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Taking Evolutionary Transitions Seriously

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ABSTRACT

The distinction between reversible and irreversible phenomena in biological information systems provides a basis for distinguishing microevolution from macroevolution. Biological transitions encompass the entire class of irreversible changes in biological systems, including physiological and developmental phenomena. Evolutionary transitions are the subset of biological transitions that have an impact on the quality and quantity of biological information transmitted to future generations. Evolutionary transitions are manifested empirically as macroevolutionary changes, i.e. evolutionary changes that can be detected only through phylogenetic analysis among groups of species sharing a unique common ancestry.

1 TWO RECENT PERSPECTIVES

The past 20 years have witnessed significant conceptual breakthroughs in understanding the fundamental nature of biological systems, and their evolutionary fate over space and through time (see, e.g., references in Brooks, 2000, 2001 and in this contribution). I believe that such conceptual advances (the 'text' of biological theory) must become embedded in ongoing empirical biological research (the 'context' of biological theory) if they are to have lasting impact. In this contribution, I will first discuss two complementary conceptual views of biological evolution, that of Brooks and Wiley (1988) and of Maynard Smith and Szathmary (1995). I will then propose a simplified taxonomy of biological and evolutionary transitions stemming from those views, within which the 'major transitions' of Maynard Smith and Szathmary (1995) nest. Finally, I will briefly discuss

some current empirical research programmes in macroevolution that can contribute directly to the discovery and evaluation of evolutionary transitions.

> ...there are two factors: namely, the nature of the organism and the nature of the conditions. *The former seems to be much more the important* for nearly similar variations sometimes arise under, as far as we can judge, dissimilar conditions; and, on the other hand, dissimilar variations arise under conditions which appear to be nearly uniform. (Darwin 1872: 32 [italics added]).

A necessary first step in encouraging working biologists to consider novel explanations for their findings is to show how such explanations (and the conceptual framework from which they stem) extend and improve the existing framework. The above statement by Darwin in the 6th edition of *Origin of Species* is a good starting point. The development of Neo-Darwinian thought during the second half of the 20th century, however, emphasized the nature of the conditions rather than the nature of the organism, often to such an extent that neo-Darwinian explanations began to sound very Lamarckian indeed. Gould and Lewontin (1979) emphasized this trend in calling research on adaptive evolution 'Panglossian.'

Two recent proposals from within evolutionary biology attempt to bring the nature of the organism back to centre stage in evolutionary biology. Both of these proposals have found it convenient to couch their discussions in terms of the dynamics of information. Brooks and Wiley (1988; Brooks, 2000, 2001) suggested that evolution is caused by the entropic increase in biological information within genetic (more properly 'inheritance systems': Jablonka and Lamb, 1995) phase space constrained historically, due to both internal (nature of the organism, or 'text') and external (nature of the conditions, or 'context') factors. They characterized evolution as stochastically generated yet having irreversible increases in informational complexity, including the emergence of new levels of organization, each of which is accompanied by the emergence of a novel form of 'cohesion', a class of material properties linking parts into wholes. Maynard Smith and Szathmary (1995) proposed that major transitions in evolution are caused by the evolution of increased efficiency of storing and transmitting information. Major transitions are characterized by contingently irreversible emergence of new levels of organization and increased complexity. One outcome of these transitions are changes that ameliorate 'conflicts of interest' (those aspects of the nature of the conditions comprising the selection arena) arising from the independently evolved 'nature of the organism' for each species. Both views converge on a common perspective: there are no strictly macroevolutionary or strictly microevolutionary processes. Rather, there are a variety of evolutionary proc-

esses, with different manifestations on different spatial and temporal scales and at different levels of biological organization (see also Maurer, 1991; Gould, 1995; Conway Morris, 1995). This means there is no single objective spatial or temporal scale for studying evolution, and evolutionary studies need to focus on finding the appropriate scale for invoking particular explanations. For this, we need a meta-theory to integrate microevolution and macroevolution.

