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The three faces of ecological fitness

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ABSTRACT

This paper argues that fitness is most usefully understood as those properties of organisms that are *explanatory* of survival in the broadest sense, not merely *descriptive* of reproductive success. Borrowing from Rosenberg and Bouchard (2009), fitness in this sense is *ecological* in that it is defined by the interactions between organisms and environments. There are three sorts of ecological fitness: the well-documented ability to *compete*, the ability to *cooperate* (as in mutualistic symbiosis), and a third sense of fitness that has received insufficient attention in evolutionary theory, the ability to *construct*. Following Lotka, it can be understood thermodynamically as the ability to maintain or enlarge the energy-circulating capacity of an ecosystem. An organism that does this could end with its gene frequency unchanged but its probability of survival enhanced since it would sustain or increase the total carrying capacity of its ecosystem. Photosynthesizers and other autotrophs are obvious candidates for organisms that are fit in the constructive sense, but any organisms, including heterotrophs, can exhibit constructive fitness if they have some mechanism for channeling external flows of free energy into their ecosystems. I will briefly examine the prospects for the human species in the light of these considerations.

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1. What could Darwinism be?

To speak of a thing called *Darwinism* suggests that one is speaking of an ideology, and this seems to be a particularly inappropriate way to describe the work of Charles Darwin, who was himself one of the most non-ideological of thinkers. Much of Darwin's greatness as a scientist stemmed precisely from his dogged determination to see things as they *are* and not as he or anyone else might have presumed that they ought to be on the basis of some set of fond preferences or established doctrine. Think of his meticulous studies of barnacles and earthworms—not to mention the infinitely painstaking way he amassed of all the biological facts he could find that might pertain to the mechanism of evolution. Darwin strove not to fit the phenomena of nature into a preconceived pattern but rather to let nature tell him the patterns it prefers. Thus it is surely not contrary to the spirit of Darwin himself to inquire whether, after everything that has been learned in the past 150 years, it is necessary to go beyond his theory in certain particulars.

If there is one component of Darwin's thought that is likely to survive, it is his core hypothesis that the evolution of species can be explained by natural selection. This profound insight has by now been exceedingly well confirmed, and there is even reason to think that it could be extended to explain the evolution of whole universes (Smolin, 1998). In modern terms, natural selection is a recursive process in which variations in the traits of successive generations are amplified or damped by feedback from the environment (Dennett, 1995). Such modulated recursivity allows for the evolution of arbitrarily complex adaptability; it could be called "design without design," "teleology without teleology," or more precisely "teleology without intentionality." It is modulated recursion that explains how evolution can get from archaeobacteria to an elephant—or a being like Charles Darwin himself. One of Darwin's great contributions, therefore, was simply to draw our attention to the importance of recursion in the natural world. The centrality of recursion in the way the world works is not surprising, since in pure mathematics it is the most general way of generating structure (Hofstadter, 1979). If there is someday a Theory of Everything

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that could be put on a T-shirt (Poundstone, 1985; Falk, 2002), it may well be a set of recursion relations, not an equation.

The aim of this paper is to critically examine and extend the notion of *fitness* in the light of these general considerations about the nature, importance, and possible limitations of Darwinism.

2. Historical sketch

Herbert Spencer (1852) had the germ of the idea of natural selection. Although he did not use the word “fitness” until his *Principles of Biology* (1866), he argued that those organisms in whom “the power of self-preservation is the greatest” (1852, p. 500) would tend to increase in numbers at the expense of other organisms, and he did not hesitate to explain this power as a consequence of traits such as strength, agility, swiftness, and (most important he thought in the long run) “sagacity.” By the sixth edition of *Origin of Species* (1872) Darwin had adopted the term “fitness” himself and, like Spencer, he took it to be virtually synonymous with natural selection. The notion of fitness (even though it was unclear) was appealing to Spencer and Darwin because it seemed to offer an intuitive explanation of why some organisms thrive while others die out. Presumably, fitter organisms survive in roughly the same sense in which fitter athletes tend to win more events; more precisely, as Gould points out (1977, p. 42), certain “morphological, physiological, and behavioral traits . . . confer fitness by an engineer’s criterion on a good design.” If an athlete’s challenge is to succeed at basketball, height is a useful trait to have; if a bird’s challenge is to fly efficiently, lighter bones are a useful trait to have. Fitness in this sense is thus *explanatory* of the ability of an organism to meet the survival challenges its environment poses for it.

