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Genetic Diversity and Environmental Future

by

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INTRODUCTION

Risk estimation has always been a problem in complex processes, especially where quantitative aspects are not known or may be mistaken by one or two orders of magnitude. Recent loss of genetic diversity of our biosphere belongs to this category. Although we can notice some obviously undesirable consequences, often seemingly compensated by short-term advantages, the mid-term and long-term effects are basically uncertain. Some of these effects, however, might well be very serious if not fatal.

The outcome of the abruptly diminishing genetic diversity cannot be predicted because of our lack of adequate knowledge. Some genetic problems still need to be solved if we are to understand quantitatively the effects of reduced genetic diversity.

GENETIC AND MOLECULAR BASIS OF GENE DIVERSITY

Classical geneticists recognized genes by their drastic mutation, the mutants being usually defective in certain biochemical functions. Detailed studies clarified the situation that, typically, such defects can be characterized by the lack of a specific functioning enzyme—in other words, one gene determines one enzyme (or, more precisely, one polypeptide chain). A 'normal' or 'wild-type' gene directs the synthesis of a functioning enzyme, while the mutant form (mutant allele) of this gene usually cannot do this.

It became obvious very soon, however, that a gene can exist in many allelic forms and that these are not just non-functioning 'mistakes'. One of the earliest examples, the human ABO blood-groups, illustrates this point. As Man is diploid, everybody can have two of the following three alleles: L^A, L^B, I (L^AL^A and L^AI produces blood-group A; L^BL^B and L^BI produces blood-group B; and L^AL^B produces blood-group AB; condition II corresponds to blood-group O). Every human population is polymorphic for this gene, and many of us are heterozygous (L^AI, L^BI, L^AL^B), having inherited different alleles from our parents.

The molecular structure of the gene is now quite well understood as a part of DNA, found as an enormously long chain in the chromosomes (cf. DuPraw, 1970; Goodenough & Levine, 1974). A single chromosome may consist of hundreds or thousands of different genes. An 'average' gene is 1000 nucleotide-pair long (a nucleotide is the building unit of DNA, while three nucleotides specify an amino-acid in the protein chain). Since there are four different nucleotides (dA, dT, dG, and dC), the simplest single-step mutation, the nucleotide substitution, can theoretically produce three different mutants at each nucleotide pair, or $1000 \times 3 = 3000$ different alleles of an average gene. (One member of the nucleotide pair determines the other member according to the pairing rule dA–dT; dG–dC.)

Two or even more nucleotide-pair alterations within the same gene are not at all unlikely, producing different alleles in very high numbers. Many of these mutants will not be acceptable for the population, but even so there remain many alleles that are maintained in large populations.

The number of genes is also very important in creating genetic diversity (cf. Grant, 1977). A single gene with two alleles gives three diploid combinations, while two genes, each with two alleles, make nine different genotypes. In general

$$G = \left[\frac{r(r+1)}{2}\right]^n,$$

where G is the number of genotypes, n stands for the number of variable genes, and r is the average number of alleles per variable genes.

The total number of genes of an organism is known with certainty in some viruses only. The smallest RNA phage (MS 2) has only three genes, the tiny DNA phage Φ X 174 carries nine genes in a peculiar way (Sanger *et al.*, 1977), while others have some tens

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or hundreds. Bacteria accommodate a few thousands, while most higher plants and animals are supposed to have tens of thousands of genes. It should be mentioned, however, that there is a discrepancy between the estimated figures for gene numbers and the amount of DNA per cell for higher plants and animals. The amount of DNA in them is usually enough to harbour 1–100 million genes, but evidence shows that this is not actually the case. The bulk of their DNA actually does not code for proteins, but, as a regulatory region of DNA (cf. Britten & Davidson, 1969), may well contribute to the quantitative aspects of polymorphism.

ESTIMATION OF GENETIC DIVERSITY

A central problem of population genetics and evolutionary studies has been the estimation of the genetic diversity present in natural populations (Murray, 1972; Lewontin, 1974; Powell, 1975). Opposite views can be illustrated by the following two genotypes:

$$1.\ \frac{a_1\ b_1\ c_1\ d_1\ e_1\ f_1}{a_1\ b_1\ c_2\ d_1\ e_1\ f_1} \qquad 2.\ \frac{a_1\ b_3\ c_2\ d_1\ e_1\ f_5}{a_3\ b_2\ c_6\ d_1\ e_2\ f_4}$$

where the double line represents homologous chromosomes, each letter corresponds to some gene, and numerical subscripts indicate allelic forms.

According to the so-called 'classical' theory (genotype 1.), a typical member of a natural population is homozygous at most of its loci for the fittest 'wild-type' allele. Heterozygosity is very rare at each locus, because natural selection usually eliminates the less-fit allele. Too much genetic variability cannot be maintained, as it creates an unbearable genetic load. (The offsprings' probability of being homozygous for any deleterious allele increases in correlation with the number of heterozygous loci.)

