

REVIEW ARTICLE

Conflicting genomes, the demic theory & biodiversity*

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ABSTRACT

Organismic-centered Darwinism, in order to use direct phenotypes to measure natural selection's effect, necessitates genome's harmony and uniform coherence plus large population sizes. However, modern gene-centered Darwinism has found new interpretations to data that speak of genomic incoherence and disharmony. As a result of these two conflicting positions a conceptual crisis in Biology has arisen. My position is that the presence of small, even pocket-size, demes is instrumental in generating divergence and phenotypic crisis. Moreover, the presence of parasitic genomes as in acanthocephalan worms, which even manipulate suicidal behavior in their hosts; segregation distorters that change meiosis and Mendelian ratios; selfish genes and selfish whole chromosomes, such as the case of B-chromosomes in grasshoppers; P-elements in *Drosophila*; driving Y-chromosomes that manipulate sex ratios making males more frequent, as in Hamilton's X-linked drive; male strategists and outlaw genes, are eloquent examples of the presence of real conflicting genomes and of a non-uniform phenotypic coherence and genome harmony. Thus, we are proposing that overall incoherence and disharmony generate disorder but also more biodiversity and creativeness. Finally, if genes can manipulate natural selection, they can multiply mutations or undesirable characteristics and even lethal or detrimental ones, hence the accumulation of genetic loads. Outlaw genes can change what is adaptively convenient even in the direction of the trait that is away from the optimum. The optimum can be "negotiated" among the variants, not only because pleiotropic effects demand it, but also, in some cases, because selfish, outlaw, P-elements or extended phenotypic manipulation require it. With organismic Darwinism the genome in the population and in the individual was thought to act harmoniously without conflicts, and genotypes were thought to march towards greater adaptability. Modern Darwinism has a gene-centered vision in which genes, as natural selection's objects can move in dissonance in the direction which benefits their multiplication. Thus, we have greater opportunities for genomes in permanent conflict.

Reviewing genetic differentiation in biodiversity

The species problem is the oldest and the least understood problem in Biology. According to the Bible, Adam faced it when he was called upon to name

species. Tito Caro Lucrezio, the Roman Naturalist and the first on record in "De Rerum Natura" to disclose our animal origin, didn't know what to do with the classification of species. To Carolus Linnaeus and the followers of the immutable archetype or the prototype of the archetype, philosophically called the platonic eidos, variations were imperfections of the species and therefore had no merit in the evolution of life. Lamarck and Darwin stressed that species did not have to be uniformly discrete (Dobzhansky, 1970). And in Down House there are several documented statements by Darwin in which he said that the origin of the species,

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even with sexual selection to cope with, was a puzzle (Desmond, 1994). Notwithstanding that modern distinguished disciples of the biological species concept such as Mayr (1942, 1963) have never given an evolutionary role to variations arising in populations, generally called varieties, Darwin concluded that "species are only strongly marked and permanent varieties, and that each species first existed as a variety (Darwin, 1859). If natural selection is instrumental in preserving species in sexual and outbreeding organisms because they are reproductive communities, as the synthetic theory of evolution claims (Huxley, 1942), then we have arguments in favor of Dawkins' theory which says that natural selection acts on genes through feedback from phenotypic effects and thus acts in preserving species unity.

Dobzhansky, one of the leading architects of the biological theory of evolution, on several occasions presented important arguments in favor of multiple mechanisms for species separation: he often spoke of hybrid inviability and sterility, ethological and ecological isolations (Dobzhansky, 1937, 1940, 1956, 1970, 1975). The phenotype that perfects isolation has better chances to survive than others which do not, because natural selection is there to improve mutual recognition of individuals in order to diminish gametic loss. In fact, genes are perpetuated through the phenotypes that have selective advantages over competing phenotypes. With this incontrovertible premise Darwin and Dawkins naturally and cogently go hand in hand into the extended phenotype because ultimately natural selection acts on genes. The phenotypic effect manifests itself in the individual, in the population and the community that houses the gene.

Thus, from the works of Darwin on natural selection acting on individuals, we can go on to Tchetverikov, Fisher, Wright and Haldane's biological theory of evolution, and to Dobzhansky's multiple mechanism that perfects and privileges isolation, to Dawkins' theory of the extended phenotype and the selfish gene as an extreme case of Darwinism.

The only obstacle to the flow of ideas that gradually passes on from early Darwinism to the more extreme forms of it is the fact that the synthetic theory emphasizes sexually reproducing species, large populations and communities as paradigmatic examples for their arguments, while Dawkins' modern Darwinian revolution applies to other non-sexually reproducing forms as well, and Hoenigsberg insists on the smallest unit of population size (Hoenigsberg, 1990).

Other recent evolutionists such as Moore (1984, p. 82) give strength to Dawkins' argument that says that natural selection would favor genes in one organism

that could successfully manipulate the behavior of another organism for their own benefit. I quote Moore "...a familiar literary device in science fiction is alien parasites that infect a human host, forcing him to do their bidding, as they multiply and spread to other hapless earthlings. Yet the notion that a parasite can alter the behavior of another organism is not mere fiction. The phenomenon is not even rare. One needs only look in a lake, a field or a forest to find it" (Moore, 1984, p. 82).