The question then becomes what sorts of traits can explain survival. T. H. Huxley, “Darwin’s bulldog,” saw fitness in competitive terms, and famously described nature as a “gladiator’s show” (1888, p. 330). The Russian expatriate biologist P. Kropotkin (1902) argued that in order to understand why some organisms flourish while others do not, the ability to cooperate is as important as the ability to compete. He coined the phrase “mutual aid” to describe the tendency of organisms to cooperate to their mutual benefit, and insisted that the capacity for mutualism was favoured by natural selection, especially in harsh environments where survival can depend upon the ability to share resources. Several late 19th century biologists (notably S. Schwendener, A. Frank, and A. de Bary) introduced the notion of symbiosis (“living together”) according to which organisms (such as lichen) survive by cooperative functionality (Sapp, 1994). Symbiosis, as understood by de Bary and most modern biologists, includes outright mutualism only as a special case; what makes a relationship between different organisms symbiotic is that they include each other in their life-cycles (metabolic or reproductive) in some regular way. For example, the complex relationship between the malaria parasite and its several hosts is paradigmatically symbiotic, though not mutualistic in any obvious way. Such relationships are among the traits of organisms that can be reinforced by natural selection.

The capacity for symbiosis may be encoded genetically or (in the cases of organisms with sufficiently complex neurosystems) behaviorally. K. S. Merezchkovskii (Sapp, 1994) introduced the term *symbiogenesis* to denote cases (such as the lichen) in which distinct branches of the tree of life merge symbiotically to form new kinds of organisms. It is possible to define a “scale of symbiosis,” running from outright Malthusian pathogenic parasitism on one end to symbiogenesis at the other, and this scale can be understood as based upon an increase in the mutualistic direction of dynamic synergicity (or, equivalently, the sharing of negentropy) (Peacock, 2010). The most dramatic example of symbiogenesis is serial endosymbiosis, the process in which eukaryotic cells formed

as symbiotic associations of prokaryotes. Serial endosymbiosis theory (SET) had been proposed by several authors in the late 19th century (Sapp, 1994) but it was not taken seriously until modern times, when it was revived by Lynn Margulis (1993) and could finally be confirmed by means of the electron microscope and various techniques in molecular biology (Gray, 1992).

Symbiosis is arguably not only an important adaptation but a source of evolutionary novelty that could be at least as important as mutation and recombination (Sapp, 2004). One of the most important aspects of symbiosis is the transition or phase change that often occurs between individual and collective behavior, and one of the central unsolved problems of biology and medicine in our time is to better understand when and how these transitions occur (Peacock, 2010). Such symbiotic phase shifts define new units of selection, in that natural selection sees the symbiotic unit as a whole under many circumstances; that is, selection acts on the *symbiome* (the term Sapp, 2004, usefully proposes for the symbiotic unit) and not just its components. It is very hard to see symbiosis as entirely due to the operation of selfish genes, especially since in symbiogenetic unions genes may actually be lost if they are redundant (Smith, 1979).

The study of symbiotic complexes such as the protist *Myxotricha paradoxa* (Peacock, 2010) suggests that one can distinguish between well-studied *external* evolution, when organisms evolve in response to adaptive challenges from other distinct organisms or the abiotic environment, and *internal* evolution (not as well studied), when a symbiotic complex evolves internally while retaining its identity as a whole (Peacock, 2010). Complex symbiomes can evolve *internally*—that is, the lineages of which they are composed can coevolve *inside* the envelope of the metagenomic symbiome—while the symbiome may retain its identity as a single, continuously living system for quite a long time, long enough for it to constitute, in effect, an environment to which its symbiotic components must adapt cooperatively. The failure to distinguish between internal and external evolution has arguably hampered the study of symbiosis from the beginning (Peacock, 2010).

