

Natural Selection: A Concept in Need of Some Evolution?

In some respects natural selection is a quite simple theory, arrived at through the logical integration of three propositions (the presence of variation within natural populations, an absolutely limited resources base, and procreation capacities exceeding mere replacement numbers) whose individual truths can hardly be denied. Its relation to the larger subject of evolution, however, remains problematic. It is suggested here that a scaling-down of the meaning of natural selection to “the elimination of the unfit,” as originally intended by Alfred Russel Wallace (1823–1913), might ultimately prove a more effective means of relating it to larger-scale, longer-term, evolutionary processes. © 2011 Wiley Periodicals, Inc. Complexity 17: 8–17, 2012

Key Words: natural selection; evolution; Alfred Russel Wallace; elimination of the unfit; survival of the fittest

CHARLES H. SMITH

Charles H. Smith is Professor and Science Librarian at Western Kentucky University, Bowling Green, Kentucky 42101 (e-mail: charles.smith@wku.edu)

1. INTRODUCTION

For over 150 years, the theory of natural selection has inspired an ever-expanding investigation into the world of adaptation—that critical element of biodiversity that draws the twin matters of ecological and evolutionary causality face to face. The focus has always been on understanding function within the natural world, and how to trace it backward through time to the origin of species. We envision, as did Charles Darwin and Alfred Russel Wallace, a “tree of life” that phylogenetically connects present forms back to their ancestors, and imagine that this tree represents not only the historical linkages between forms but also an actual coming-into-being process.

There can be no doubt that these links represent real evolutionary *associations*; beyond our increasing knowledge of DNA sequences, which seemingly proves this outright, one needs look no further than Wallace’s “Sarawak Law” essay of 1855 [1], which pointed to an otherwise unexplainable connection between most closely related species and their distributions in space (geographical range) and time (the fossil record). Nothing other than a diverging—evolving—pattern of relations could explain such a thing. For its own part, the concept of natural selection is based on elements that themselves can hardly be denied: there really *is* variation within natural populations, and a limited resource base that could in theory be over-run by the high native rates of procreation within species. Unless one argues that what would generally be understood as “less fit” individuals on the average should compete as well as more fit ones—and one cannot—it seems inescapable logic that

the latter will tend to prevail and preferentially pass their genes along to their progeny.

However, natural selection has always found itself under attack, and sometimes for good reasons. Although lending itself perfectly well to interpretations of many immediate relationships—that is, to the facts of adaptation—it has proved largely ineffectual in contextualizing the larger scale: especially, the causes of variation, divergence, and speciation [2], other key (and empirically evident) products of biological evolution. There is evidently a disconnect in the theory between its ecological enactment and its historical “accumulations” (as both Darwin and Wallace referred to them), recapitulated both in the DNA molecule and its manifest expressions as functioning individuals and populations. Darwin was largely oblivious to this difficulty but Wallace was not; this is perhaps not surprising as the former looked at the entirety largely from a geologist’s historical vantage point, whereas Wallace was more the ecologist and geographer. The Darwinian version of natural selection soon found itself attacked as a tautology. As Lewontin once put it, “The process is adaptation and the end result is the state of being adapted.... The problem is how species can be at all times both adapting and adapted [3].”

Generations of biologists and historians have identified various differences between Darwinian and Wallacean understandings of natural selection. There are many particulars, but for now two main ones may be emphasized: (1) Darwin viewed competition as occurring mainly between individual organisms, whereas Wallace emphasized the dynamics between varieties, and (2) Wallace tended to regard environmental pressures such as climate or geological change as the main selection-generating forces, whereas Darwin looked more to individual competition for resources, including sexual selection, as of pri-

mary import. In what follows I will, perhaps surprisingly, not play to a favorite: I believe both discussions represent red herrings. Instead, I would like to start by re-examining the basic question of what natural selection is—or perhaps better yet, what it is not—and then consider how a more limited view of natural selection—a more Wallacean view—might help us to identify some interesting causalities within the evolutionary process.

2. NATURAL SELECTION AS THE ELIMINATION OF THE UNFIT

In 1888, C. Lloyd Morgan, in some quarters referred to as the father of comparative psychology, made a presentation entitled “Elimination and Selection” to the Bristol Naturalists’ Society. Despite Morgan’s fame, this is a little known work, as it was published in the Society’s obscure “Journal” series [4]. As the first three paragraphs of the paper well introduce the present thread, they may be reproduced in full:

Those who have read the recently published “Life of Charles Darwin” may remember a footnote in which Mr. A. R. Wallace criticizes the phrase “Natural Selection.” “The term ‘Survival of the Fittest,’” he says, “is the plain expression of the fact; ‘Natural Selection’ is a metaphorical expression of it, and to a certain degree indirect and incorrect, since Nature does not so much select special varieties as exterminate the most unfavourable ones.” Mr. Darwin, while admitting with his wonted candour the force of this criticism, urges in support of the use of his own phrase, first, that it can be employed as a substantive governing a verb; secondly, that it serves to connect artificial and natural selection; and thirdly, that its meaning is *not* obvious, and that this leads men to think the matter out for themselves.