Any good review of papers in the journals of Parasitology, Animal Behavior, Behavioral Ecology and Sociobiology reveals rich sources of information on *Gammarus* (and other fresh water amphipod crustaceans) whose behavior drastically changes when visited by parasitic acanthocephalan worms such as *Polymorphus paradoxus*, *Polymorphus marilis* and *Corynosoma constrictum* (reviewed in Cronin, 1994). Holmes and Bethel (1972), Bethel and Holmes (1973, 1974, 1977), Moore (1984), and Dawkins (1990), who published their important researches some 23 years ago, produced Dawkins' data for his extended phenotype theory. Of course, the selfish gene already showed how genes can manipulate hosts to increase their adaptive value (Dawkins, 1976). As we see it, the only difference from neo-Darwinian evolution is that the emphasis now is on the gene that codes the phenotype and the individual that hosts it, instead of the individual itself.

Whatever this new vision has brought, it has not challenged the essence of Darwinian evolution. New theories such as the selfish gene and the extended phenotype not only do not change the biological or synthetic theory of evolution, but also reinforce it by finding a gene-based platform on which natural selection acts to produce evolutionary change (Dawkins, 1976, 1978, 1979, 1980, 1981, 1982b, 1990). What we have now is the same natural selection acting not on individuals but on genes in a round-about-way from phenotypic effects. Genes are perpetuated because they give rise to phenotypes with selective advantages over competing phenotypes. Since the selfish gene promotes itself through the phenotype, then the gene can also perpetuate itself by "dominating" the phenotype in all those "other" manifestations in which selective advantages are present or appear. Those "other" manifestations constitute the extended phenotype. For example, beak formation for a bird that uses it for nest building is readily accepted as a classical phenotype coded by genes. The extended phenotype extends the idea to the nest itself. Thus, as I see it, biodiversity becomes even more diverse and variable because it has an extended projection for every variant phenotype. We, geneticists, have often considered

phenotypes to be limited to the body of the organism: the phenotypes of a tree lie in its body, stems, flowers, seeds, etc., the phenotype of a fly should be looked for in its wings, abdomen, thorax, bristles, eyes, etc., the body phenotype of a bird, as in the other case, lies in its body, feathers, beak, wings, legs, etc. In the new and revolutionary theory of the extended phenotype, phenotypic variability should be examined beyond the body structure. In the case of the male bowerbird, for example, nests and bowers are also phenotypes coded by the species' genes. Thus, we have in parasites and in their host extended phenotypes on which genes exert a pressure to multiply their type.

Now, Darwinian evolution has another tool to use, the extended phenotype. Male bowerbird nest construction varies from austere ornamentation flat on the ground, to baroque elaborations. Cronin (1994, p. 62) has presented several populations of bowerbirds according to their extended nest phenotype: there are toothbilled, archbold, MacGregor's, striped gardener, golden, Australian regent, satin, greatgray, and lauterbach's bowerbirds.

Therefore, to improve mutual recognition of individuals in order to diminish gametic loss, Darwinism now counts on characters of the extended phenotype that reinforce mutual recognition of the individuals that share a great many adaptive genotypes. Therefore, while neo-Darwinian population geneticists counted on genes, gametes and genotypes to show potential variability in sexually reproducing species, now we can include even greater variability in extended phenotypes.

Outlaw genes and organismic adaptive variability, old and new

Darwin in his many works (Darwin, 1845, 1859, 1862a,b, 1865, 1868, 1871, 1872, 1876a,b, 1877; Darwin and Wallace, 1858) showed a tendency to be organism-centered.

Classical Darwinism and Wallace's extreme adaptationism analyze the workings of natural selection through what individuals and their progeny do and not necessarily through what their characteristics do and stand for. Modern Darwinian Theory is about genes and the phenotypes they control, although admittedly genes do not present themselves as base-pairs of DNA to the scrutiny of natural selection. Genes as replicators or interactors lurk inside organisms and their reproductive success is mediated by what tails, colors, shells, and muscles do. Although natural selection acts on organisms and phenotypes, it also acts ultimately on genes through feedback from phenotypic effects.

However, Darwin (1871, p. 155, 161) also hinted at a gene-centered view in his altruistic behavioral analysis although he never came out with a cogent theory on how other behavioral phenotypes could participate in the improvement of adaptation.

The extended phenotypic manipulation presents itself in full when sexual selection and the evolution of emotional signals, as in altruism, make their appearance in Darwinism. Traditional Darwinism went as far as regarding the individual's genes and genotypes as the epitome of harmony. But when the genes are viewed as natural selection's target to improve phenotypes and adaptation, harmony breaks up. The best example is segregation distorter genes (SD): in this phenotype meiosis is influenced so that more than half of its chance of ending up in a sex cell produces a considerable increase in its frequency.