Despite the rather obvious ways in which the reality and importance of symbiosis challenges the Huxleyan competitive paradigm (and it may indeed be “Huxleyism” rather than Darwinism that I am questioning here), and despite its widespread occurrence throughout nature, symbiosis was almost entirely ignored by mainstream evolutionary biologists during most of the 20th century—except perhaps as one of those odd adaptations that life may occasionally have. Instead, evolutionary theory took a positivistic turn with the creation of population genetics (Provine, 1971). Fitness becomes simply a measure of competitive success, the tendency of an organism to increase the representation of its genes in successive generations. (This insistence on considering only the *outputs* of complex functionality has a parallel in behaviorism in psychology, which was a major trend around the same time that classical population genetics arose.) Population genetics is a mathematical theory with considerable predictive power; however, debate continues (Rosenberg & Bouchard, 2009) about its meaning and whether it does encompass all of the phenomena that should be of interest to an evolutionary biologist. It is often accused of being tautological; furthermore, from the symbiotic point of view a major weakness is that it implicitly takes competition to be the only strategy that could explain survival. An extreme version of this interpretation is Richard Dawkins’ “selfish gene” theory (1976), which treats the gene essentially as a virus (Peacock, 2010).

Another problem with the classical view of fitness is that it fails to take account of the tension between local and global constraints, which is of central importance in understanding symbiosis. Gould (1977) defends an explanatory conception of fitness, but says that for Darwin it amounted to adaptation to the “immediate, local environment” (p. 45); as I shall argue in more detail below, this

can't be the whole story of fitness, since a species' ability to survive, especially for more than a relatively few generations, can depend critically upon its adaptation to global, long-range, and long-term environmental demands as well as those that are local and immediate.

Several more nuanced notions of fitness have been explored. An important distinction can be made between fitness as reproductive success in the next generation (winning it all now) and fitness as long-term survival (staying in the game). Sober (2001) calls the former *viability* and the latter *fertility*. The notion of *inclusive fitness* can go a long way toward explaining how symbiosis can be favoured by natural selection (Trivers, 1971), but it is not clear that it can fully explain symbiogenesis. It is necessary to reformulate the problem that the concept of fitness is supposed to solve.

3. A larger canvas

Let us recall that the problem Darwin originally set himself was to explain the *origin* of new species—that is, what he took to be the observed fact that new species evolve over the long course of geological time. Natural selection explains this brilliantly (even granting the neglect of symbiosis). However, framing the problem this way naturally draws attention to the *competitive* survival strategies that members of new species may use to assert their place in the world. If one's problem is to explain how a novel variant may turn into a distinct species, one must indeed look for an explanation of why the numbers of its individuals increase or (in more modern terms) why its representation in the total gene pool increases.

However, it has been apparent for a long time in the field of ecology (Odum, 1971; Tansley, 1935) that the evolution of new species is not the only strategy that life has for continued survival, and a number of authors have attempted to bring an awareness of this fact into the mainstream of evolutionary thought (Bouchard, 2008; Thoday, 1953; van Valen, 1973). From this broader explanatory perspective, we need to understand fitness as whatever traits, propensities, or properties life may possess that enables it to continue to remain life. Darwin and Spencer saw fitness as explanatory of evolution. But reproduction itself (and the speciation and Darwinian evolution consequent upon it) is really just one of perhaps a variety of survival strategies or propensities possessed by life that collectively constitute fitness. The very ability of life to evolve is *itself* a form of fitness. Therefore, in order to understand fitness today, 150 years after the publication of the *Origin*, we must focus our attention on a larger problem than the one that Darwin himself considered; that is, we need to investigate not only the origin of species but their persistence in the complex ecological settings that they, themselves, help to create and maintain.