I propose here briefly to consider Mr. Wallace’s criticism; to suggest provisionally the use of the phrase, “Natural Elimination,” which *can* be employed as a substantive “governing a verb”; and to indicate the advantages which would attend the use of such a term, not the least of which is, that it serves to distinguish between artificial selection and “natural selection.”

Mr. Herbert Spencer’s term, “Survival of the Fittest,” says Mr. Wallace, is the plain expression of the fact; “Natural Selection” is a metaphorical expression of it. Yes; but in the first place, Mr. Spencer’s phrase gives no inkling of the process by which such survival is brought about; and, in the second place, it is questionable whether any phrase, which does so indicate the process, can escape the charge of being in some degree metaphorical. The sting of Mr. Wallace’s criticism, therefore, would appear to lie (appropriately) in the tail, where he points out that Nature does not so much select special varieties as exterminate the most unfavourable ones. This seems to me a valid criticism; one which Mr. Darwin does not sufficiently meet; and one which still holds good. I would, however, venture to suggest that the word “eliminate,” though somewhat metaphorical, is more satisfactory than Wallace’s word, “exterminate”; and I further venture to suggest that the use of the phrase, *Natural Elimination*, would emphasize the fact that, whereas in artificial selection it is almost invariably the fittest which are chosen out for survival, it is not so under Nature; the “survival of the fittest” under Nature being in the main the net result of a slow and gradual process of the elimination of the

unfit. The well-adapted are not selected; but the ill-adapted are rejected; or rather, the failures are just inevitably eliminated.

This was not the only occasion on which Morgan made these points [5], nor he was the only one to consider the matter [6], but the term “natural elimination” never caught on. Wallace himself apparently became more aware that his view differed from Darwin’s as time passed. He had referred in print to this notion of the removal of the unfit at least as early as 1877 [7]; it is not known whether Wallace knew of Morgan’s essay, but by 1890, in one of his most famous essays, “Human Selection,” he straightforwardly states: “The survival of the fittest is really the extinction of the unfit [8].” In an 1894 interview, he remarks “I believe that the unfit will be gradually eliminated from the race, and human progress secured,” [9] and a year later, in “The Method of Organic Evolution,” he writes “Without making some numerical estimate of this kind it is impossible to realize the severity of the struggle continually going on in nature and the resultant “elimination of the unfit.” [10]

If Wallace believed, and surely he did, that “elimination of the unfit” was what “survival of the fittest” really came down to, why did he bother using the second term at all? The reason seems evident from the following passages from two other late works of his:

Herbert Spencer suggested the term “survival of the fittest,” as more closely representing what actually occurs; and it is undoubtedly this survival, by extermination of the unfit, combined with universally present variation, which brings about that marvellous *adaptation to the ever-varying environment*. . . [11]

This continual weeding out of the less fit, in every generation,

and with exceptional severity in recurring adverse seasons, will produce two distinct effects, which require to be clearly distinguished. The first is the preservation of each species in the highest state of adaptation to the conditions of its existence; and, therefore, so long as these conditions remained unchanged, the effect of natural selection is to keep each well-adapted species also unchanged. The second effect is produced whenever the conditions vary, when, taking advantage of the variations continually occurring in all well-adapted and therefore populous species, the same process will slowly but surely bring about complete adaptation to the new conditions. And here another fact—the normal variability of all populous or dominant species, which is seldom realized except by those who have largely and minutely compared the individuals of many species in a state of nature—comes into play. There are some writers who admit all the preceding facts and reasoning, so far as the action of natural selection in weeding out the unfit and thus keeping every species in the highest state of efficiency is concerned, but who deny that it can modify them in such a way as to adapt them to new conditions, because they allege that “the right variations will not always occur at the right time.” This seems a strong and real objection to many of their readers, but to those who have studied the variability of species in nature, it is a mere verbal difficulty dependent on ignorance of the actual facts [12].

He thus apparently acknowledged that “elimination of the unfit” *per se* does not well lend itself to the notion of “adapting” in an evolutionary sense.

Yet, while “elimination of the unfit” might only serve to keep species in “the highest state of adaptation,” Wallace could fall back on the understanding that changing conditions are what stimulate the kind of directional selection process leading to evolution. This is where, I believe, Wallace goes wrong. “Changing conditions,” on whatever scale, are themselves a function of evolution (not necessarily just biological ones, of course, but the whole system is integrally interconnected), and cannot merely be assumed. A chicken-or-egg situation has been set out in which the initial conditions of causality have not been specified.

Another way of putting this is to suggest that just as negentropy is not merely the “opposite” of entropy, neither does evolution imply something that is automatically the opposite of “elimination of the unfit.” Evolution of any kind, including biological in particular, implies a movement away from chaos and toward higher levels of order. The thoughts of the late Stephen Jay Gould and others notwithstanding, evolution as witnessed on this planet, and probably universally (even if only locally), is progressive. Whether it is progressive toward some predestined end, as some would suggest, is quite another matter, but one cannot sensibly argue that insects, for example, whatever their numbers and diversity, individually or as a group display responses to impinging stresses that are as advanced as those by vertebrate species. If Wallace—and the rest of us—wish to show how the “non-unfit” are really contributing to evolution, we must show how their (ecological) actions are producing a net increase in the overall information content of the active earth surface layer.

