
AN ECOLOGY OF REPLICATORS

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Daniel Dennett went only a *little* too far when he wrote, at the beginning of *Darwin's Dangerous Idea* (1995): "Let me lay my cards on the table. If I were to give an award for the single best idea anyone has ever had, I'd give it to Darwin, ahead of Newton and Einstein and everyone else."

He wasn't talking about evolution itself, which was not Darwin's idea, but natural selection, which pretty much was. Today, notwithstanding local school boards in various backwoods and boondocks of the United States, no educated person doubts the truth of evolution. Nor do they doubt the force of natural selection. Natural selection is not the only driver and guide of evolution. At least at the molecular level, random drift is also important (Kimura 1983) but selection *is* the only force capable of producing *adaptation*. When it comes to accounting for the stunning illusion of design in nature, there is no alternative to natural selection. The one idea that might, for a moment, have seemed to be a conceivable alternative, Lamarckism, is not, as has sometimes been suggested, a good alternative theory which just had the misfortune to be false. It isn't even a good alternative theory. The Lamarckian theory is not a big enough theory to account for adaptation. It couldn't work, even on some hypothetical planet where acquired characteristics were inherited (Dawkins 1982a).

If a biologist denies the importance of natural selection in evolution, it is pretty safe to assume *not* that he has some alternative theory but that he simply underrates adaptation as a dominant property of life that needs explaining (Mayr 1983). Probably he has never set foot in a tropical rain forest, or set flipper over a coral reef, or set eyes on a David Attenborough film.

Nowadays, questions about adaptation are high in the consciousness of field biologists. It has not always been so. My old maestro Niko Tinbergen (1963) wrote of an experience when he was a young man: "I still remember how perplexed I was upon being told off firmly by one of my zoology professors when I brought up the question of survival value after he had asked 'Has anyone an idea why so many birds flock more densely when they are attacked by a bird of prey?'"

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Today's student is more likely to be perplexed about what the professor could possibly have meant by his question if *not* survival value. People in Tinbergen's own field of ethology now complain of a stampeding backlash in the other direction, towards an overwhelming preoccupation with Darwinian survival value, at the expense of studies of behavioral mechanisms.

But still when I was learning biology at school, we were warned against a dire sin called 'teleology'. This was actually a warning against Aristotelian final causes, not against Darwinian survival value. Nevertheless, it perplexed me because I had never found final causes the slightest bit tempting. Any fool can see that a 'final cause' is not a cause at all. It is just another name for the *problem* which, eventually, Darwin solved. Darwin showed how the illusion of a final cause could be produced by comprehensible efficient causes. His solution is the only workable one that has ever been suggested, and my hunch is that it will never be superseded. It has of course been refined, by the giants of the Modern Synthesis including Ernst Mayr. Darwin and his twentieth century successors have solved biology's deepest mystery: the source of the illusion of design which pervades the living, but not the nonliving world.

The illusion of design is at its strongest in the body shapes and behavior patterns, the tissues and organs, the cells and molecules of individual creatures. The individuals of every species, without exception, show it powerfully. But there is another illusion of design which we notice at a higher level: the level of ecology. Design seems to reappear in the disposition of species themselves, in their arrangement into communities and ecosystems, in the dovetailing of species with species in the habitats which they share. There is a pattern in the intricate jigsaw of rainforest, say, or coral reef, which leads rhetoricians to preach disaster if but one component should be untimely ripp'd from the whole.

In extreme cases, such rhetoric takes on mystical tones. The womb is of an earth goddess, all life her body, the species her parts. Yet, without giving in to such hyperbole, there *is* a strong illusion of design at the community level, less compelling than within the individual organism but worth attention. The animals and plants that live together in an area seem to fit one another with something like the glove-like intimacy which the parts of an animal display as they mesh with other parts of the same organism.

A cheetah has the teeth of a carnivore, the claws of a carnivore, the eyes, ears, nose and brain of a carnivore, leg muscles that are suitable for chasing meat, and guts that are primed to digest it. Its parts are choreographed in a dance of carnivorous unity. Every sinew and cell of the big cat has meat-eater inscribed through its very texture, and we can be sure that this extends deep into the details of biochemistry. The corresponding parts of

an antelope are equally unified with each other, but in pursuit of a different route to survival. Guts designed to digest plant roughage would be ill-served by claws and instincts designed to catch prey. And viceversa. A hybrid between a cheetah and an antelope would fall flat on its evolutionary face. Tricks of the trade cannot be cut from one and pasted into the other. Their compatibility is with other tricks of the same trade.