That meta-theory comes from considering biological information as a statistical mechanical phenomenon. All evolutionary dynamics are statistical in nature, forming microstates (organisms and groups of organisms) that can be described ecologically by something like the Hutchinson niche and in evolutionary terms by demes and populations. The statistical summation over all members of any evolutionary lineage (a 'community of descent' *sensu* Darwin, 1872) are the macrostates, which can be described ecologically by something like the Elton niche and in evolutionary terms by Simpson's (1944, 1953) *Evolutionary Species Concept* (see also Wiley, 1981) and his view of adaptive zones, embodying a fundamental duality in which macroscopic biological systems were simultaneously genealogical and ecological entities—hence his use of the term *Quantum Evolution* (for an excellent review of the debate within mainstream evolutionary biology about micro- and macroevolution see Eldredge) (Eldredge, 1985).

As noted above, Maynard Smith and Szathmary (1995) proposed that the major transitions in evolution are characterized by the evolution of increased efficiency of storing and transmitting information. Brooks and Wiley (1988) proposed that cohesive properties, ranging from molecular affinities to cell-cell adhesion to genetic compatibility, mate recognition, and genealogy, are analogous to inertia in physical systems, and are essential in allowing the emergence and persistence of macroscopic properties. The major transitions in evolution discussed by Maynard Smith and Szathmary (1995) are all associated with the emergence of new forms of cohesion, which permit information to be stored and transmitted more efficiently. It is in the recognition of the significance of cohesive properties that we find the key to understanding microstate/macrostate distinctions in biological systems. A recent discussion of the nature of species illustrates this point.

2 THE NATURE OF SPECIES

Species comprise historical lineages forming 'communities of descent' (Darwin, 1859, 1872) that comprise, at any given time, spatially-distributed complex information systems (Brooks and Wiley, 1988; Brooks & McLennan, 2002). Kornet (1993a,b; Kornet and

McAllister, 1993; Kornet et al., 1995) added an important dimension to this perspective. Viewing species as historical lineages subdivided into smaller historical lineages extending through time she proposed that when one of these smaller lineages experiences a permanent, or irreversible, split from the others, the relationship between that lineage and the others changes from a microevolutionary to a macroevolutionary one. The divergent lineage is called a *macrospecies* to indicate that permanent split from its ancestor and may now produce its own complement of smaller lineages extending through time, which constitute its own *microspecies.*

'Microspecies' is a general term encompassing all those assemblages of conspecific organisms that biologists have called demes, subspecies, differentiated populations, geographical races, or incipient species. Two implications link these terms. First, the group of organisms being considered can be distinguished objectively in some manner relevant to the dynamics of inherited biological information. Second, there is a probability that this group will become a (macro)species in its own right, but has not done so yet (an event often difficult to determine empirically). Microspecies thus represent the realm of what is happening right now and the realm of possibilities for the future. The microspecies of any given macrospecies may be relatively numerous and locally differentiated yet highly similar due to their close common history, so naturally replicated exemplars will abound, including the locally adapted populations of Williams (1992) and the coevolutionary mosaic of Thompson (1994).

Demographic phenomena, such as local extinctions and fusions with other microspecies as a result of dispersal and gene flow, limit the number of microspecies that become macrospecies in their own right. This is exactly the emerging pattern in studies of *Phylogeography* (Avise, 2000). Phylogeographers are interested in describing the "deployment of genetic variation within species" (Zink 1996:308). This deployment is uncovered by reconstructing phylogenetic relationships among populations then examining the effects of relatedness (phylogeny) and geography on differences in the genetic structure of those populations (microspecies). One major generalization arising from these studies is that relationships among populations within a species are complex and reticulated, often showing only moderate to very little differentiation, as indicated by the occurrence of numerous, equally parsimonious or statistically indistinguishable phylogenetic trees. Although relationships among microspecies are often ambiguous, many phylogeographic studies have detected statistically significant groups of populations which exhibit unambiguous phylogenetic relationships among themselves.