Unfortunately, while we can prove easily enough that evolution really has taken place, it is not so easy to demonstrate that natural selection as usually conceived is responsible for this progression of complexification (both in individual forms, and doubtlessly at

the entire environmental level as well). Actually, and even assuming it operates as Darwin envisioned, at least five related causalities (or lack thereof)—and undoubtedly others—can be posed that might, in the absence of countervailing forces, stop it in its tracks.

First, and again, what is there in the natural selection concept that actually argues for a process of complexification over time, as opposed to mere change, or even diversification? That is to say, why is the planet not populated by no more than an endless array of microorganisms that merely morph over time into further endless arrays of microorganisms? (And for that matter, just how effective has natural selection been in explaining speciation into discrete population entities?: not very.)

Second, what is there in the logic of the process of natural selection (as opposed to its supposed observed results, that is) that demonstrates that the physical environment is not so fickle and changeable as to present too difficult a challenge for selection to overcome? And there is beyond this the possibility that as that environment itself evolves into wholly new sets of relationships, it could do so in ways that natural selection is powerless to address.

Further, we may be confident at this point that mutations introduce new diversity into the biological system, but can natural selection tell us whether this diversity is of a productive type frequently enough, or even under what circumstances it might be? Perhaps, the rate of mutation is so great, and its usually evil effects so prevalent, that some other force is needed to steer its results in a productive direction.

Perhaps worst of all, is it actually *evolutionarily*—as opposed to *ecologically*—productive in all instances to adapt? More specifically, where adaptation results in highly specific ties to various (physical or biological) elements of the environment, what are the long-term downsides to this kind of associa-

tion? One, of course, is proneness to extinction, but another perhaps further-reaching one is an unlikelihood of further diversification into forms with an ability to enter into substantially new kinds of associations, or indefinitely perpetuating ones. Insects, for all their great number and diversity, have never given rise to any other class of organized beings since they themselves came into existence. Diversification, in mere terms of *speciosity*, is only one element of evolution, and perhaps not even its defining element.

Finally, and most interesting, what if there are *a priori* limitations to the nature of complex structure that natural selection must work around to function at all? The DNA molecule, for example, seems to display a rather similar structure all the way up and down the living world, and we have tacitly assumed that the reason for this lies in an unconstrained random-walk-modified-by-negative-feedbacks kind of evolutionary process—just the same assumption we have made regarding the history of emergence of living variety in general. Even if this is to some extent true, there still may well be overarching constraints on the structure of complex systems that create absolute limits to that process, or that push it in certain directions.

And, as if these suppositions were not enough to cause some worries, many years of diligent study by paleontologists have shown that many or most populations in fact do *not* change in a manner reflecting the basic Darwinian dictum of slow, continual adaptation. We are now aware of many species that have shown little if any alteration for even many tens of millions of years. It appears to be more common that short bursts of innovation take place that push species into new adaptive equilibrium states for varying periods of time. Wallace suspected as much; in 1880 he wrote: "... the *extreme slowness* of the action of natural selection, on which Mr. Darwin repeatedly dwells, is by no means an essential characteristic of

it... if, as must often have happened, conditions have changed with comparative rapidity, then the enormous amount of individual variation, which would be taken advantage of *every year* by the survival of the fittest, might effect changes in a single century quite as great as those which distinguish nearly allied species [13]."

Now understand that this is not to try to suggest that any of these forces *necessarily* have unduly complicated, or impeded, the evolutionary process. Instead, the point I am trying to make is that in our efforts "to make natural selection work" a lot of potentially interesting irregularities are merely being explained away. The Darwinian approach to natural selection tacitly assumes that all of these possibly extenuating influences *must* have been overcome—thus, natural selection emerges as a transcendental force that simply supersedes all and any such agencies. Yet, it provides limited insight into how this is accomplished.

Such considerations should make us wary of attempts to conceptualize natural selection as a process model. It may be more fruitful to begin with the unassailable—the facts of super-ample rates of procreation, limited resources, and genetics—and agree with Wallace that natural selection represents no more than the notion of the elimination of the unfit, and its consequence of the "highest state of adaptation to the conditions of its existence; and, therefore, so long as these conditions remained unchanged, the effect of natural selection is to keep each well-adapted species also unchanged [14]." This fairly exact starting point allows us to ask without fear of circularity: what conditions surrounding those that *do* survive are tending to push the overall state of negentropy on the planet's surface to higher levels?

While it is undoubtedly true that there are genetic differences between those individuals in any population that do not survive very long and those that do, it is arguably not these differ-

ences *per se* that drive evolution. Instead, and technically speaking, it is the fact that the second group has a greater opportunity to engage with its environment (defined broadly) in a nonrandom fashion that ultimately drives phylogenesis. So, we are speaking most fundamentally of assembly rules here. On the average, adaptive arrays that better suit ecological conditions (again, physical and/or biological) will more likely be embraced by them, but this is not a tautological statement because the causalities that are coming together are quite distinct in nature. The individual organism, once in existence, is little more than an automaton, programmed by its DNA. The environment, by contrast, is infinitely complex, offering varying and continually changing probabilities of success of engagement over time—and beyond this there is the further complication that such probabilities are spatially autocorrelated: all of them are the more or less so in an actual spatial context. Evolution takes place as this two-way set of relationships works out ever more intricate intercausalities.