In Crow's paper "Genes that violate Mendel's rules" (Crow, 1979) one reads on SD genes that "the Mendelian system works with maximum efficiency only if it is scrupulously fair to all genes", and continues to say that Mendelism is "in constant danger, however, of being upset by genes that subvert the meiotic process to their own advantage...many refinements of meiosis and sperm formation whose purpose is apparently to render such cheating unlikely. And yet some genes have managed to beat the system". In fact SD genes are considered to be antisociable, or outlaw genes, because notwithstanding their deleterious effect on the rest of the genome, SD can increase its survival by manipulating meiosis. Therefore, there are genes that have phenotypic effects that favor their own survival, even when they are deleterious to other genes in the genome. Moreover, an individual can be considered a mosaic of conflicting phenotypes, and sometimes of conflicting genes. But this point brings us to consider genetic warfare as an inconvenient conflict in which the genome gets the worst part. Since genes are selected for their ability to be good partners with other genes in a background of many genes in the gene pool, how can we reconcile the presence of outlaw genes with the individual's adaptation? The genome's integrity in the gene pool needs harmony in order to offer comparative survival. The genetic information passed from generation to generation is discrete and Mendelian. The information is coded singularly.

Notwithstanding the logical necessity for the genome's integrity and harmony in order to have universal Mendelian genetics throughout the genome, no one can deny a conceptual crisis in biology produced by several unresolved questions like: 1) Often gametes of the two sexes are of different sizes (anisogamy), interpreted in the light of Hamilton's selfish genes

(Hamilton, 1970) as an adaptation to prevent the phenotypic expression of the haploid genome (Dawkins, 1989, p. 143). If genes expressed themselves in their haploid state, outlaws would be favored without control (Dawkins, 1989, p. 142). However, natural selection has just worked on sperm genes to control the expression of their phenotypes, for if it had not acted on gametic genes their recessive and recent mutants would have been wiped out. The harmony and the amount of expressed variability that emerges in the diploid genotype would have suffered tremendously. Therefore, the explanation of Beatty and Gluecksohn-Waelsch (1972) that the sperm phenotypes are not under the control of their genes, but rather under the control of the diploid genotype of the father genes because they do not possess cytoplasm, which is the raw material for phenotypic construction, is correct. But Dawkins offers his "arms race between haploid genes for increased competitive ability among spermatozoa, on the one hand, and genes expressing themselves when in the diploid genotype of the father, on the other hand, causing sperms to become smaller and therefore unable to give phenotypic expression to their own haploid genotypes."

To my view the most spectacular theoretical example of genome's overall incoherence and disharmony is that outlaw genes, which are subject to suppression by modifiers in the rest of the genome, threaten the whole population with extinction. Hamilton's computer simulated experiment (Hamilton, 1967) with just a single mutant male with SD, or "driving Y", chromosome manipulating males into having only sons, introduced into a population of 1000 males and 1000 females, in just fifteen generations managed to drive the simulated population to extinction for lack of females. Lyttle (1977) demonstrated this effect in the laboratory. Hamilton showed in the same paper (1967) that X-linked drive probably has the same effect on populations as Y-linked SD's, but tends to take many more generations to reach extinction.

In grasshoppers there is a very interesting example of the genome's overall disharmony, simply because a whole B-chromosome that decreases the individual's fitness can multiply in the center of a species range where the population displays high levels of chromosomal variation (Sequeira *et al.*, 1995). In fact, the results permit two models to explain the maintenance of B-chromosomes in natural populations. The selective model supports that B-chromosomes may increase fitness in frequency dependence (when in less number). Actually so far there is little data to support this hypothesis. According to the parasitic hypothesis, supernumerary chromosomes would persist in natural populations exclusively through an accumulation

mechanism which counteracts the lower fitness of the individuals (Ostergreen, 1945; White, 1973). Ostergreen (1945) was the first to postulate the "outlaw nature" of B-chromosomes in grasshoppers, although he limited himself to refer to it as having a parasitic nature. Here we have an example of a "selfish" structure which acts against the rest of the genome and yet manages to multiply. How does B-polymorphism in *Dichroplus elongatus* manage to be temporally stable (Remis *et al.*, 1993)? Not unlike the P-elements in *Drosophila*, B-chromosomes in grasshoppers produce deleterious effects on sperm formation (Loray *et al.*, 1991; Clemente *et al.*, in press) and meiotic instability as other outlaw genes, which, however, Remis and Vilardi (1986) call accumulation mechanism, following Ostergreen (1945). However, Jones calls them selfish (Jones, 1985).

The P-elements are a family of several thousands of base-pairs of nucleotides which, despite their low fitness in transpositions, spread rapidly through *Drosophila*'s natural populations. These are genes that include elements that excise and integrate and have a regulation that governs their movement within the genome. These mobile sequences of DNA:

1. Can catalize their own mobility by encoding a transposase necessary for excision and integration.
2. Regulate mobility by tissue-specific differential splicing of the transposase in m-RNA.
3. Have alternative splicing of the P-element in RNA which may produce a protein capable of repressing the mobility of P-elements.
4. Have a genome which may contain both complete and truncated copies of P-elements.