This is hardly to minimize the importance of evolution. It is, to say the least, a good survival strategy when environmental conditions change, and since the survival problems posed by ecological conditions are always changing (though from time to time to significantly different rates) evolution will always occur. As Thoday put it, "life could not arise except in a changing world, and once arisen life itself is change and must accommodate itself to the change of which it becomes part cause" (1953, pp. 111–112). However, as Thoday insisted, the persistence of life is certainly favoured in many situations by ecological stability, and also by the sorts of cooperative and constructive functionality that are especially apparent in the study of symbiosis (Bouchard, 2008; Peacock, 2010). Evolution and speciation are not the only survival strategies, and therefore fitness is not merely that which explains evolution; it must also be that which explains the persistence and stability of life itself.

It is helpful to think of the workings of evolution in terms of feedbacks. Systems theory distinguishes both positive and negative feedback. Positive feedback is a response to a signal that increases

the strength of that signal, while negative feedback decreases the strength of an initial signal. Positive feedback therefore amplifies a signal while negative feedback damps it. We can think of the appearance of a novel heritable variation as a signal. The evolution of a new species is a phase of ecological disequilibrium in which the composition of the populations of organisms from which that species emerges must shift. During the evolutionary phase, when the number or genetic representation of a new species increases, positive feedback must necessarily be dominant. Positive feedback can often lead to the very rapid amplification of a signal, and this could be part of the explanation for the punctuated equilibrium controversially noted by Gould and Eldredge (1977). However, ecosystems can also exist in states of dynamic quasi-equilibrium; such quasi-equilibria are prone to shift at the slightest provocation, but often they can also persist for quite long periods of time (essentially for thermodynamic reasons—they are efficient generators of entropy) and exhibit surprising stability in the face of external perturbations. Periods of relative stability are characterized by a balance of positive and negative feedbacks. For instance, an emergent organism may claw out for itself a place at the ecological table by out-reproducing other organisms with similar resource needs, but there will come a point at which its reproduction is balanced as predators and parasites become adapted to it or as critical resource limitations impose themselves; at that point, the organism's best survival strategies (the strategies that enable it to leave any offspring *at all*) may well be symbiotic.

Robert Brandon (2008) states, "Biology starts when reproduction begins." But this is surely not the whole story about how life begins, and not merely because most organisms do not spend more than a small proportion of their lives reproducing. I won't attempt here a full characterization of what distinguishes life from non-life, but one can certainly say, at least, that biology on this planet started when a certain type of self-maintenance becomes possible in dissipative systems constructed out of carbon-chain molecules. Reproduction is one of the most important and effective means of self-maintenance but not the only one, and there could conceivably be organisms that do not reproduce at all, at least in the sense of the multiplication of discrete individuals. There could even be organisms for which reproduction is a relatively unimportant method of self-propagation; a possible dramatic example, adduced by Bouchard (2008), is the quaking aspen. Groves of these trees are often a single massive clone, acres in extent, and in some cases possibly up to a million years old. For many organisms, the need to reproduce is minimized by successful long-term survival (a fact that Spencer correctly guessed; 1852). Just as there is often selection for the ability to expand rapidly, there is also selection for stability and longevity.

These ecological factors are often ignored in literature on population ecology, where the *only* signs of ecological success are measures of the tendency of a species or variant to increase its representation in successive generations (Hamilton, 2009). That notion of fitness is relevant only to the expansion phase of an organism's history, which could be a relatively short period in its tenure on Earth. Competitive ability may explain why a new species was able to establish itself, but it could be insufficient to explain why the organism remains in business for (in the cases of some species) millions of years. Some broader conception of fitness is needed.