3. A NATURAL SELECTION TYPOLOGY

Starting with the basic notion that a population's array of adaptations gives it the *potential* to engage its environment in a spatially nonrandom way that is implicitly information-accruing, it is possible to construct a typology of interaction types that might, or do, influence the way biological evolution in the longer term sense plays out. In some of these, the changes anticipated and how they occur coincide fairly closely with conventional Darwinian interpretations, but in some they do not. We may call this typology the "Opportunities and Constraints" model. We begin with the opportunities.

3.1. Opportunities for Adaptation

Natural selection of a Darwinian type is most straightforwardly apparent

when some easily modified part of an organism's body undergoes selection resulting in an adaptation that accrues a specific and immediate significant advantage. A good example is protective mimicry, in which a usually less common form comes to resemble a more common, and in one manner or another noxious, species. In general, any environment will provide a range of opportunities for productive engagement, so the longer term question in this instance is whether such engagement results in a narrowing, or expansion, of evolutionary opportunities and inertias. A short term advantage may be accrued by assuming a coloration or bodily shape that provides camouflage, but this specialization will be to of no avail in the longer term if the host species is suddenly eradicated through disease or competition.

Still, this form of adaptation is undeniably very widespread, and under the right circumstances leads to great levels of diversification over long periods of time. Parasitism falls into this category of engagement. Many parasitic species undoubtedly have coexisted with their hosts throughout the latter's entire period of existence, and by implication before it. The hosts themselves, of course, continue to counter-modify in response, as the Red Queen Hypothesis suggests [15].

3.2. Constraints on Adaptation

At first it may be difficult to appreciate how added *constraints* on the range of adaptive potential might stimulate evolutionary diversity, but there are some complex considerations here. Let us group these under the headings "Conventional," "Implicit," and "Explicit."

3.2.1. Conventional Constraints

Under "Conventional," we may recognize all those factors, many long understood, that directly force adjustments in organic development and function. Historically, attention was first drawn to

those resources whose relative rarities seemed to affect presence and absence; the work which popularized this kind of thinking, giving us the concept of limiting factors, was Justus von Liebig's "Organic Chemistry in its Applications to Agriculture and Physiology" in 1840. In the decades that followed, biogeographers and climatologists investigated larger-scale factors of the same general kind, some arguing for deterministic influences on evolution that seemed to imply a Lamarckian kind of process. In the 20th century, ecologists identified further possibly relevant factors; in a relatively little known paper, for example, Hutchinson [16] argued that local deficiencies of trace but necessary nutrients might have a dampening effect on organismal success. More recently, students of biodiversity have used advanced monitoring techniques to expose variations in ambient yet potentially important evolutionary causal factors—for example, the relations between high diversity and high-energy environments [17].

Presence-and-absence thinking of this kind is something of a dead end, however, because at most it identifies correlations between particular factors and organisms. While it is clear that ecological conditions represent various combinations of lack or surplus of resources and organisms must be adapted accordingly to persist, the evolutionary question is more how such relations change in an organized, synergistic fashion. In 1984, I made the following observations:

It is apparent that any resource that is vital to all forms of life but is only available part of the time and/or in some places will dictate certain spatial strategies of existence on the part of living things. Specifically, they will need to apportion a significant part of their total energy budget to the development and operation of means of being "in the right place at the right time"

to obtain and conserve the resource. This directed behavior, whether active or passive, will lead to the development of non-random movements through time and space (for sedentary organisms the patterns will devolve as spatially-varying rates of successes and failures of individuals over time). I interpret this deviation from random movement in time and space to represent a direct mapping of the stress upon the system. The greater the stress (i.e., the more discontinuous the rate and spatial patterns of provision of the vital resource), the more non-random the movement we should expect.

Such non-random patterns of direct interaction between the biotic sector and the abiotic sector will of necessity extend to the pattern of interaction among organisms. An obvious example is the well-known fact that in times of drought, carnivores often hunt near the waterholes their prey frequent [18].

The basic idea here, which I have also discussed elsewhere [19], is that the more the need to be in “particular places at particular times,” the more the organism’s energy—and genetic—budget must be tied up in supporting specialized adaptive responses. Conversely, less stressful environments will be less demanding in this respect, allowing selective drift, and the evolution of generalist species. Models identifying the nature and measure of this kind of stress can be imagined; from these geographical clines of same can be envisioned which should affect the rate and directionality of both in-dispersal and removal of forms (per related rules of assembly). In my doctoral dissertation, support was found for one such model, involving the soil moisture cycle. More recently, I performed a follow-up analysis: if in fact

the species that inhabit low-stress areas are more genetically diverse (at least in the sense of their promoting further phylogenesis), then they should exhibit a higher incidence of subspeciation throughout their range. This turned out to be markedly so (<http://people.wku.edu/charles.smith/once/dissadds.htm>). It would also be interesting to investigate this matter in terms of the so-called “Neutral Theory of Molecular Evolution” (as developed especially by Motoo Kimura and Masatoshi Nei [20]), as one can project that genetic drift would likely play a greater role in identifying new viable structures under a regime of low environmental stress of this type. Recent work by Wagner [21] might also be relevant in this context, as stepwise mutation to the ends of adaptation in the sense he describes might also be more likely in environments which are not so dominated by being “in particular places at particular times.”

