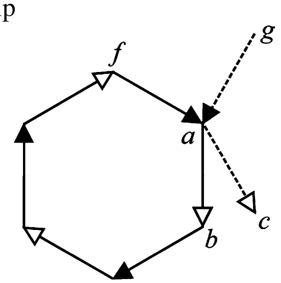
The symbiotic relationship



(36)

is the sharing (or, in the parasitic case, the siphoning off) of the metabolite *b*, a scenario that I discussed in the illustrative example of the previous section. The symbiosis is represented by the sequential composition $g \circ f$.

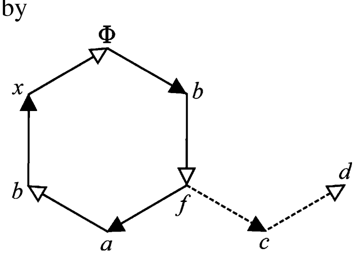
The symbiotic relationship



(37)

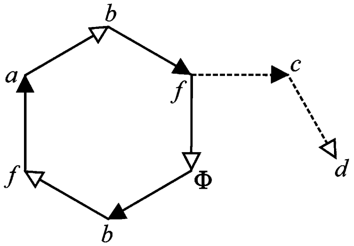
is similar, in this case the sharing of the metabolite *a* (or the competing for the resource *a*). Note that in both diagrams (36) and (37), the processor *g* of the symbiont simply takes its material cause from the host, in a strictly metabolic arrangement.

The interaction modes when the symbiont appropriates an efficient cause from the host are represented by



(38)

and

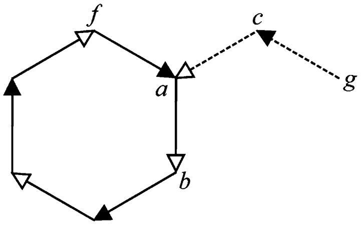


(39)

In each of these cases, the host resource shared with the symbiont is an enzyme, a catalytic processor of a metabolic mapping.

10 Infection

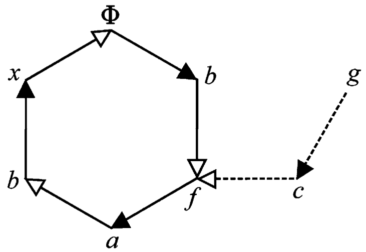
When the processor *g* of the symbiont supplies its final cause (effect) to the host, the result is often harmful to the latter. In a metabolic interaction, one has



(40)

The metabolic process f of the host, instead of its original mapping $f : a \mapsto b$, now becomes the composite $f \circ g : c \mapsto g(c) \mapsto f(g(c))$. Stated otherwise, the material cause a of f is replaced by $g(c)$, so the original product $b = f(a)$ in the hierarchical cycle of the (M, R)-system of the host is then replaced by the different metabolite $b' = f(g(c))$. This foreign material may be considered an infective agent. Most bacterial and fungal infections of organisms are relational biological interactions of this mode.

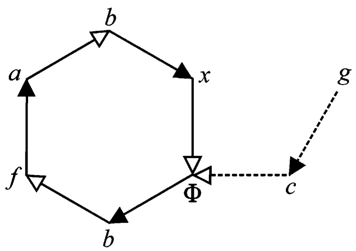
When the substituted node of the host is an efficient cause rather than a material cause, the infection is often more devastating. The interaction



(41)

displaces the original enzyme f with an antigen $f' = g(c)$, and the surrogate enzyme catalyses a different metabolic process $f' : a' \mapsto b'$ instead of the original $f : a \mapsto b$. Since now a new efficient cause is in place (and not, as in diagram (40), just a new material cause which may be of limited supply), the host is infected to produce its own infective material. Prions, and some bacteria and fungi, are infectious agents with relational biological interactions of this mode, on a higher hierarchical level.

On an even higher hierarchical level still, the genetic interaction



(42)

replaces the original gene Φ with the rebel $\Phi' = g(c)$. Now the host executes a new genetic instruction $\Phi' : b' \mapsto f'$ instead of the old $\Phi : b \mapsto f$, thus producing new copies of the antigenic enzyme f' for further metabolic devastation. This is the mode of infection of the obligate intracellular molecular parasites that are viruses.

11 Peroratio

Biology is a subject concerned with organization of relations. This fact is epitomized in relational biology by our definition of an organism as the realization of an (M, R)-system, a closed-to-efficient-causation entailment network in a nutshell (*cf.* Postulate of Life, p. 283 of Louie 2009). The biological interaction of organisms is, therefore, the realization of the relational interaction of (M, R)-systems. This paper shows how various aspects of symbiosis are modelled in relational terms, as a result of single-node connections between host and symbiont, and the entailments of our theory are already consequential. The power of our approach that is relational biology is evident: each of the six modes of interaction has a realization in symbiotic terms. This idea of model-realization duality is expressed poetically in Friedrich von Schiller's *Columbus* (1795):

Mit dem Genius steht die Natur im ewigen Bunde,
Was der eine verspricht, leistet die andre gewiss.

[With genius Nature ever stands in solemn union still,
And ever what the One foretells the other shall fulfil.]

The next exercise will be a consideration of multiple-node connections.

Symbiosis—in our general sense of commensalism and parasitism in addition to mutualism—is ubiquitous in the living world and is, indeed, an essential aspect of life itself. It may even be said that competition and symbiosis are the two driving forces of the biosphere. The importance of symbiosis in evolutionary innovation is evident when one understands its role in the determination of phenotypes and genotypes, as illustrated by the various entailment modes between symbiont and host. One may even extend the definition of 'organism' to be more than single genetic entities, and include symbiotic units. But in relational biological terms, this generalization is already made: a union of interacting (M, R)-systems (or better, their *join* in the *lattice* of (M, R)-systems) is itself an (M, R)-system.

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