On the other hand, model genotype 2. indicates that most of the loci are heterozygous, because there are so many forms of alleles for each gene; homozygosity is an exception rather than the rule. A large amount of polymorphism is maintained by various forms of balancing selection (according to the 'balanced polymorphism theory'). There is no ideal or fittest 'wild-type' allele, because the environment is extremely complex and changes continuously.

The development of modern biochemical methods (particularly gel electrophoresis and electrofocusing) has unequivocally demonstrated the great number of allelic forms (allozymes) present in natural populations (e.g. Singh *et al.*, 1976); thus the 'balanced polymorphism' view appeared to be the right version of the above alternatives. The situation, however, is not so simple. Although an average of approximately 40% of the protein loci that have been studied are polymorphic for electrophoretically detectable alleles (and the actual percentage might possibly approach 100%), this polymorphism may well be selectively neutral, and therefore irrelevant to adaptation (Kimura & Ohta, 1971; Nei, 1975; etc.). In other words, the majority of allelic forms detected by electrophoresis (molecular polymorphism) do not necessarily mean functional polymorphism. According to this hypothesis (the 'neo-classical' view), random processes determine the frequencies of these neutral alleles. As comparative amino-acid sequence analyses indicate the importance of mutations in evolution, stochastic processes of neutral alleles (fixation and loss) are the main factors of evolution ('non-Darwinian evolution').

The rate of fixation of neutral alleles in evolution (per species per generation) is equal to the rate of occurrence of such neutral mutations (per gamete per generation) (Kimura, 1968). This theory regards natural selection as nothing but a clearing agent that eliminates the obviously deleterious mutant forms. The observed protein polymorphism represents a transitory phase in the random fixation and loss of alleles. Clearly, the problems of the meaning and maintenance of polymorphism have not been solved.

THE MEANING OF GENETIC DIVERSITY

The interpretation of the observed genetic polymorphism is of crucial importance regarding damage caused by its loss. Both 'balance' and 'neo-classical' theories admit fitness differences in certain alleles, but the balance theory states that such adaptively non-neutral alleles are in the majority, while the neo-classical concept holds that they are rare. If genetic diversity is lost in a certain population, there will be decreased genetic adaptability in both cases, but the magnitude of damage is very different.*

In order to get an answer to this important problem, selective neutrality *versus* different fitness values ought to be demonstrated for many allelic forms of several loci. To design a suitable experimental test is not a simple task. The study of a single locus would be preferable, with the following restrictions (Clarke, 1975):

(*a*) The organism should be typically polymorphic and allogamous.

(*b*) The chosen locus should direct a single enzyme with known physiological function.

(*c*) This physiological function should be influenced by a quantifiable habitat factor.

* Even the 'neo-classical' theory states, however, that the larger the size a population is, and the shorter the generation-time, the higher will be the evolutionary rate. Thus, even if adaptation were not important in evolution, a reduction of the effective number of a population would inevitably slow down the evolutionary change (Ohta & Kimura, 1971).

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d) Wild populations of this organism should differ in this habitat factor.

There are a limited number of studies where these prerequisites were met (e.g. lactate dehydrogenases in fish, alcohol dehydrogenases in fruit-flies, and α-glycerophosphate dehydrogenase in butterflies). These studies have established that, under most circumstances, *selection is the major force maintaining genetic polymorphism* in populations. The type of selection can be heterozygote superiority (heterosis), frequency-dependent selection saving the rare allele (cf. Murray, 1972; Clarke, 1975, 1976), or multiple-niche selection (providing fit genotypes for diverse microhabitats). It follows that the ability of giving an adaptive response to changing environment is determined by the amount of genetic diversity present in the population. Without adequate genetic polymorphism, a population will die out in a changing environment although it can prove superior in a stable one.

RECENT LOSS OF GENETIC DIVERSITY

Keeping in mind the difficulties of estimating genetic diversity,* any calculation of genetic loss can only be the crudest approximation. Because of random combination of alleles in different chromosomes and the genetic recombination of linked ones by crossing over, practically every single individual in a panmictic population represents a unique genotype. By genetic loss we mean the loss of certain allelic forms and not their particular combination into a genotype.

An allele can be lost by directive or dispersive forces. The former is realized by selection, and perhaps by mutation, for Kimura & Ohta (1971), Nei (1975), and others believe that mutational pressure alone (without selection) can also totally replace the previous allele. When a recessive allele with q frequency is affected in the recessive phenotype (assuming complete dominance of the other allele), the decrease of q can be calculated as:

$$\Delta q = -\frac{sq^2(1-q)}{1-sq}$$

where s is the selection coefficient. It can be seen that selection becomes very ineffective if q is small, and consequently cannot eliminate this allele unless we are dealing with a finite population (cf. Li, 1955; Crow & Kimura, 1970).

The size of the population is extremely important. The number of samplings at each newer generation introduces variance into the otherwise stable frequency (Hardy–Weinberg equilibrium). The extent of this can be formulated as follows:

$$\sigma^2_{\Delta q} = \frac{q(1-q)}{2N}$$

where N is the number of individuals in a diploid population. This 'random walk' of the q might eventually reach q = 0 or q = 1, where the allele is lost or fixed (Kimura, 1970; Wright, 1970).