In sum, if it can be shown that range change in populations is non-random, and slowly tends in those (geographical) directions that permit integration into generalist-promoting ecological settings, then we will have an understanding of how complexification in an evolutionary sense works—that is, how the constraints on biological function are lifted, rather than imposed. Such processes will undoubtedly be relatable to certain conditions of the environment, but it will probably be some spatial/temporal integration of these that will constitute the driving force, and not just large or small amounts of one thing or another [22].

3.2.2. *Implicit Constraints*

There are many exact ways that a species can go extinct, but apart from catastrophic events for very localized populations (as on a small island), these usually involve no longer being able to make use of some vital resource (including other members of

the species). While such outcomes can often be understood after the fact as a simple inability to select responses to various stresses fast enough, one can imagine other, less immediate, causal scenarios. One involves conflicting causal inertias. For example, it is not *a priori* implausible that the demise of some higher taxa throughout history has been due to their adopting a physiological plan at one time that later would no longer work because of ambient environmental changes whose impact was of such a nature as to supersede available selection options. As a possible example of this, briefly consider the evolution and extinction of the dinosaurs.

A 2002 summary of the evolution of atmospheric oxygen levels [23] suggests that after an early Mesozoic peak its percentage constitution of the atmosphere dropped sharply, then increased fairly continuously to double its original level by the end of the Mesozoic. This corresponds very closely to the period of time during which the dinosaurs evolved and existed, and one might relate the two facts as follows. Suppose that evolving endothermy under relatively low levels of atmospheric oxygen necessitated one of two means of balancing heat loss and retention: (1) small size (to promote heat loss under high temperature conditions) combined with external insulation (to promote heat retention at low temperatures), or (2) large size (to promote heat retention) combined with internal or negligible insulation (to promote heat loss). Let us further suppose that the second strategy, while workable under low ambient oxygen level conditions, has no guarantee of working well—or at all—under much higher level conditions. Dinosaurs thus eventually would have faced a problem, as it might have been impossible to select an adaptive response that at one time reduced their rates of oxygen processing, yet supported active ecological engagement.

This theory, if true, would help in explaining a number of peripheral historical phenomena: for example, that all dinosaurs were at least relatively large (and thus all would have been affected); the reason for the survival of birds, mammals, and other (not endothermic) reptiles; the expansion of dinosaur populations to colder climates in the Cretaceous; the increasing number of morphological peculiarities of dinosaurs (crests, sails, etc.), which might have aided in heat regulation; the extinction of whole families and orders (suggesting causes based more in physiological commonalities than in single ecological stresses); and an apparent tendency of primitive current-day representatives of ancient groups to be associated with oxygen-poor environments.

For a second possible instance of an “implicit constraints” kind of selection regime, we turn to wildlife’s 10-year cycles in the Northern boreal forests. In the New World, the cycling population levels of the varying hare, *Lepus canadensis*, are thought to lie at the center of this phenomenon, as it is a primary food source for most of the creatures whose numbers also cycle. Many years of study have established critical elements of the demography of the cycling populations, but no clear model of underlying causes. In this instance, the key to the phenomenon may lie in what early literature [24] referred to as the “shock disease” that seems to be linked to cycling hare populations, an affliction characterized by skin lesions, internal organ degeneration, and aberrant behavior—symptoms also connected to photosensitivity disorders [25], which are more common at such latitudes. Suppose that during the height(s) of the Ice Age, the hare population was pushed southward, and while there experienced selection pressures resulting in a loss both of its white color and resistance to ingested photosensitive pigments. With their return north-

ward, selection for white color again became imperative, but this conflicted with a renewed need to be protected from photosensitive pigments (dark pelage helps protect organisms from this problem). It has been suggested [26] that two different morphs within the snowshoe hare population are battling it out for supremacy. As photosensitivity also affects reproduction in lagomorphs and other animals [27], perhaps at the low point in the cycle the one factor is favored, but as population levels rise this selection conflicts with its socio-demographic dynamics.

Both of these examples are based on supposition at the moment, but these are the kinds of lagged effects that cannot be ruled out as natural selection responds to a succession of immediate circumstances, without anticipating ultimate implications of the larger-scale system’s path (<http://people.wku.edu/charles.smith/once/finalc.htm>).

3.2.3. Explicit Constraints

Finally, we come to the potentially most interesting kind of constraint that could be operating on the “removal of the unfit”: *a priori* structural limitations.

Although it is apparent that most mutations are deleterious and result in individuals that are either aborted after conception or cannot compete and die before reproducing, the full controls affecting these eventualities are undoubtedly far from fully known. The DNA molecule is a highly stable one, both as an immediate organizer of biochemical activity and as an evolutionary structure, but we have no way of knowing at present whether its evolution is solely due to a stochastically arrived-at random walk over time, or further influences of a prior structural type. Beyond this, the same can be said for the environment outside the organism.