Something similar can be said of communities of species. The language of the ecologist reflects this. Plants are primary producers. They trap energy from the sun, and make it available to the rest of the community, via a chain of primary, secondary and even tertiary consumers, culminating in scavengers. Scavengers play a recycling 'role' in the community. Every species, in this view of life, has a 'role' to play. In some cases, if the performers of some role, such as scavengers, were removed, the whole community would collapse. Or its 'balance' would be upset and it might fluctuate wildly, out of 'control' until a new balance is set up, perhaps with different species playing the same roles. Desert communities are different from rainforest communities and their component parts are ill-suited to other such communities just as—or so it seems—herbivorous colons are ill-suited to carnivorous teeth or hunting instincts. Coral reef communities are different from sea bottom communities, and their parts cannot be exchanged. Species become adapted to their community, not just to a particular physical region and climate. They become adapted to each other. The other species of the community are an important—perhaps the most important—feature of the environment to which each species becomes adapted. In one sense, the other species of the ecosystem are just another aspect of the weather. But unlike the temperature and the rainfall, the other species are themselves evolving. The illusion of design in ecosystems is an inadvertent consequence of this coevolution.

The harmonious role-playing of species in a community, then, resembles the harmony of the parts of a single individual organism. The resemblance is deceptive and must be treated with caution. We must not fall for the excesses of group selectionist panglossianism such as the ludicrous concept of 'prudent predators' (Slobodkin 1961). Given my biases, it feels like pulling teeth to say so, but the analogy between organism and community is not completely without foundation. It is one of my purposes in this article to argue that there is an ecology within the individual organism. I am not making the now commonplace point that a large metazoan body contains a community of bacteria, including mitochondria and other modified bacteria. I am making the much more radical suggestion that we should recognize the entire gene pool of a species as an ecological community of genes. The forces that produce harmony among the parts of an organism's body are not unlike the forces that produce the illusion of harmony in the species of a community. There is balance in a rainforest,

structure in a reef community, an elegant meshing of parts whose coevolution recalls coadaptation within an animal body. In neither case is the balanced unit favored *as a unit* by Darwinian selection. In both cases the balance comes about through selection at a lower level. Selection doesn't favour a harmonious whole. Instead, harmonious parts flourish in the presence of each other, and the illusion of a harmonious whole emerges. A helpful language for explaining the emergence of such harmony is the game-theoretic language of evolutionary stability (Maynard Smith 1982).

At the individual level, to rehearse an earlier example in genetic language, genes that make carnivorous teeth will flourish in a gene pool containing genes that make carnivorous guts and carnivorous brains, but not in a gene pool containing genes for herbivorous guts and brains. At the community level, an area that lacks carnivorous species might experience something similar to a human economy's 'gap in the market.' Carnivorous species that enter the area find themselves flourishing. If the area is a remote island which no carnivorous species has reached, or if a recent mass extinction has devastated the land and created a similar gap in the market, natural selection will favour individuals within non-carnivorous species that change their habits and eventually their bodies, and become carnivores. After a long enough period of evolution, specialist carnivore species will be found to have descended from omnivorous or herbivorous ancestors.

Carnivores flourish in the presence of herbivores, and herbivores flourish in the presence of plants. But what about the other way around? Do plants flourish in the presence of herbivores? Do herbivores flourish in the presence of carnivores? Do animals and plants need enemies to eat them in order to flourish? Not in the straightforward way that is suggested by the rhetoric of some ecological activists. No creature benefits directly from being eaten. But grasses that can withstand being cropped better than rival plant species, really do flourish in the presence of grazers—on the principle of 'my enemy's enemy.' And something like the same story might be told of the victims of parasites—and predators, although here it is more complicated. It is still misleading to say that a community 'needs' its parasites and predators like a polar bear needs its liver or its teeth. But the enemy's enemy principle does lead to something like the same result. It can be right to see a community of species as a kind of balanced entity which is potentially threatened by removal of any of its parts.

The idea of community, as made up of lower level units that flourish in the presence of each other, pervades life. But, as I have said, I want to go beyond the familiar point that animal cells are communities of hundreds or thousands of bacteria. This is not to downplay the importance of bacterial symbioses. Mitochondria and chloroplasts have become so comprehensively integrated into the smooth workings of the cell that their

bacterial origins have only recently become understood. Mitochondria are as essential to the workings of our cells as our cells are to them. Their genes have flourished in the presence of ours as ours have flourished in the presence of theirs. Plant cells by themselves are incapable of photosynthesis. That chemical wizardry is performed by guest workers within the cells, originally bacteria and now relabelled chloroplasts. Plant eaters such as ruminants and termites are themselves largely incapable of digesting cellulose. But they are good at finding and chewing plants. The gap in the market offered by their plant-filled guts is exploited by symbiotic micro-organisms who possess the biochemical expertise necessary to digest plant material efficiently, and to the benefit of their herbivorous hosts. Creatures with complementary skills flourish in each other's presence.