4. Is life necessarily a struggle for existence?

The subtitle of Darwin's great work refers to the "preservation of favoured races in the struggle for life." Darwin understood that there is struggle both between organisms competing amongst themselves for resources, and also (more figuratively speaking)

against the hostility of the abiotic world. But the metaphor “struggle” is misleading. Life, dare we say it, is *natural* in certain broadly favourable circumstances; its early origins on Earth and long persistence could not be explained otherwise. A hawk floating effortlessly on an updraft could hardly be said to be struggling. It’s more like a struggle, albeit brief, for the mouse that the hawk stoops upon. But both hawk and prey and their supporting ecosystems float, as it were, on an updraft of free energy (provided largely by the sun). To an important degree life survives by *not* struggling, but rather fitting itself gracefully to the flows of energy and matter that our universe (harsh though it can be) often so generously provides. Much of fitness is “*fit*”-ness—the ability to accommodate to flows of energy, materials, and information in highly efficient ways. The metaphor of competitive struggle is appropriate during the expansionary phase of an organism’s evolution, or in the periods of crisis that inevitably obtrude from time to time during the career of a species or individual, but it cannot be the whole story about how life conducts its business. This is another respect in which seeking a “balanced, overall view of life” (in the words of an anonymous referee) requires us to paint on a larger canvas than the one used by Darwin himself—since Darwin’s main concern was specifically to solve the narrower problem of evolution.

5. What, then, could fitness be?

In order to understand why some organisms flourish and others do not, one needs to look behind the phenomenology of competitive fitness and inquire into those dispositions and traits that conduce to survival. There is nothing scientifically wrong with trying to broadly categorize how organisms meet the survival challenges they face, any more than there is nothing misleading about noting that a hawk’s superb eyesight suits it especially well for hunting. Perhaps if we were to re-run the history of evolutionary biology it would have been less confusing to introduce a new technical term to denominate differential reproductive success. Then one could explore the ways in which such a parameter was a function of fitness. Instead, I will borrow the term *ecological fitness* from Rosenberg and Bouchard (2009) to describe those traits, dispositions, and properties of organisms that tend to suit them for (and are thereby explanatory of) survival—where (as indicated above) survival is understood as not *merely* reproduction. That we speak of *ecological fitness* is meant to respect four key facts. First, what enables an organism to survive may be a function of the organism’s complex interactions with broad features of its ecology. Second, organisms affect and even partially construct or constitute their own supporting ecologies in fundamental ways. Third, the primary habitat of many organisms is some other organism, or an ecosystem defined and operated by other organisms. Fourth, because organisms must adapt to the habitats they themselves have constructed or affected, evolution involves feedback loops in which organisms must adapt to changes they themselves have caused.

Remarks by Simpson capture the evolutionary importance of the complex relationships between organisms and their habitats:

Adaptation is a fitting together of organisms and, in the very broadest sense, environments. . . the physical environment has its own ‘fitness’ . . . [and] it is adapted to life as well as life to it . . . adaptation is a reaction between the two and not of one to the other . . . (1953, p. 181).

It is essential, therefore, to make room for broader conceptions of fitness than those based merely on competitive ability. Orthodoxy says that the fittest organisms are those who increase their gene frequency in succeeding generations—at the expense of other species or varieties. This implicitly treats *all* forms of life as parasitical, and it can’t be the whole story of fitness. An organism that somehow maintained or increased the carrying capacity of its

ecosystem would thereby protect or increase its own long-run probability of survival, even if its gene frequency stays roughly the same from one generation to the next. Indeed, there are known to be examples of such organisms, commonly called “plants.” I do not mean to suggest that many plant species would not increase their numbers in succeeding generations if they got the chance, just as Malthus said they would; rather, I am saying that most plants have become superbly adapted to holding the course, so that their net interactions with other life-forms are, on the whole, mutualistic in the key sense that they share the free energy they have garnered from the sun in ways that supports many other forms of life and thereby their own habitats as well.