In 1986, I advanced a model [28], derived in part from the thoughts of

the philosopher Benedict de Spinoza, that involved a curious idea: that all natural systems might be underlain by a single, common, form of structural organization related to the way they subsystemize internally. In the years that followed, a particular version of this theory emerged; this is amenable both to simulation and empirical application. A number of simulations and pilot studies followed, all of which continue to support the potential viability of the approach. Further details are not important at the moment, but the notion that there could be *a priori* constraints on the nature of diversification is an interesting one to contemplate.

In such a world, not only would many structures not have come into being (as a matter of chance or stochastic inevitability), but their existence, as a functioning element of physical space, would be impossible *a priori*. This is not to say that an infinite number of forms and eventualities would not still be possible, just that a “larger” infinite number would not be. Otherwise put, a “final cause” would be introduced into play that would absolutely restrict natural expression of form and structure to a subset of what might otherwise be viewed as possibly resulting from a simple (or constrained at the time) “random walk”-like process.

Natural selection—the removal of the unfit—would operate locally in exactly the way Wallace imagined, keeping populations “up to snuff.” But its results would become more and more a function of organization taking place at a more remote level as global biogeochemical cycles came into equilibrium with the “final cause” and established local spatial/temporal conditions of turnover of all fundamental resources. Thus, the opportunities for “being in the right place at the right time” would tend to become more subtle, more stable, and less confining: actually, in one sense *less* diverse, if one considered the matter in terms of extremes of condition only.

Meanwhile, the DNA molecule itself would be affected in interesting ways. As its own system having to conform to the basic structural limitations implied by the final cause (of internal pattern of subsystemization), most significant changes away from its already-existing form would not be possible, thus thwarting either the initial stages of reproduction (including fertilization itself), or later ones. Some such processes arguably would represent a selection process that was *not* natural selection as we (or for that matter Wallace) would recognize it, as it would remove individuals from existence before they could environmentally (or even developmentally) engage. Yet it could also be argued that natural selection was being influenced by this process, because the individuals produced under this constraint would no longer represent a “random” sample of the totality of imaginably emergent structures, but one from which a nonrandom sample of forms had been removed *a priori*.

The particular general systems theory model I have introduced in this regard may or may not prove to mirror reality, but even if it does not, a conceptually more apt approach might yet retain some of its properties. The notion of the possible existence of *a priori* constraints on structural *complexity* in a physical, dimensional, world, is a fascinating one, and one not necessarily so hard to demonstrate as one might initially imagine.

Whatever the fate of the individual theoretical scenarios briefly described above, the more general point with regard to natural selection still stands. This is, as Wallace understood many years ago and others have since, that the actual causal basis of a model of change that relies on tautological ideas is likely to remain obscure. To examine the root factors for a process as complex as evolution, we need to identify potential causalities in a way

that does not confuse causes with results.

4. CONCLUSION

I am not alone in thinking that some fresh approaches are in order. Bowler has recently expressed some reservations about the “Darwin industry,” stating: “modern Darwinians may actually benefit from diverting some of their energy to uncovering and making more visible the work of those evolutionists who looked for other ways of trying to explain the development of life on Earth [29].” In another recent column, historian and sociologist Stephen Shapin aptly writes:

‘Adaptationists’ take it as securely established that organic change proceeds through the natural selection of individual traits, each of which improves the organism’s reproductive chances, that each trait’s evolutionary end-point represents an optimum, and that no other process is needed for an evolutionary lineage to move along through time. But adaptationism has distinguished critics within biology departments—Richard Lewontin, Niles Eldredge, and the late Stephen Jay Gould among them—and they have argued that there is a difference between asserting adaptation as a possible means of getting smoothly from evolutionary point A to point B and establishing that this is in fact how organic change has occurred. Maybe there are developmental constraints on how traits change, and change with respect to other traits; maybe some traits are accidental by-products of changes in other traits; maybe evolutionary change is in fact discontinuous; maybe there is a dialectical causal relationship between

organisms and the environmental niches to which they ‘adapt’; maybe processes other than adaptation are at work but we just don’t know much about them yet. The adaptationist camp includes Dawkins, Dennett, and Pinker—some of the most enthusiastic Darwin Year celebrants. Adaptationists tend to give spectators a misleading picture of the scientific state of play, while at the same time laying claim to a founding father who in fact had reservations about the power and sufficiency of natural selection. There is a struggle among scientists for Darwin’s soul. It is understandable that modern evolutionists should configure history as best suits present purposes, but truth in advertising should be part of the exercise [30].

Chomsky [31], Deacon [32], and others, meanwhile, have expressed reservations with the Darwinian approach to the evolution of language. Similar reservations may be found in works regarding other adaptationism-related evolutionary subjects [33]. Meanwhile, in his study of explanation in Darwinian evolutionary theory Bock [34] agrees with me that “Natural selection is better treated as either survival of the fit (*i.e.*, not *fittest*), or as elimination of the unfit.”

Despite the basically critical nature of my remarks here, I feel that a “demoted” natural selection—Wallace’s “elimination of the unfit”—is likely to result in a clearer understanding of how selection promotes an evolutionary agenda. In particular, a greater focus on longer term, larger-scale environmental interdependencies, should invigorate ecological and biogeographical studies, and give us new kinds of insight into those natural processes that have made us who and what we are.