My point is that the process is mirrored at the level of every species' 'own' genes. The entire genome of a polar bear or a penguin, of an iguana or a guanaco, is a set of genes that flourish in each other's presence. The immediate arena of this flourishing is the interior of an individual's cells. But the long-term arena is the gene pool of the species. Given sexual reproduction, the gene pool is the habitat of every gene as it is recopied and recombined down the generations.

This gives the species its singular status in the taxonomic hierarchy. Nobody knows how many separate species there are in the world, but, thanks largely to Ernst Mayr, we at least know what it would mean to count them. Arguments about whether there are 30 million separate species, as some have estimated, or only 5 million, are real arguments (Wilson 1992). The answer matters. Arguments about how many genera there are, or how many orders, families, classes or phyla have no more status than arguments about how many tall men there are. It's up to you how you define tall, and it is up to you how you define a genus or a family. But—as long as reproduction is sexual—the species has a definition which goes beyond individual taste, and does so in a way that really matters. Fellow members of a species participate in the same shared gene pool. The species is defined as the community whose genes share that most intimate of arenas for cohabitation, the cell nucleus—a succession of cell nuclei through generations.

When a species spawns a daughter species, usually after a period of accidental isolation, the new gene pool constitutes a new arena for inter-gene cooperation to evolve. All the diversity on earth has come about through such splittings. Every species is a unique entity, a unique set of coadapted genes, cooperating with each other in the enterprise of building individual organisms of that species. The gene pool of a species is an edifice of harmonious co-operators, built up through a unique history. Any gene pool, as I have argued elsewhere, is a unique written record of ancestral history. Slightly fanciful perhaps, but it follows indirectly from Darwinian

natural selection. A well-adapted animal reflects, in minute detail even down to the biochemical, the environments in which its ancestors survived. A gene pool is carved and whittled through generations of ancestral natural selection, to fit that environment. In theory a knowledgeable zoologist, presented with the complete transcript of a genome, should be able to reconstruct the environmental circumstances that did the carving. In this sense the DNA is a coded description of ancestral environments, a 'genetic book of the dead' (Dawkins 1998, chapter 10). George Williams (1966) had already said it more economically: "A gene pool is an imperfect record of a running average of selection pressures over a long period of time in an area often much larger than individual dispersal distances."

The gene pool of a species, then, is the rainforest in which the ecology of the genes flourishes. But why have I called my article an ecology of *replicators*? In answering this, I need to step back and look at a controversy in evolutionary theory, one in which Ernst Mayr has been an eloquent partisan. It is the controversy over the unit in the hierarchy of life at which natural selection may be said to act. In Richard Alexander's phrase, "The fittest *what*?" Ernst Mayr and I have both coined a word—'Selection' in his case, 'Optimon' in mine—for the sole purpose of asking the *question* "What is the entity about which you may say that an adaptation is good for it?" Is it for the good of the group, the individual, the gene, life as a whole, or what? My own answer to the question—the gene—is not the answer Ernst Mayr would give—the organism. I shall try to show that the difference is apparent, not real. It will disappear when terminological differences are sorted out. After such presumptuous—not to say impertinent—promise, let me try to deliver on it.

The wrong way to set up the debate is as a competition between rungs on a ladder, of which the gene is the lowest: gene, cell, organism, group, species, ecosystem. What is wrong with the ladder of levels is that the gene is really in an entirely different category from all the rest. The gene is what I have called a replicator. All the rest are, if anything, 'vehicles' for replicators. The justification for treating the gene as special in this list of levels was clearly presented by Williams in 1966:

The natural selection of phenotypes cannot in itself produce cumulative change, because phenotypes are extremely temporary manifestations. The same argument holds for genotypes... Socrates' genes may be with us yet, but not his genotype, because meiosis and recombination destroy genotypes as surely as death... It is only the meiotically dissociated fragments of the genotype that are transmitted in sexual reproduction, and these fragments are further fragmented by meiosis in the next generation. If there is an ultimate indivisible fragment it is, by definition, 'the gene' that is treated in the abstract discussions of population genetics.

Philosophers now call this “genic selectionism,” (Sterelny and Kitcher 1988) but I doubt that Williams regarded it as a radical departure from orthodox neo-Darwinian ‘individual selection’. Nor did I, when I reiterated and extended the same argument a decade later in *The Selfish Gene* and *The Extended Phenotype*. We thought we were just clarifying what orthodox neo-Darwinism really meant. Yet both critics and supporters misunderstood our view as an attack on the Darwinian idea of the individual organism as the unit of selection. This was because we had not then made sufficiently clear the distinction between *replicators* and *vehicles*. Of course the individual organism is the unit (or at least a very important unit) of selection if you mean unit in the sense of vehicle. But it isn’t a replicator at all.