Kornet's criterion of reversible and irreversible splits for distinguishing microspecies from macrospecies thus provides a clear component differentiation in micro- and macroevolution. That component is not one of magnitude, but of quality. It embodies the quality of the cohesion holding the microspecies together as a single 'collective entity', as well as time and history. New macrospecies are the fundamental products of evolutionary transitions. As Futuyma (1989) suggested, population/demic-level changes are likely to have no net evolutionary impact unless they are partitioned by speciation, meaning the production of new macrospecies. Thus, while there may only be one fundamental kind of evolution, there can be two fundamental kinds of evolutionary outcomes, reversible ones and irreversible ones. I propose that *biological transitions* encompass the entire class of irreversible changes, including physiological and developmental phenomena, and that *evolutionary transitions* are the subset of those irreversible changes that have an impact on the quality and quantity of biological information transmitted to future generations.

3 CLASSES OF EVOLUTIONARY TRANSITIONS

Evolutionary transitions encompass a wide range of irreversible phenomena in biology, but not all evolutionary transitions produce equally significant outcomes. Therefore, it might be fruitful to attempt to classify various kinds of transitions. Brooks and McLennan (2002) characterized three categories of evolutionary transitions thus:

Category 1: Playing the game, or taking advantage of opportunities permitted by the game

Such evolutionary transitions are the easiest to achieve (least costly in time and genetic change), yet provide the least evolutionary payoff in terms of diversification. They require only altered environmental conditions, such as geographic isolation leading to speciation. To return to Darwin, such transitions require only a change in the nature of the conditions, and not the nature of the organism. Janzen (1985) generalized this with his concept of *ecological fitting*. For example, most biologists also believe that parasitism is a one-way street, so that once a lineage becomes parasitic, it remains parasitic until or unless it goes extinct. Siddall et al. (1993), however, showed that the common ancestor of the diplomonad flagellates was parasitic, and that within the group *Hexamita inflata* and members of *Trepomonas* have reverted to the free-living mode of existence. What makes this case congruent with ecological fitting is the recognition that all free-living diplomonads live in anaerobic aquatic sediments which often contain high levels of decaying organic matter and their associated bacteria, similar to the intestinal environments in which

their relatives live. In other words, the 'nature of the conditions' for both free-living parasitic species in this group are similar enough that the division between 'parasitic' and 'free-living' is almost arbitrary. Similarly, Trouvé et al. (1998) reported that the life history traits of parasitic flatworms are most similar to the life history traits of their free-living relatives, indicating that these species do not have a 'parasitic' but rather a 'platyhelminth' (phylum Platyhelminthes, also known as flatworms, including the familiar free-living forms called planarians and parasitic forms called flukes and tapeworms) mode of life which functions well in a host-parasite context. Thus, even the adoption of a new mode of life, whose outcome is highly significant in evolutionary terms, may not require an equally significant origin.

Category 2: Changing the rules of the game – changing the dimensions of the evolutionary arena

Ross (1972) established a major component of the foundation of historical ecology when he discovered that only approximately one out of every thirty speciation events for a variety of insect groups was correlated with shifts from the plesiomorphic (ancestral) ecology to any apomorphic (derived) ecology. Ross concluded that though such shifts were important components of insect community structure and complexity, they occurred much less frequently than the origin of new species. Furthermore, he felt that there were no predictable patterns explaining the shifts that did occur and suggested that ecological diversification in evolution comprised a biological 'uncertainty principle'. In other words, we cannot predict when and where a new set of rules for playing the 'game' of surviving and reproducing in a given ecosystem will evolve, though we can document their origin and subsequent effects.

Category 3: Changing the game—creating new evolutionary arenas

This type of evolutionary transition involves explanations for the origins of major modes of life that also depend on specialized morphology, behavior, or ecology often correlated with special conditions. The most fundamental of these transitions, as recognized by Maynard Smith and Szathmary (1995) is the origin of life itself (see also Wicken, 1987; Depew and Weber, 1995). Such transitions are the most difficult to achieve, because they require the conjunction of at least two innovations, each one improbable in itself. (Maynard Smith and Szathmary (1995) noted that such conjunctions would be sufficient to make such transitions effectively irreversible, at least long enough to serve as constraints on future evolution (Brooks and Wiley 1988; Brooks, 2001). As great as the 'cost' (difficulty) of achieving such innovations, the evolutionary payoff for such transitions can be

very large; such transitions lie at the base of explanations for many species-rich, widely-distributed and abundant groups. Maynard Smith and Szathmary's major transitions are all examples of this category.