As a thought experiment, imagine the following hypothetical case: Suppose there is an organism that never exists in more than a vanishingly small proportion of the population. However, like a benign gardener it manipulates or affects its surroundings in ways that stabilize the carrying capacity of its environment against perturbations. Its immediate interactions with other organisms in the system are minimal (or occasionally perhaps even locally destructive, like a gardener who pulls weeds). But it is a covert mutualist in the sense that the system might not exist, or at least in such richness, without it. Let us call such a hypothetical organism an “anti-parasite;” it would be among the fittest of organisms, for the result of its interactions with its environment would increase its own probability of long-term survival as well as its supporting ecosystems as a whole. The existence of such beings is possible, at least in principle.

Despite the work of many authors (including but not limited to Brooks & Wiley, 1986; Corning, 1983; Depew & Weber, 1995; Lotka, 1922; Odum, 1971; Schneider & Kay, 1994; Schneider & Sagan, 2005; Wicken, 1987), insufficient attention is still being paid to the biophysics of the kind of mutualism described here, in which organisms help to maintain or even expand the ecosystems in which they participate. In order to understand the ways in which organisms can be fit it is essential to understand the thermodynamics of ecological interactions. Ecosystems and the organisms of which they are in part composed belong to the class of physical systems called dissipative structures (Prigogine, 1980). These are stable cyclic patterns that form spontaneously in flows of free energy and matter far from thermodynamic equilibrium. Such structures are notoriously difficult to analyze mathematically, and the conditions under which they form are still not well understood. Nevertheless, the concept of the dissipative structure is extremely general and it can be expected to find increasing applications.

All dissipative structures require a continuous flow of external free energy for their maintenance. Most ecosystems on Earth are directly or indirectly powered by the sun although not necessarily so; for example, the rich communities around deep-sea hydrothermal vents are powered largely by geothermal energy (Searce, 2006). Dissipative systems are favoured thermodynamically because they are an especially efficient way of degrading free energy into waste heat—or equivalently of generating entropy. (This could be because the feedback loops typical of a dissipative structure allow the system to sample its possible microstates very quickly, although this point still does not seem to be well understood.) Ecosystems function, in effect, as biotic storage batteries and the greater the energy circulating in the system the more complexity they can support.

The energy that powers an ecosystem is typically absorbed by autotrophic organisms, such as plants or chemoautotrophic bacteria, which can derive energy directly from inorganic sources by mechanisms such as photosynthesis. Abstractly, the autotrophs act like valves, diverting external energy flows into the system. They must use some of the energy they capture to run their own metabolisms, but they contribute to the system by capturing *more* free energy than they need for themselves. Heterotrophs (such as

humans) must derive their energy from organic sources, and they are therefore dependent upon the autotrophs. However, heterotrophs (including humans in principle) can be *indirectly* or vicariously autotrophic by *arranging* for autotrophs to do their work (Peacock, 1999). For instance, humans can increase the amount of photosynthesis taking place by appropriate soil cultivation. The evolution of heterotrophic life greatly increased the ecological opportunities for autotrophs, and therefore heterotrophs and the autotrophs they depend upon can be mutualistic in many ways. Humans can be indirectly or vicariously autotrophic *via* technology; there are a variety of means by which we can tap into flows of inorganic energy, including wind power, geothermal power, solar power, nuclear power, or simply the planting of trees. In the (perhaps unlikely) event that we achieve controlled nuclear fusion then we could become independent of the Sun and in principle independent of autotrophic life.

Some neglected observations by A. J. Lotka point to the evolutionary importance of the kind of mutualistic biophysics described above:

But the species possessing superior energy-capturing and directing devices may accomplish something more than merely to divert to its own advantage energy for which others are competing with it. If sources are presented, capable of supplying available energy in excess of that actually being tapped by the entire system of living organisms, then an opportunity is furnished for suitably constituted organisms to enlarge the total energy flux through the system. Whenever such organisms arise, natural selection will operate to preserve and increase them. The result, in this case, is not a mere diversion of the energy flux through the system of organic nature along a new path, but an increase of the total flux through that system (1922).