Here we have an outlaw family of genes that will always survive in horizontal transfers because they can mobilize in trans by the expression of the complete copies even when they are deleted! (Clark and Kidwell, 1995).

When P-elements introduce themselves into a naive genome they can spread rapidly, and their mobility in the germline is responsible for the phenomenon of hybrid dysgenesis (= aberrant phenotypic trait) (Kidwell *et al.*, 1977). The reduction of organismal fitness can be found in Mackay, among others (Mackay, 1986). In short, hybrid dysgenesis consists of temperature-sensitive sterility, reduced viability and fecundity that lead to a reduction of fitness.

The fact that gametes carry Y and X chromosomes that do not contribute with genes in the same manner has inspired several workers to invent "thought experiments..." Imagine a gene on a Y which orders its possessor to kill off his daughters. Such a driving Y chromosome is a disequilibrating gene to the genome, for the sex ratio would move against females

and the population would face extinction. The result of this disequilibrating action is that the advantages derived from sexual reproduction in a Mendelian connubium vanish and with them the possibility to safeguard the potential variability of the population.

Be them X-linked, autosome-linked or Y-linked outlaws, their disequilibrating effects have forced natural selection to repair the damage done by enlisting modifiers to curve or avoid the deleterious or lethal action.

Indeed, a phenotypic effect of a gene is the combined product of the gene and its environment, including the genomic environment. Thus, neither dominance nor recessiveness or any other phenotypic effect can avoid being subject to evolution in the way Fisher taught us, i.e., through the selection of other genes elsewhere in the genome. The fact that Fisher's theory of dominance admits that the rest of the genome can be enlisted to protect disharmony that can endanger the local adaptation of the population, means to admit that the gene pool and the individual genome should not be considered a perfect harmonious finished product of natural selection's wondrous jobs in the past. These adaptations are not just the perfection of harmony with the environment where genes are all in optimum equilibria, as in Muller's conception of the classic theory of population genetics. It is not as far-fetched as it used to be a few years ago, to visualize several steps previous to complete and fulfilled adaptation.

Before the organism reacts adaptively when outlaw genes of various kinds and forms disarrange the genome, the physiological mechanism endowed to answer now, as homeostasis is in charge, reacts to correct what can be corrected immediately, and in other cases just to adjust temporarily things which are adjustable, for the benefit of the whole genome's survival, before a more permanent adjustment can be made. Some selective agencies are more demanding in rapid actions to make immediate survival possible. Thus, what could be the mechanism that acts in one way or another homeostatically so that this organism now may survive and reproduce even suboptimally?

At this point we must be able to diagnose each adaptive change according to how close immediate adaptation is to final adaptation.

Neo-Darwinian harmony vs. modern Darwinian disharmony

Organismic-centered Darwinism tacitly took harmony for granted! So much so that when the methods of systematics are cladistic, there is only

controversy because Willi Hennig's 1966 book implies acceptance of phylogenetic systematics or Hennigian systematics or simply cladism. My personal view on the virulence of this controversy is that, being a technique for characterizing a hierarchy of groups, the biologists involved, such as Mayr (1974), Simpson (1975), Van Valen (1978), Dupuis (1979), Platnick (1980), Nelson and Platnick (1980) or Patterson (1982), necessarily are organismic-centered and thus do not reflect on the fundamental aspects of adaptation and the various entities that intervene in the micro-evolutionary phenomena. Mayr's (1974) main points in that controversy constitute the best example of taking harmony for granted simply because when you see woods from above you cannot see disharmony and biodiversity flat on the ground.

Mayr referring to cladistics says:

"Cladists have altered the meaning of terms like phylogeny, relationship and monophyly by defining them in terms of common ancestry." But in another part of the same paper he says that cladists neglect the difficulty of deciding whether characters are primitive or derived and of discriminating parallel and convergent evolution. For those who have not followed the bitter controversy, Hennig, the father of cladistics and a convinced evolutionist, argued that classification should follow "phylogeny", in other words, the evolutionary relationship of organisms. This statement nurses within at least two problems (Mayr says five). 1) In view of anagenetic changes (rates of evolution) how can we best deduce phylogenetic relationships? 2) What are we going to do with traits that can be used in similarities among sister groups to classify samples taken from nature when not all similarities have equal weight: some are similarities in derived traits (= apomorphs, monophyletic), others are similarities in primitive traits (= plesiomorphs, paraphyletic)? For example, men, bats and lizards have five fingers, but this is not evidence of a close relationship because the origin of this characteristic is primitive in land vertebrates. Chimpanzees and men have facial gestures and this is evidence of a close relationship because having facial gestures is recent. But beyond this difficulty there is the problem of considering essential to evolution and to the species problem a new platonic stereotype, namely that harmony prevails and therefore that when we say "species" we mean uniformity. I tend to think of it as an argument about names, not about the real world (Hoenigsberg, 1989).