A replicator is anything of which copies are made. An individual organism is not a replicator in this sense, and individual reproduction is not replication. Not even where it is asexual, clonal reproduction. This is not a matter of fact but a matter of definition. If you doubt it, you have not grasped the significance of the term ‘replicator’.

For an operational criterion for whether an entity is a true replicator, ask what is the fate of *blemishes* in entities of this class. An individual organism, such as a clonally reproducing aphid or stick insect, would be a true replicator only if blemishes in the phenotype—say an amputated leg—were reproduced in the next generation. And of course they are not. Note that a blemish in the genotype—a mutation—*is* reproduced in the next generation. Of course it may then show itself in the phenotype too, but it is not the phenotypic blemish itself which is copied. This is no more than the familiar principle of the non-inheritance of acquired characteristics, or—its molecular version—Crick’s Central Dogma (1958).

There could be a form of life on some distant planet where individual reproduction really *is* true replication. This would be so if the body were scanned, say by some biological version of magnetic resonance imaging, and every atom of the original parent copied in manufacturing the offspring. Needless to say, this is not what happens in any life form known to us. But the informational equivalent does happen to germ-line DNA.

I have described (Dawkins 1982b) a replicator as ‘active’ if something about its nature affects its proficiency in being copied, which implies that blemished replicators may be less proficient, or more proficient than the original (in practice because of what we are accustomed to calling ‘phenotypic effects’). The true unit of selection in any Darwinian process, on any planet, is an Active Germ-line Replicator. On this planet, it happens to be DNA.

Williams has returned to the matter in his more recent book, *Natural Selection: Domains, Levels and Challenges* (1992). He agrees that the gene does not belong in the same hierarchical list as the organism: “These

complications are best handled by regarding individual selection, not as a level of selection in addition to that of the gene, but as the primary mechanism of selection at the genic level.”

‘Primary mechanism of selection at the genic level’ is Williams’s way of saying what I would call the ‘vehicle’, and David Hull (1980) would call the ‘interactor’. Williams’s version of my ‘replicator’—in other words his way of singling out the gene from all vehicles—is to coin the phrase *codical domain*, as opposed to *material domain*. A member of the codical domain is a codex. The information coded in a gene is firmly in the codical domain. The atoms in the DNA of the gene are in the material domain. The only other candidates I can think of for the codical domain are self-replicating computer programs, and units of cultural inheritance. Which is to say that both these are candidates for the title of Active Germ-line Replicator, and candidates for the basic unit of selection in a hypothetical Darwinian process. The individual organism is not even a candidate for a replicator in any Darwinian process, however hypothetical.

But I haven’t yet done justice to the criticisms of the idea of genic selectionism. The most cogent of these criticisms have come from Ernst Mayr himself, using arguments foreshadowed in his famous attack on beanbag genetics, and in the ‘Unity of the genotype’ chapter of *Animal Species and Evolution*. In that chapter, for example, he said: “To consider genes as independent units is meaningless from the physiological as well as from the evolutionary viewpoint.”

This beautifully written book is a favourite of mine, and I agree with every word of the ‘Unity of the genotype’ chapter except its take-home message, which I disagree with profoundly!

The important thing is to distinguish between the role of genes in embryology and the role of genes in evolution. It is undeniably the case—but completely irrelevant to the levels of selection debate—that genes interact with each other in inextricably complex ways in embryology, even if not all embryologists would go so far as Mayr (1963) in saying: “Every character of an organism is affected by all genes and every gene affects all characters.”

Mayr himself acknowledges that this was exaggerated. I am happy to quote it in the same spirit. Happy to quote it because, even if it were literally true, it would not undermine, not even to the tiniest extent, the status of the gene as the unit of selection: unit in the sense of replicator, that is. If this sounds like a paradox, the resolution is actually given by Mayr himself (1963): “A given gene has as its genetic environment not only the genetic background of the given zygote on which it is temporarily placed, but the entire gene pool of the local population in which it occurs.”

This really is the key point. Every gene is selected for its ability to survive in its environment. We naturally think first of the external environment.

But the most important elements in the environment of a gene are the other genes. This 'ecology of genes', in which each is separately selected for its ability to flourish in the presence of the others in the sexually recombining gene pool, is what creates the illusion of 'unity of the genotype'. It is emphatically not right to say that because the genome is unified in its embryological role, it is therefore also unified in its evolutionary role. Mayr was right about embryology. Williams was right about evolution. There is no disagreement.

DEDICATION

Dedicated, with the very deepest respect, to Professor Ernst Mayr FRS, Hon. D. Sc (Oxford) on the occasion of his hundredth birthday.

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