From the broader perspective sketched in this paper, we can now say that there are three faces of ecological fitness:

1. The ability to compete for a bigger slice of a given ecological pie. This aspect of fitness is (to say the least) well-documented, and is obviously the dominant survival factor in many cases—especially when the ecological pie is large enough that (for a period of time) its finitude can be ignored.
2. The ability to cooperate, defined as an ability to share a given ecological pie in a mutually beneficial way. Cooperative fitness is the basis of mutualistic symbiosis; the extent to which it operates remains controversial. Extensive studies of symbiosis show that there is such a thing, even though there is still much to learn about it, especially the central problem of better understanding the conditions in which assemblages of organisms phase-shift from competitive to cooperative modalities.
3. The ability to construct a bigger pie. I'll call this *constructive* or *Lotkan* fitness. There are a myriad of ways in which organisms exhibit this kind of fitness.

The existence of constructive fitness is recognized in recent work on niche construction by J. Odling-Smee, Laland, and Feldman (2003), and an awareness of the extent to which organisms can alter their supporting habitats constructively has been implicit in ecosystem ecology from the beginning of that discipline. Odling-Smee's term "niche construction" is perhaps too narrow, however; *habitat* construction might be better, because it suggests that constructive organisms do not merely hollow out for themselves a small space within a pre-existent environment, but rather, in many cases, alter the whole fabric of their environments. As Jones, Lawton, and Shachak (1994) indicate, organisms can be "ecosystem engineers," and one "cannot identify any habitat on earth that is not engineered in some way by one or more species" (Jones et al.,

1994, p. 383). However, the fact remains that the ability to be constructive is still the least acknowledged and studied aspect of fitness. I will discuss its possible practical significance for humans below; its theoretical significance in understanding evolution is enormous. The possibility of ecosystem intensification pointed to by Lotka suggests that even if our aim is to explain why the gene frequency of a certain species increases we would not necessarily be looking for a competitive explanation (though that often enough turns out to be what has gone on). It may be that the new species has constructive abilities allowing it to enlarge the total carrying capacity of its ecosystems in ways that make more of the kind of room it needs for itself. It is not a given that this need be done at the expense of other life-forms; even expansion is not necessarily competitive, if there are sufficient reserves of free energy available to the ecosystem.

6. Implications and questions for *Homo sapiens*

With this broader concept of fitness in mind, what is fitness for the human species?

The evolution of the kind of intelligence that enables language and technology has occurred very late in the history of life on Earth. Evolutionary thinkers in the nineteenth century presumed that this manifests some sort of "progress." Spencer took what we would now call increasing adaptive complexity to be the expectable result of evolution and the appearance of intelligence to be its culmination (Spencer, 1852). But is it really the case that humans are capable of acting intelligently? Our unique neurology has allowed for *short-term* dominance of the terrestrial ecosystem. But could our cleverness be in the end our ecological downfall? Up to now, the predominant human modality has been parasitical in a literal sense, with far more of our technological ingenuity directed to extracting resources from the "found" ecology than maintaining that ecology. Historian William McNeill observed that the human capacities for language and technical ingenuity

allowed human cultural evolution to impinge upon age-old processes of biological evolution . . . Time and again, a temporary approach to stabilization of new relationships occurred as natural limits to the ravages of humankind upon other life forms manifested themselves. Yet sooner or later, and always within a span of time that remained miniscule in comparison with the standards of biological evolution, humanity discovered new techniques allowing fresh exploitation of hitherto inaccessible resources . . . Looked at from the viewpoint of other organisms, humankind therefore resembles an acute epidemic disease, whose occasional lapses into less virulent forms of behavior have never yet sufficed to permit any really stable, chronic relationship to establish itself (McNeill, 1976, p. 23).

It is possible that this process of leap-frogging evolutionary constraints is at last coming to an end, with the imminent depletion of key natural resources such as forests and petroleum upon which complex human societies depend, and the very real possibility of catastrophic climate change consequent upon our short-sighted exploitation of these resources (Hansen et al., 2007). Knowledgeable observers warn of the possible "end of ingenuity" (Homer-Dixon, 2006). These uncomfortable facts point to an understanding of what fitness *for humans* must consist of.