It can be seen that classifying large taxa (genera, families, etc.) can bring us to the extreme of the "transformed cladists" who discovered that Hennig's proposal for cladograms (the trees representing

relationships) can be carried out quite satisfactorily without having evolution in mind. Therefore, they conclude that maybe evolution is not necessary as a hypothesis in Biology. This makes me refuse to get involved or excited about it.

I brought this controversial issue up because it represents the kind of scientific methodology, mind you of enormous importance, that necessarily has a built-in belief in the genome's uniformity and harmony. The language used by cladists, transformed cladists, and phylogenetic evolutionists when discussing classification and the biological species concept is not congenial to the spirit of this paper.

I am not saying that natural selection produces phenotypic disharmony in individuals because its action is on genes; or that the individual's harmony is in conflict with its own genome. Nobody can say that. Neither can anyone say that natural selection acts not on individuals but on the phenotypic effects of their own selfish replicators. What one can say from concrete evidence coming from parasites that manipulate suicidal behavior in their hosts, from a driving-Y gene, or from a driving-Y chromosome causing males to have only sons and from the segregation distorter genes that manipulate and subvert the meiotic process to propagate their own kind in detriment to the other ordinary genes, is that phenotypes are the end product of the effects of multiple compromising genes in the genome. The final result could be disharmonious and incoherent simply because "outlaws" sometimes may have the upper hand in the crisis (Alexander and Borgia, 1978). In other words, we have to be open to the possibility of conflicts of interest between genes within an individual genome and even between genes of individuals within populations, and finally between genes of individuals that belong to different species as in cases of horizontal transfer of P-elements (= Jumping genes by Barbara MacClintock).

Disharmony in the phenotype also results when new mutations arise. Indeed the pleiotropic effects of new mutations are usually quite deleterious. Therefore, all those new genes that enter the previous generation's genome are temporarily, in that sense, "outlaws".

Can disharmony and unadaptation survive?

Since the work of natural selection is to keep individuals alive, to compete for mates, to have offspring and to care for them, the final result after doing its job well for many generations is to adapt the individual to its surroundings. And this is a job that

ultimately requires many genetic compromises between conflicting genes, for often there will not be immediate adaptation. On the road to adaptation, there will be combinations of genes and of their genetic effects that before becoming selected for their compatibility with other genes within the same genome, may produce unadaptive, neutral, exaptive, pseudoadaptive phenotypes (Hoenigsberg, 1990). Finally, genes are never selected individually in isolation. What natural selection does is to choose them against the background of other genes in the genome or of other genes in the gene pool. Thus selection chooses those genes that mix well with other genes. These are interactors in Hoenigsberg's idea (Hoenigsberg, 1990) because they are entities that have specific effects on phenotypes, and as such they may produce at least three kinds of traits: 1) Traits that are currently selected for a certain function, and their presence now results from successful historical selection. 2) Traits called by some exaptive because they are selected now in reference to a particular role but they have not emerged through historical selection. They could have resulted because unusual hybrids between marginal localities that seldom cross produce such traits; or because of random drift (we shall see cases in courtship elements in *Drosophila pseudoobscura* below); or because sampling errors can permit uncontrolled traits that decrease the average fitness of the population. 3) Interactors may also code for traits that seem adaptive, but only because they have been linked with others that are directly selected. This can result from sorting when not selecting. 4) Interactors can code for traits that are neutral now and therefore not subject to selection but that may be later. Others like Vrba and Gould (1986) have anticipated our ideas to some extent, although with not as many possible phenotypic traits, resulting from many interactors rather than replicators. But the most genial anticipation and pioneer theory in this line of thought is Darwin's (1859) when he recognized that there have to be characters that although useful may not be "adaptations" and that there may also exist characters that are not relevant to natural selection (Darwin, 1859).

What makes us offer many more interactive entities than those considered by Dawkins as units of selection is the magnificent and exuberant tropical biodiversity. Our interactive entities manifest their presence in characteristics which are also necessary to function in the evolutionary process. When interactors interact with the environment, adaptive, exaptive, neutral, unadaptive and even maladaptive characters appear, covering all the range of phenotypic biodiversity in a continuum of expressions in

components of fitness of conventional phenotypes and so many more in extended phenotypes (see before).

Interactors and the environment act in concert when there is harmony in the individuals' genome; each gene and its alleles behaving in a Mendelian fashion without stridency, smoothly obeying Fisherian increase in fitness (Mayo, 1990). These interactors will always produce adaptive traits. But there are other interactors that do not act in concert with harmonious backgrounds of genes.