4 DISCOVERING EVOLUTIONARY TRANSITIONS

> 'The processes of life can be adequately displayed only in the course of life throughout the long ages of its existence' (Simpson 1960: 9).

We want to know something about the history of life on earth that can be deduced from properly understood relationships of groups of species—rare and old events, processes occurring on time scales longer than the lifespan of single species, events that had a significant impact on the evolution of species and the ecosystems they form. For evolutionary explanations, the nature of the organism is most strongly embodied in phylogeny, the history of descent with modification which accounts for most similarities among organisms as well as the evolutionary lineages they form.

Phylogenetic systematics provides biologists with a rigorous methodology to help study both the patterns and mechanisms of evolution (Brooks and McLennan, 2002). As a consequence of that and renewed interest in a broader and more inclusive view of evolutionary theory, a new perspective has emerged within empirical biology, based on the concept that evolution is a complex phenomenon resulting from various interacting processes, termed 'forces' or 'constraints,' operating on different temporal and spatial scales. Evolutionary processes that occur at rates fast enough to be manifested as change within a single macrospecies are included within the domain of microevolution. By contrast, processes that occur at such slow rates that their effects are manifested in among-species patterns, are macroevolutionary. Microevolution and macroevolution are thus considered to be inextricably entwined as parts of a more inclusive whole, each domain represented by the hierarchical nature of biological systems (Salthe, 1985, 1993). If macroevolution is neither autonomous from, nor reducible to, microevolution, robust evolutionary explanations must integrate require data from both sources. For example, because macroevolutionary processes operate so slowly, they help define the boundaries within which microevolution takes place. That is, they can affect the ways in which and the extent to which local populations respond to selection pressures.

5 THE SIGNIFICANCE OF HISTORY

Brooks and Wiley (1988) asserted that history plays a central role in evolutionary irreversibility. Maynard Smith and Szathmary (1995) gave form to this intuition by suggesting that biological processes become effectively irreversible whenever two or more individually improbable events (stemming from either the nature of the organism or the nature of the conditions) effect an inheritable change in the nature of the organism. The odds against two improbable events occurring at the same time in the proper sequence for a specific biological system at any particular time under particular circumstances are astronomically large. History decreases those odds when the first improbable event becomes incorporated into the retained evolutionary history (heredity transmitted information) of a species. The second improbable event can now occur at any time, in any place, and the species will respond accordingly. In other words, history increases the probability that the first improbable event will still be part of the system when a second improbable event occurs.

Brooks and Wiley (1988) further suggested that cohesive properties of biological systems ranging from cell-cell adhesion and recognition, to sexual reproduction and specific mate recognition systems, to common phylogenetic history, are especially important to evolutionary explanations. For them, cohesive properties of living systems limit both the ways and the extent to which populations can respond to environmental selection, and are the 'glue' of functional integration and hierarchical organization so characteristic of biological systems (Wake and Roth, 1989). Many biological processes that give rise to irreversible behaviour manifest such changes as a result of interactions among cohesive factors, which tend to keep biological systems intact and stable in the face of environmental perturbations, and diversifying factors, which tend to split them into separate systems. Speciation in sexually reproducing species, for example, results when developmental and reproductive constraints acting as cohesive forces maintaining a macrospecies as a single lineage are overridden by environmental forces—the best known of which is geographic isolation severing information flow that splits the lineage apart into descendant macrospecies (Wiley, 1981). This is the reason Maynard Smith and Szathmary (1995) associated the origin of sex with the origin of true biological species—sex (including the self-repair capabilities of DNA in sexual reproduction; Bernstein et al., 1988) is informationally cohesive at the level of multiple local lineages (microspecies). Brooks and Wiley (1988) thus proposed that the cohesive nature of sex was a critical part of resolving the dilemma of the 'cost of sex'. In a complementary fashion, the environmental boundaries within which each species lives might be pronounced enough in some cases to be consid-