Recall Gould's explication of fitness as Darwin apparently understood it, as adaptation to the "immediate, local environment." If this were the only kind of adaptation of which life was capable, it would have long ago obliterated itself in a planetary-scale Hardinian "tragedy of the commons" (1968). In fact, it is possible for local adaptations to cohere symbiotically, but only given the right sort of feedbacks. A central problem for life at all levels

of complexity from prokaryotes on up is to maintain coherence between local and global survival imperatives. Life often, but not always, solves this problem. Cancer is an important example of a Hardinian or perhaps Malthusian crisis in which some cells (for reasons still not understood) get out of touch with globally-appropriate regulatory signals. Micro-organisms and individual metazoan cells must depend upon biochemical signals for symbiotic self-regulation. Organisms with sufficiently complex neurology, however, need not merely react to local stimuli but can sometimes anticipate the future. This is a survival trait that would be powerful indeed, if it could be made to operate reliably.

There are two striking facts about human intelligence. The first is the enormous range and variability of individual neurological capabilities. (This is probably a reflection of the complexity of the human brain, which allows for large fluctuations in performance about the mean.) The second is the jarring disparity between individual intelligence at its best and the collective intelligence exhibited by human societies—not only at their worst, but on average. T. Homer-Dixon has argued that the major challenge of our time is to generate not only technological ingenuity, but also ecologically appropriate *social* ingenuity (Homer-Dixon, 2000). The latter must include the creation of socio-political structures that somehow bring human ingenuity at its best to bear on the large-scale survival problems our species faces today—problems that are largely unintended consequences of the unique neurological adaptations evolved by our immediate ancestors during a long period of turbulent climate change (Wright, 2004).

What is the chance we will succeed? On the basis of reasonable astronomical assumptions, we should have contacted extraterrestrial intelligence by now; but we have not. So where are they? Enrico Fermi first posed this question in 1950, but it has been made acute by the recent discovery of over 300 exoplanets. As Alan Boss observes, “All the evidence gathered to date by over 10 years of planet hunting implies that Earth-like planets should be common” (2009, p. 205). And yet, there is no satisfactory evidence that any beings at least as intelligent as humans, in the way that we are intelligent, are within earshot. One possible answer to Fermi’s Question could therefore be that linguistic-technological intelligence does not conduce to the long-term survival of a species.

On the other hand, there are encouraging precedents, especially apparent in microbiology but found throughout the kingdom of life, which show that transitions from parasitism to mutualistic modalities are not uncommon (Odum, 1971); indeed, they may be precisely what made the long tenure of life on this planet possible. As Kropotkin argued, this mutualistic transition especially tends to occur in constrained environments where cooperation is favoured (Jeon & Jeon, 1976; Margulis, 1998), but it is not guaranteed to happen. If humans are capable of such a symbiotic transition, it can only happen when we *decide* to pay collective attention to the signals our overstressed supporting ecology is sending us.

Our capacity for what a referee for this paper called “teleological engagement” (ironically evolved by means of the ateleological processes identified by Darwin) is both our greatest peril and our greatest hope. Fermi’s interesting astrobiological problem notwithstanding, the most pressing question in our time is whether there is intelligent life on earth—in the sense that true intelligence, understood as a form of fitness that conduces to long-term survival, must entail constructive adaptation to the demands and constraints of the “long-range, global environment.”

7. Summary

Darwin’s theory of evolution by natural selection provides a brilliant and well-tested explanation of the evolution of new

species. However, if Darwinism includes the continued application of the preconception-free, inquisitive methodology of Darwin himself, then it must now paint on a larger canvas than did Darwin, for ecology and studies of symbiosis since his time have shown that the problem is not only to understand how species evolve, but how they persist in the complex ecological settings they have themselves modified. From this viewpoint, the flourishing and persistence of organisms (including humans) can be explained by at least three kinds of ecological fitness: competitive, cooperative, and constructive.

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