These are the genomes that have conflicting genes, that code conflicting phenotypes as we have discussed before, and they do not always have to produce adaptive traits. When such outlaws act "selfishly" or when they obey Hamilton's rule (1964) (which is really Fisher's, since he had proposed it 50 years before, in 1914, see Mayo, 1990, p. 2), we have many more traits and some of them are bound to be part of the range in a continuum of expressions outside adaptation. Hoenigsberg's pleiotropic interactors still fall short of what we are proposing now. Because then, in 1990, we kept within the classical Darwinian harmonious genome. Now, we are saying that the potential biodiversity of any species and population is much greater when conflicting and non-harmonious genomic backgrounds are taken into account within demes. We are aware that there is much unadaptiveness, semi and sublethality, and mutants that cannot repair in time to avoid lethality in demes that frequently have to cope with conflicting and non-harmonious genomes. In my view, the large amount of homozygosity inherent in small populations with little relative variability, called demes, and which at times when isolated from the main bulk of the species distribution as in depauperated *D. pseudoobscura* from Bogotá, Colombia, present sexual isolation, (Hoenigsberg and Rojas, 1995) is instrumental in generating strange deviations such as recently reported (Campos and Hoenigsberg, 1995). Remember that in small demes with as little as an average of 1.03 alleles per locus (Hoenigsberg *et al.*, 1988) selection will wipe out a great part of the next generation as a price to pay for generating even more biodiversity in "strange" deviations. Thus, I agree with Lewontin (1978) and with Gould and Lewontin's idea of spandrels (1979, pp. 581-584, 595-597). They claim that many characteristics reported as adaptive may not be adaptations at all; they may be mere side effects.

When we say that this one gene has a certain particular phenotypic effect we automatically have to admit that the gene may also cause variability in other traits! These unintended phenotypic effects are side effects of selection. Darwin himself recognized that,

"we should bear in mind that modifications ... which are of no service to an organism ... cannot have been ... acquired (by natural selection). We must not however, ... forget the principle of correlation, by which ... many strange deviations of structure are tied together ... so that a change in one part often leads ... to other changes of quite unexpected nature..." (Darwin, 1871, pp. 151-152 taken from Cronin, 1994 reprinted).

Darwin means by correlation the overall coherence implicit in development and growth so that variations that have not resulted from natural selection (on the road to real adaptation, unadaptive or maladaptive) and that are of no service to an organism can be accumulated through natural selection by virtue of being tied together in the genome (Darwin, 1859). Therefore, Darwin accepts that we might as well attribute such cases to the pleiotropic effect of genes that tie up characteristics that are unadaptive in the embryological development to other traits that natural selection is selecting for. Therefore, they appear with the real adaptive ones as part of the overall biological package.

If we had only perfect coherence thanks to natural selection and no unadaptive or maladaptive phenotypes in the traits that have survival value, then there would be no permanent and continuous cases of strange deviations, for natural selection would immediately cancel out those codes. What we have always seen is that phenocopies, and in general strange deviations, present themselves at a certain recurrent rate in the small demes of *D. pseudoobscura* from Colombia.

To summarize, there are several kinds of apparently strange unadaptive or maladaptive variants: 1) Those that result from the action of "outlaw" genes; 2) Those that appear when P-elements interfere in the embryological course of development; 3) Those that emerge when pleiotropical side effects are set in motion by selection for other adaptive traits which are tied together; 4) Many of the variants that appear are the result of genomes that have not produced a stable homeostatic mechanism yet. We saw before that the genome's incoherence is, in some instances, the consequence of "selfish genes" within. Before relative harmony sets in for the benefit of full adaptation many disharmonious genomes result; 5) There are cases reported in the literature (Hoenigsberg, 1968) in which a fluctuating temperature may produce such embryological imbalance on the road to normality that within a certain range a phenotype will appear monstrous. We will not stress this example because it is not permanent; 6) Strangely, enough elaborate ornamentation in males due to female selection should

also be considered a strange deviation from the general average. Sexual selection has had two interpretations. One is Wallace's view; he claimed that the female bird chooses ornamented males because ornamented males are also the most healthy, perseverant and vigorous. In other words, Wallace's theory is that there is a strong positive correlation between ornamentation and useful qualities (Wallace, 1905). But the other theory, that of Darwin (1871, p. 399) and Fisher (1930), says that sexual selection is the sphere in which adaptation can be costly. Indeed for Darwin sexually selected characteristics should be considered the end result of a trade-off: survival vs. mating advantages (Darwin, 1871, p. 279). Therefore, for Darwin adaptation can generate inconvenient or unadaptive traits in different components of fitness.

When genes are viewed as the target

When genes are considered as the target, several old phenomena such as kin selection and altruism find logical solutions. Darwin declared that social insects, Hymenoptera (ants, bees and wasps) and Isoptera (termites), represented the most serious special difficulty to natural selection (Darwin, 1859, p. 242). And Williams wrote in his famous book that "there is no more important phenomenon than the organization of insect colonies" (Williams, 1966, p. 197). Williams has considered altruism a challenge to genes as target. But what worried Darwinians, until Fisher came along, was that there are species of insects in which sterile workers dedicate their care to the rest of the colony. They care for the offspring of their fellows and they devote their existence to the survival and reproduction of others, but they have no offspring of their own. The puzzle is how could natural selection, working on organisms that pass on heritable adaptations, give rise to such behavior? How do sterile workers benefit from their self-sacrifice?