REFERENCES

- Wallace, A.R. On the law which has regulated the introduction of new species. *Ann Mag Nat Hist* 1855, 16, 2nd series, 184–196.
- (a) Wolf, B.W.; Lindell, J.; Backström, N. Speciation genetics: Current status and evolving approaches. *Phil Trans Roy Soc B* 2010, 365, 1717–1733; (b) Langerhans, R.B. Predicting evolution with generalized models of divergent selection: A case study with poeciliid fish. *Integr Comp Biol* 2010, 50, 1167–1184; (c) Reznick, D.N.; Ricklefs, R.E. Darwin's bridge between microevolution and macroevolution. *Nature* 2009, 457, 837–842.
- Lewontin, R.C. *Adaptation*. In: *Conceptual Issues in Evolutionary Biology*, Sober, E., Ed.; MIT Press: Cambridge, MA, 1984; on pp 237–238.
- Morgan, C.L. Elimination and selection. *Proc Bristol Naturalists' Soc* 1888, 5, 273–285.
- (a) Morgan, C.L. *Animal Life and Intelligence*; Ginn: Boston, 1891, pp 79–80; (b) Morgan, C.L. Natural selection and elimination. *Nature* 1888, 38, 370.
- (a) Hutton, F.W. Darwinism and Lamarckism, Old and New; G. P. Putnam: New York, 1899, p 128; (b) Thompson, J.A. The endeavour after well-being. *Nat Sci* 1896, 8, 21–26; (c) Weed, C.M. The hibernation of Aphides. *Psyche* 1896, 7, 351–362; (d) Poulton, E.B. *Theories of evolution*. *Hope Rep* 1894, 1, 371–393.
- Wallace, A.R. The colours of animals and plants. I. The colours of animals. *Macmillan's Mag* 1877, 36, 384–408, on p 405. Considerably earlier, in an 1866 letter to Darwin, he wrote: "Natural Selection . . . does not so much select special variations as exterminate the most unfavourable ones" (Alfred Russel Wallace Letters and Reminiscences); Marchant, J., Ed.; Harper: New York, 1916; on p 141.
- Wallace, A.R. Human selection. *Fortnightly Rev* 1890, 48, on p 337.
- Tooley, S.A. Heredity and pre-natal influences: An interview with Dr. Alfred Russel Wallace. *Humanitarian* 1894, 4, 80–88.
- Wallace, A.R. The method of organic evolution. II. *Fortnightly Rev* 1895, 57, 435–445, on p 438.
- Wallace, A.R. The world of life: As visualised and interpreted by Darwinism. *Fortnightly Rev* 1909, 85, on p 424.
- Wallace, A.R. *Evolution*. In: *The Progress of the Century*; Harper & Brothers: New York, 1901; on p 26.
- Wallace, A.R. The origin of species and genera. *Nineteenth Century* 1880, 7, 93–106, on p 104.
- On page 62 of Wallace's original natural selection essay of 1858 (On the tendency of varieties to depart indefinitely from the original type. *J Proc Linn Soc: Zool* 1858, 3, 53–62), he describes the action of natural selection through a now famous analogy: "The action of this principle is exactly like that of the centrifugal governor of the steam engine, which checks and corrects any irregularities almost before they become evident; and in like manner no unbalanced deficiency in the animal kingdom can ever reach any conspicuous magnitude, because it would make itself felt at the very first step, by rendering existence difficult and extinction almost sure soon to follow." In 1972 Gregory Bateson suggested that with these words Wallace had become the first cybernetician: ". . . The steam engine with a governor is simply a circular train of causal events, with somewhere a link in that chain such that the more of something, the less of the next thing in the circuit . . . If causal chains with that general characteristic are provided with energy, the result will be . . . a self-corrective system. Wallace, in fact, proposed the first cybernetic model . . . Wallace saw the matter correctly, and natural selection acts primarily to keep the species unvarying . . ." (Steps to an Ecology of Mind; Chandler Publishing Co.: San Francisco, 1972, on p 435). For a recent perspective see: Bell, G. Fluctuating selection: the perpetual renewal of adaptation in variable environments. *Phil Trans Roy Soc B* 2010, 365, 87–97.
- (a) Van Valen, L. A new evolutionary law. *Evolutionary Theory* 1973, 1, 1–30; (b) Ridley, M. *The Red Queen: Sex and the Evolution of Human Nature*; Penguin Books: New York, 1995.
- Hutchinson, G.E. The influence of the environment. *Proc Natl Acad Sci* 1964, 51, 930–934.
- (a) Qian, H.; Wang, S.; Li, Y.; Wang, X. Breeding bird diversity in relation to environmental gradients in China. *Acta Oecologica* 2009, 35, 819–823; (b) Keil, P.; Simova, I.; Hawkins, B.A. Water-energy and the geographical species richness pattern of European and North African dragonflies (Odonata). *Insect Conserv Divers* 2008, 1, 142–150; (c) Hawkins, B.A.; Porter, E.E. Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. *Global Ecol Biogeog* 2003, 12, 475–481; (d) Hawkins, B.A.; Porter, E.E. Water-energy balance and the geographic pattern of species richness of western Palearctic butterflies. *Ecol Entomol* 2003, 28, 678–686; (e) Hawkins, B.A.; Field, R.; Cornell, H.V.; Currie, D.J.; Guégan, J.-F.; Kaufman, D.M.; Kerr, J.T.; Mittelbach, G.G.; Oberdorff, T.; O'Brien, E.M.; Porter, E.E.; Turner, J.R.G. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 2003, 84, 3105–3117.
- Smith, C.H. *The Dynamics of Animal Distribution: An Evolutionary/Ecological Model*. University of Illinois: PhD Dissertation, 1984, on p 62. Available at: <http://people.wku.edu/charles.smith/DISS/dissertation.htm>. Accessed March 27, 2011.
- (a) Smith, C.H. A contribution to the geographical interpretation of biological change. *Acta Biotheor* 1986, 35, 229–278; (b) Smith, C.H. Historical biogeography: geography as evolution, evolution as geography. *New Zealand J Zool* 1989, 16, 773–785.
- (a) Kimura, M. *The Neutral Theory of Molecular Evolution*. Cambridge University Press: Cambridge, UK, 1983; (b) Nei, M. Selectionism and neutralism in molecular evolution. *Mol Biol Evol* 2005, 22, 2318–2342.
- Wagner, A. Neutralism and selectionism: A network-based reconciliation. *Nat Rev Gen* 2008, 9, 965–974.
- In a recent paper (Links between global taxonomic diversity, ecological diversity and the expansion of vertebrates on land. *Biol Letters* 2010, 6, 544–547) S. Sahney, M.J. Benton, and P.A. Ferry have made related arguments in trying to understand dinosaur diversification as a function not of competition, but of occupying new environments.
- Lane, N. *Oxygen: the Molecule that Made the World*; Oxford University Press: New York, 2002.
- (a) Chitty, D. A note on shock disease. *Ecology* 1959, 40, 728–731; (b) Christian, J.J. The adreno-pituitary system and population cycles in mammals. *J Mamm* 1950, 31, 247–259; (c) Green, R.G.; Larson, C.L. A description of shock disease in the snowshoe hare. *Am J Epidemiol* 1938, 28, 190–212; (d) Green, R.G.; Larson, C.L. Shock disease and the snowshoe hare cycle. *Science* 1938, 87, 298–299.