ered extrinsic cohesion in the form of stabilizing selection (Collier, 1998, 2000). Again, each of the major transitions of Maynard Smith and Szathmary (1995) are associated with the emergence of a novel form of cohesion. Interestingly, this view returns us to Darwin (1872: 158), "Homologous parts tend to vary in the same manner, and homologous parts tend to cohere."

6 EVOLUTIONARY TRANSITIONS IN A COEVOLUTIONARY SYSTEM

The coevolutionary history of leaf beetles (*Ophraella*) and their host plants presented by Knowles et al. (1999) provides an excellent illustration of all three categories of evolutionary transitions (see Figure and for further details, see Brooks and McLennan, 2002).

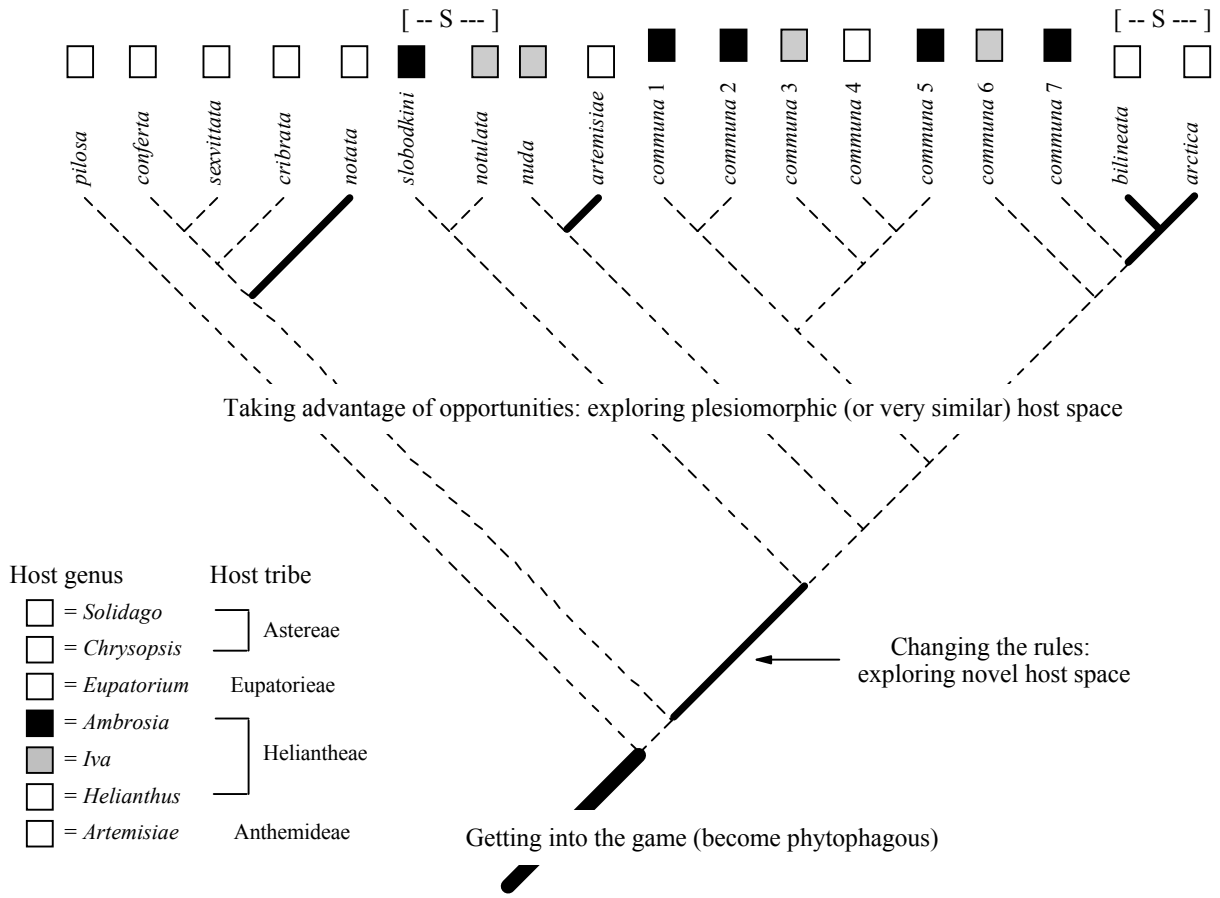

Figure 1: Three categories of evolutionary transitions in coevolution in the evolution of Ophraella. Dotted lines = category 1; bold lines = category 2; thick line at base of phylogenetic tree = category 3 (this occurred prior to the origin of Ophraella).

Most of the speciation in the group took place within the context of the ancestral host resource, i.e. staying with the ancestral host during speciation, or speciating in association with host switching among members of the same tribe (transition category 1). Many of those events evidently occurred in a burst during the Plio-Pleistocene, a time of substantial environmental change (Knowles et al., 1999: see Brooks and McLennan, 2002 for other studies suggesting periodic bursts of speciation). This implies that rates of speciation may have increased during that period of environmental crisis because the beetles were given the opportunity to host switch e.g., increased sympatry of previously allopatric hosts bearing the plesiomorphic resource as organisms were forced together in rapidly shrinking refuge areas. These transitions occurred as a result of a change in the nature of the conditions alone. Colonization of more distantly related host plants (transition category 2) encompasses fewer events, and as yet there is no indication that