The answer comes from kin selection (Fisher, 1930, p. 177; Haldane, 1932, p. 130, 207; Hamilton, 1963, 1964) that says that offspring are not the only road to gene transfer, and therefore to reproductive success. In some species of Hymenoptera, brothers and sisters can be as valuable as offspring. What developed from the new vision of genes as target is known everywhere and I do not have to dwell on it except in certain aspects that serve as the main point of this paper. When the emphasis moved from organisms violently fighting to obey the Darwinian dictum of the survival of the fittest to genes that try to multiply their type through the phenotype, the ruthless efficiency of 19th century Darwinism was modified. It does not pay for a species to be that efficient, for too great efficiency that kills off

other actual and potential variants in the vicinity may cause a species to eliminate its own food and starve to death. Indeed this is the new truth that has provided ground to explain the enormous tropical biodiversity. It may not be amiss to state that the extreme form of natural selection mellowed itself with the social insects.

When Sewall Wright explained shifts in adaptive peaks, thanks to random drift and natural selection, because populations break up into smaller inbred groups, the panoramic scenery of population genetics was set to attempt an explanation with groups instead of individuals (Wright, 1932, 1945, 1951). A group of inbred individuals in a subpopulation could exhaust additive variation and end up with the least well-adapted individuals. A subpopulation with much inbreeding would not be a candidate for natural selection's work to uplift adaptive success. Such a depauperated genetic pool unable to go back to the parent population is then forced to travel other roads. Natural selection could set this population on a new destiny. Who knows, it may even reach a higher peak of adaptedness! Random drift and natural selection can push a group of individuals that broke up from the original larger population out of local optima. Wright conceived as highly possible that having acquired higher adaptive peaks, they would, in time, eventually swamp the other subpopulations and populations because of intergroup selection. The whole point that makes this theory weak is that, by the time a higher level of adaptation swamps other adaptations controlled in other loci and by other gene interactions, other subpopulations will arise in other places in geographical sympatry, with exactly the same possibility of running away from local optima, as the previous one. Thus, it may be said that notwithstanding its mathematical beauty, Sewall Wright's theory does not offer a real stable solution. Moreover, there is a developmental constraint because a small group of individuals with high inbreeding and reduced developmental homeostasis produces not just allelic variants but strange deviations that do not contribute to adaptation. In such subpopulations these P-elements or segregation distorters, that subvert the meiotic process, or parasites whose extended phenotype can make havoc of their hosts phenotype, may conduct the group to extinction. And yet such impoverished genetic legacy caused by random drift can have in some cases a real possibility to make a more or less quasi-adaptive peak and survive. The rate of survival can be much higher than that offered by chance if a subpopulation of highly inbred individuals crosses with other subpopulations equally inbred but for other alleles, to give rise to uniformly heterozygous. Thus, there is a way out of

extinction, even when conflicting instead of harmonious genomes are present. But this was not Wright's theory. There is still another possibility for survival in such groups that move out of local optima: To have altruistic individuals only and never to be invaded by selfish individuals; this is, of course, a very unlikely condition (Williams, 1966, pp. 92-250).

The general consensus is that genes, not groups, are the units of selection. In kin selection and altruism, individuals share more genes with siblings than with offspring. Individuals, then, are vehicles of replicators in Dawkins' terminology (Dawkins, 1976, 1982a, 1989 and others). The story goes like this: if I have a gene for altruism, then my siblings are just as likely to bear copies of it as my children. Thus, in the struggle for survival Haldane's altruism says, "make my siblings survive for they can be as valuable as my offspring." This increases biodiversity!

Just as there is a beginning of demic theory in Wright's impoverished gene pools that through drift move away from local optima, there is a more definite statement in its favor in Hamilton's inbreeding within and outbreeding without to explain termites' breeding cycles (Hamilton, 1972). I will explain how this is a formula, maybe even an axiom, to inject survival that makes the demic theory a more universal answer to break away and maybe to speciate.

Let us have a case study in termites (Hamilton, 1972; Bartz, 1979, 1980, see e.g. Myles and Nutting, 1988). If one of the original difficulties of the demic theory was that the marginal and isolated group of very small numbers can slip into rapid extinction, then, by analyzing the characteristics of the natural history of the individuals that find themselves in such hardship of genetic poverty, we find that new adaptive peaks can be had if other circumstances of population dynamics are satisfied. As pockets of few individuals that break away from the ephemeral central part of the geographical distribution in the tropics, where K selection dominates in intensive brother-sister inbreeding stratagems, most loci will become subject to natural selection's efficacious elimination of some outlaws, of genes that produce dysgenesis in P-element transfers and of detrimental extended phenotypes. Thus, with this population dynamics in which close inbreeding sets in, followed by outbreeding with neighboring but relatively isolated demes, there is a stage for extremely profitable altruism that will change biodiversity within the species, and in apparently close sympatry.

In the amazonian tropical rain and dense forests, physical isolation of small groups of individuals can happen rapidly even within a few meters because

of the organic matter that decomposes in abundance in proliferating and in multiplying habitats. This is the ideal ecological scenery where drift can operate rapid genetic impoverishment of the local genome. Then with the help of strong selection in all loci that become homozygous before extinction appears, a few selected individuals will scout for better places to establish. This new colony will outbreed with other such individuals which had escaped from extinction in another deme. For recolonization in *D. pseudoobscura* see Hoenigsberg and Dobzhansky (1987).