25. (a) Graham, K. Entomological, ecological, and evolutionary implications of photodynamic action. *Can J Zool* 1972, 50, 1631–1636; (b) Selas, V. UV-B-induced plant stress as a possible cause of ten-year hare cycles. *Popul Ecol* 2006, 48, 71–77.
26. Sinclair, A.R.E.; Chitty, D.; Stefan, C.I.; Krebs, C.J. Mammal population cycles: Evidence for intrinsic differences during snowshoe hare cycles. *Can J Zool* 2003, 81, 216–220.
27. (a) Ben Saad, M.M.; Maurel, D.L. Long-day inhibition of reproduction and circadian photogonadosensitivity in Zembra Island wild rabbits (*Oryctolagus cuniculus*). *Biol Reprod* 2002, 66, 415–420; (b) Hague, E.B.; Hague, T.E. Aspects of intra-relevancies of photoperiodism: A review. *J Interdisciplinary Cycle Res* 1970, 1, 89–93.
28. Smith, C.H. A general approach to the study of spatial systems. I. The relational representation of measurable attributes. *Int J Gen Syst* 1986, 12, 359–384.
29. Bowler, P.J. Do we need a non-Darwinian industry? *Notes Rec R Soc* 2010, 63, 393–398.
30. (a) Shapiro, S. The Darwin show. *London Rev Books* 2010, 32, 3–9. See also parallel remarks in (b) Safina, C. Darwinism must die so that evolution may live. *The New York Times*, 10 February 2009, D3; (c) Damiani, G. Corrections to chance fluctuations: quantum mind in biological evolution? *Rivista di Biol* 2009, 102, 419–446.
31. Chomsky, N. Three factors in language design. *Ling Inq* 2005, 36, 1–22.
32. Deacon, T.W. A role for relaxed selection in the evolution of the language capacity. *Proc Natl Acad Sci* 2010, 107 (suppl 2), 9000–9006.
33. (a) Kutschera, U. Symbiogenesis, natural selection, and the dynamic earth. *Theory Biosci* 2009, 128, 191–203; (b) Reiss, J.O. *Not by Design; Retiring Darwin's Watchmaker*; University of California Press: Berkeley, 2009; (c) Wainwright, M. *The origin of species without Darwin and Wallace*. *Saudi J Biol Sci* 2010, 17, 187–204.
34. (a) Bock, W.J. Multiple explanations in Darwinian evolutionary theory. *Acta Biotheor* 2010, 58, 65–79. (b) Fogel, G.B.; Fogel, D.B. Simulating natural selection as a culling mechanism on finite populations with the hawk–dove game. *Biosystems* 2011, 104, 57–62; (c) Venette, R.C.; Kriticos, D.J.; Magarey, R.D.; Koch, E.H.; Baker, R.H.A.; Worner, S.P.; Gómez Raboteaux, N.N.; McKenney, D.W.; Dobesberger, E.J.; Yemshanov, D.; De Barro, P.J.; Hutchison, W.D.; Fowler, G.; Kalaris, T.M.; Pedlar, J. Pesk risk maps for invasive alien species: a roadmap for improvement. *BioScience* 2010, 60, 349–362.