these events were correlated with each other or with any particular episode of environmental change. These transitions likely involved the evolution of novel abilities enabling the insects to utilize new host resources (a change in the nature of the organism) leading to novel *Ophraella*/plant associations, adding to the evolutionary complexity of the dimensions of the arena and adding new rules to the game (in the form of new types of associations).

Finally, that *Ophraella* spp. are herbivores in the first place is phylogenetically conservative in the Chrysomelidae (all of which are herbivores). Is the evolution of herbivory an example of transition (transition category 3)? To answer this question, we must consider the origin of herbivory in animals in general. I believe herbivory is a good candidate as a major transition in evolution, although not immediately recognizable as such. That there are tremendous ecological benefits and impacts of herbivory on both the power and stability of ecosystems (Ulanowicz, 1986, 1997) and on the structure of communities (Brown, 1995; Maurer, 1999) is uncontested. The link between the stability, resilience, and persistence of ecosystems in which herbivory plays a role and increased efficiency of information storage and transfer associated with Maynard Smith and Szathmary's major transitions is indirect but clearly inferred from those ecological benefits.

No metazoan has ever evolved the ability to digest cellulose. Whether this means it is impossible, or merely that it is so improbable that is has not yet happened, is unknown. Nonetheless, in order for metazoans to be herbivores, they need help. Three things must happen, each of which is *a priori* improbable: (1) obtain a source of cellulose-digesting microbes or protists; (2) provide a suitable environment for them in the intestine; and (3) provide a mechanism for passing them on to your offspring. According to Maynard Smith and Szathmary (1995), this should be sufficient to ensure that the adoption of herbivory is