Genes as units of selection produce conflict and increase the probability of speciation

Brahmachary in June 1995 reminded us that certain bacteria resident in an aphid kill all males and propagate through the females. This is one of the first cases of feminist DNA. Such foreign DNA has been known to parasitize some 5-10% of insects. Gadagkar (1995) mentions B-chromosomes in a parasitic wasp, the most selfish DNA known. There are classic examples of invasive bacteria, meaning their DNA, in cockroach eggs, which make them attain normal size (Henry, 1967). Thus, recent and old observations point to genomes that harbor DNA from other species. We have previously shown how conflict within genomes makes for altruistic phenotypes, which in classic organismic-centered Darwinism could not be understood, a simple and straightforward phenomenon of selfish DNA.

The gene-centered (instead of the organismic-centered) unit of natural selection has to have the following properties: 1) It must be able to produce copies of itself; 2) It has to replicate but with occasional and slight mistakes both in its molecular structure and in its combining structure as interesting entities because these alterations introduce differences into the population; 3) The self-replicating entities have to influence directly or indirectly the probability of increasing or decreasing their frequency, and this is produced through influencing their survival, reproduction and competitive ability. Anything in the genome with such properties is either a replicator or an interactor. Genes qualify as units of selection because they reproduce themselves more or less faithfully and their phenotypic effects influence their frequency.

Other candidates for units of selection are organisms, groups of individuals and even species. However, none of them is able to replicate facsimiles of themselves, for organisms do not reproduce what they acquire in their lifetime, only what their germplasm has. The other higher levels for selection do not have a mechanism for self replication. While genes can be

replicators and interactors that project themselves into the future by generating adaptations in their phenotypes for their own good, even against the organism that harbor them, the other higher levels as units of selection cannot.

The smallest unit of population is the deme, where a high degree of homozygosity can take place and therefore where the units of selection can be readily selected out to improve their cohesion for the benefit of adaptations. Adaptation is the mechanism for increasing the frequency of replicators and interactors. The organism is the vehicle; it is the way by which the genes multiply their copy (Dawkins, 1976). When certain phenotypes cannot be understood with an organismic-centered evolution – and such is the case for altruism – the time is ripe to use the only serious candidate for unit of selection that can interpret altruism and genomes in permanent conflict. However, the entity for selection to operate on has to have an immediate stage, the local deme with a high degree of consanguinity, even the product of a single gravid female, occasionally punctured with some outbreeding in another deme.

Here we go back to the properties that anything would need to be a unit of natural selection. Firstly to replicate, but secondly with occasional change. In the level of individuals this property can be satisfied with the deme and its occasional outbreeding.

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RESUMO

O darwinismo centrado nos organismos, para usar fenótipos diretos para medir os efeitos da seleção natural, requer harmonia e coerência uniforme do genoma, além de populações de grande tamanho. Contudo, o darwinismo moderno, centrado no gene, tem encontrado novas interpretações para dados que falam de incoerência e desarmonia genômica. Como resultado dessas duas posições conflitantes, uma crise conceitual nasceu na Biologia. Minha posição é que a presença de demes de diminuto tamanho, é importante para gerar divergência e crise fenotípica; além disso, a presença de genomas parasitas, como em vermes acantocéfalos, que chegam a manipular comportamentos suicidas em seus hospedeiros; distorcedores de segregação

que alteram a meiose e as taxas mendelianas; genes egoístas e cromossomos inteiros egoístas, tais como no caso de cromossomos B do gafanhoto; elementos P da *Drosophila*; cromossomos Y que manipulam as taxas sexuais, fazendo com que os machos sejam mais freqüentes, como no “drive” ligado ao X de Hamilton; e genes estratégia macho e fora-da-lei são exemplos eloqüentes da presença de genomas conflitantes reais e de uma coerência fenotípica e harmonia genômica não uniformes. Assim, nós propomos que a incoerência e a desarmonia em geral geram desordem, mas também geram mais biodiversidade e criatividade. Finalmente, se os genes podem manipular a seleção natural, eles podem multiplicar as mutações ou as características indesejáveis e mesmo as letais ou deletérias, daí o acúmulo de cargas genéticas. Genes fora-da-lei podem mudar o que é conveniente adaptativamente, mesmo no sentido do caráter que se afasta do ótimo. O ótimo pode ser “negociado” entre as variantes não apenas porque os efeitos pleiotrópicos assim o exigem, mas também, em alguns casos, porque genes egoístas ou fora-da-lei ou elementos P ou manipulação fenotípica externa assim o requerem. Com o darwinismo organismico, o genoma na população e no indivíduo era considerado como agindo harmoniosamente sem conflitos e os genótipos caminhavam em direção a uma maior adaptabilidade. O darwinismo moderno tem uma visão centrada no gene, em que os genes, como objetos da seleção natural, podem mudar em dissonância no sentido que beneficia sua multiplicação. Assim, existem maiores oportunidades para os genomas que estão em permanente conflito.

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