irreversible—it is an evolutionary transition. The fossil record suggests that this is so; during the major extinction events, herbivores become extinct, and the re-emergence of terrestrial ecosystems is associated with the evolution of herbivory in a few surviving lineages of faunivores (Sues, 2000). The evolutionary cost of herbivory is that it is difficult to achieve, thereby explaining why herbivory is not the ancestral feeding mode in any major metazoan group (with the possible exception of the Mollusca), why it has *originated* so few times, and why its origin cannot be predicted in advance (Sues, 2000). The evolutionary benefits are manifestly large, sufficient to structure and power terrestrial ecosystems globally, thereby explaining the evolutionary success (in terms of geographic distribution, species richness, and total biomass) of the lineages in which it arises. This is the manner in which herbivory is associated with increased efficiency of information storage and transfer, an essential aspect of Maynard Smith and Szathmary's concept of major transitions. Finally, we need to ask if herbivory requires special conditions. I believe this may be true, although again in an indirect manner. Given the enormous evolutionary payoffs accruing to those lineages that become herbivorous, it is possible that the first lineages adopting this mode of life proliferate and diversify so rapidly that they themselves effectively change the nature of the conditions such that it become increasingly difficult for new lineages to establish themselves at all, and or them to become widespread if they do become established (pre-emptive competition, or 'survival of the first'). In population genetics, this is known as the Allee Effect; a further implication of this is that the newer version of a trait may actually be better adapted than the older, but not so much that the advantage of the ubiquitous nature of the older trait can be overcome by displacive competition. New origins of herbivory are inhibited unless those conditions are fundamentally changed again, as in the case of major extinctions due to global environmental catastrophes or change. In this manner, a fundamental (but *a priori* difficult to achieve) change in the nature of the organism leads to a fundamental change in the nature of the conditions. Maynard Smith (1976) noted that much of the environment (nature of the conditions) relevant to biological systems consists of products of genealogical processes (see also Brook and Wiley, 1988). I thus believe that herbivory qualifies as a major transition in evolution.

7 EVALUATING EVOLUTIONARY TRANSITIONS

The above discussion invokes a simple cost/benefit argument to help classify a particular type of evolutionary transition. I believe this is potentially a useful means of evaluating proposed evolutionary transitions. The informational nature of the organism

ensures the existence of independent relatively autonomous entities occupying the same space at the same time, which also provides the possibility of evolutionary conflicts of interest. As evolutionary diversification proceeds from the origin of life, the diversification of species, all confined to this single planet, made such conflicts inevitable. Biological research has demonstrated that such conflicts of interest abound; indeed, the existence of such conflicts arising from the relatively autonomous nature of the organism creates the various selection arenas (Brooks, 2000, 2001). More fundamentally, in a world controlled by the Second Law of Thermodynamics there is no free lunch; everything is a trade-off, beginning with the most fundamental issues of trade-offs between energy used and work done, between energy stored as structure (biomass, including the information system itself) and energy dissipated as a result of making and maintaining that structure. To the extent that biological information has a material basis, it must have an energetic cost, which must be assessed in the context of survival.

8 THE MACROEVOLUTIONARY COST/BENEFIT ARENA

The simplest cost/benefit arena can be depicted as a 2 X 2 contingency table, depicting interactions between two binary variables. Each of the four cells in such a table represent evolutionary outcomes, sometimes called strategies, each of which specifies a set of costs and benefits. Again in the simplest case, the cell which represents the greatest net benefit is predicted to be the strategy observed in nature. Departures from expectations imply additional factors influencing the system. Large amounts of biological complexity can be added to cost/benefit analyses, and microevolutionary studies have used this approach with great success.

To convert this to a macroevolutionary arena, we need to consider the evolutionary history, i.e., the *origins*, of variables representing any putative evolutionary transition, to help us explain what irreversible events *happened* and why, complementing predictions of what reversible dynamic changes *might happen*, and why. Consider the simple case in which one variable represents changes in the nature of the organism as 'easy to achieve' (cases of ecological fitting and vicariant speciation being special cases in which no change was necessary) or 'difficult to achieve' while the other variable represents changes in the nature of the conditions, represented as 'not required' and 'required'. In the simple classification presented above, category 1 transitions would be 'easy to achieve' and 'no special conditions required', category 2 transitions would be 'easy to achieve' and 'special conditions required' (2a) or 'difficult to achieve' and 'no special

conditions required' (2b), and category 3 transitions would be 'difficult to achieve' and 'special conditions required'.

When an evolutionary transition is associated with the origin of a species, we can envision a set of such tables summed over the evolution of a clade (e.g., *Ophraella* as discussed above) permitting us to ask questions such as, where did the clade enter the game. Eexpanding the scale of the study phylogenetically can also answer the questions of when did the clade enter the game and what game was it playing before? What was the sequence of exploration of the cells? Are there any empty cells? If there are multiple occurrences of the same cell, did it arise form the same source and in the same manner in each case? Did any member of the clade ever leave the game, and if so, from which cell, and where did it go—including the case of going extinct?

Adopting the perspective of cost/benefit analyses also enables us to understand the most fundamental benefit of retained history – it lowers the cost of evolution. Retained history lowers the cost of innovation, because innovations are modifications of only part of pre-existing information. New traits need not be produced de novo, and their expression is 'pre-screened' through developmental dynamics based on the non-modified components which determine whether or not the innovation is 'permitted' i.e. if it disrupts overall developmental, including reproductive integrity (cohesion). Retained history also lowers the cost of specialization—specialists on widespread persistent ancestral resources have options for survival and evolutionary diversification under changing conditions (ecological fitting). Finally, retained history lowers the cost of adaptability, as most adaptability is accumulated history.

9 A RESEARCH PROGRAM FOR MACROEVOLUTIONARY COST/BENEFIT ANALYSES

The past decade has witnessed an explosion of experimental studies informed by phylogenetic information directly documenting evolutionary mechanisms, even those operating in the distant past. David Wake (1991) proposed that an understanding of the evolution of biological form required an integration of 'neo-Darwinian functionalism and biological structuralism, in a context of rigorous phylogenetic analysis' (see also *Historical Structuralism* of Brooks and Wiley, 1988). This has led to two macroevolutionary research programs, *Historical Ecology* (Brooks, 1985; Brooks and McLennan, 2002) and *Integrative Biology* (Wake and Roth, 1989). The goal of both research programs is to

provide rigorous explanations for the origin, persistence (stasis), and diversification of the species traits that provide the foundation for complex evolutionary systems.

The *Ophraella* patterns discussed above are an example of historical ecology, and set the stage for studies in integrative biology. Wake (1991) described the integrative biology perspective as the desire to differentiate instances of evolutionary change due to selection (nature of the conditions) and those due to 'design constraints' (nature of the organism). Integrative biology involves efforts in diverse fields including functional morphology, neurobiology, physiology, reproductive biology, and developmental biology (for a list of relevant publications, see Brooks and McLennan, 2002). Placing the results of studies in integrative biology in a cost/benefit context provides a powerful research program for evaluating the nature of evolutionary transitions. Mechanistic components of integrative studies can tell us the costs and benefits; phylogenetic studies can tell us where each lineage got into the game, and how many times and in what sequence it took advantage of the opportunities, changed the rules, or even changed the game.

Retained phylogenetic history thus allows considerable biological complexity to evolve, and survive through ecological fitting, extending the time period during which evolutionary experiments, leading to evolutionary transitions can occur. It lowers the global cost of evolutionary origins and persistence while not sacrificing the benefits of local adaptation.

10 SUMMARY

The conceptual framework summarized above treats organisms and the systems they form as information systems retaining much of their phylogenetic history. I believe this contribution provides a glimpse of the power of that perspective in linking theoretical ('text') and empirical ('context') research programs. There is still much to be accomplished, in terms of priorities, terminology, and better understanding of both general and specific phenomena through both empirical studies and modelling efforts. Nonetheless, I believe it is time to consider all such debates to be part of the vigorous activities of a growing and progressive research program, rather than a collection of mutually exclusive competing alternatives. This will lead us back to the panoramic view of biology in an evolutionary context first articulated by Darwin. It will also provide hope of encompassing the enormous amount of biological discoveries since Darwin, along with more fundamental developments in statistical mechanics, non-equilibrium thermodynamics and self-organization, information theory, and complexity theory (for additional discussion

and references, see Wicken, 1987; Weber, Depew, and Smith, 1988; Csanyi, 1989; Matsuno, 1989; Kampis, 1991; Kauffman, 1993; Depew and Weber, 1995; Van de Vijver, Salthe, and Delpos, 1998; and Taborsky, 2000) in a truly unifying, if not unified, theory of biology.

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