Estimation of the loss of genetic diversity can also be approached from the expected decrease of heterozygosity. In a small isolated population, the average initial heterozygosity (H_0) will decrease in each generation (t). The new average heterozygosity at t^{th} generation is (Li, 1955):

$$H_t = H_0(1-\frac{1}{2N})^t .$$

According to this equation, in small, isolated populations, sooner or later each locus will be homozygous (with allogamy for the same allele). In a large, open population a very small amount of loss is still possible, but this is compensated by migration and mutation in addition to heterosis, frequency-dependent selection, and multiple-niche selection. A population of less than a few thousand individuals, however, is usually subjected to gene-pool diminution.

Modern agriculture takes the short-term advantage of genetic polymorphism. If there is a polymorphism in genes controlling productivity, why should we keep the less favourable allelic forms? A monomorph population of highly productive genotype can temporarily increase the yield!

This breeding for uniformity has reduced genetic polymorphism in most of our cultivated plants and animals. In the last two decades, the International Biological Programme, FAO, and other agencies, have been attempting to prevent further loss by organizing and establishing 'gene-banks' to store taxa upholding genetic diversity for future use (Collins, 1975; Lawrence, 1975).

On the other hand, very little if any attention has been paid to the global loss of gene diversity of the total biosphere. In order to illustrate the magnitude of the loss, consider a natural area of 100 km² 'untouched by Man'. This area is covered by a deciduous forest. Such an area can maintain about 10^6 individual trees of a single species. Assuming 2×10^4 genes in a diploid zygote, the whole population represents 10^6 zygotic combinations of 2×10^{10} ($=10^6 \times 2 \times 10^4$) genes, though the number of different genes within

* A precise estimation of *genetic diversity* should also consider the allelic frequency values according to the well-known formula of entropy measure (cf. Wilson & Bossert, 1971): $H_a = -\sum_{i=1}^{a} p_i \ln p_i$ [in this case H_a is the total genetic diversity; p_i is the frequency of the ith allele in the ecosystem's total allele pool (a)]. At present, however, even the number of genes and their alleles are difficult to calculate. The frequency values are known for only a tiny fraction of genes.

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this gene-pool will of course be smaller. Supposing only 50% polymorphic loci, there are 5×10^3 variable genes in the population. Although they all can mutate into at least 3,000 different alleles producing 15×10^6 different alleles, only a small fraction of these can be accepted by the population. If this fraction is about 7%, there remain maintained a million kinds of alleles of this single tree species alone.

Making a moderate guess, let us consider a thousand different plant and animal species living in this area. Most of these are obviously less abundant and consequently possess smaller gene-pools than are contributed by the dominant tree species. If we calculate for each of them an average of 10% of the genetic diversity* of this tree species, their total contribution of genetic diversity* is made up of $10^3 \times 10^5 = 10^8$ different genes and alleles.

Now, under some 'civilized' conditions, the natural forest is replaced by man-made ecosystems. If the trees are changed to a highly productive, vegetatively propagated single genotype, the previous gene-pool value (10^6) of this tree population is reduced to less than 2×10^4. Similarly, there will be considerable reduction also of the number of species, and the new gene diversity will be somewhere between one-hundredth and one-thousandth (1% to 0.1%) of that of the original natural system.

Removing the whole forest and replacing it with sophisticated, modern agriculture, may leave a dozen or so of crop plants with their pests and weeds. The crop is uniform, with almost no variability, and the pest animals and weeds are also fairly uniform (being '*r* selectionists'; cf. Wilson & Bossert, 1971). The total diversity in this case drops further to between one-thousandth and one ten-thousandth of that of the original.

Most of our man-made or -modified ecosystems consist of less than 1% of the natural gene diversity. Considering the global proportion of such areas, we may end up with the alarming conclusion that, within historical times, we have possibly (though not necessarily) already lost as much as 90% of the total genetic diversity of the biosphere!†

Human population is rapidly increasing, being estimated in 1977 to total some 4.3 thousand million people—six times as many as two hundred years ago. In addition, each year nearly 2.2% are added to the total (May, 1976, 1977). With this rate of growth we could theoretically reach 40 thousand millions in another hundred years. It is hoped, however, that this high Malthusian parameter ($r = 0.022$) will be reduced soon by more sensible family planning. Yet we have to realize that, even in the very unlikely case that every newly-married couple decides to have two children only, human population will grow further for two or three decades, because of the present age-distribution (cf. Pianka, 1974). Consequently the increasing demand for food production and urban areas on our finite Earth will obviously lead to further loss of natural ecosystems and of genetic diversity.

POSSIBLE OUTCOME OF GENETIC DIVERSITY REDUCTION

Short- and Medium-term Consequences

Reductions of polymorphism in cultivated plants and animals are usually advantageous in the first few years. Breeding by selection usually means preferential propagation of certain allelic combinations at the expense of others. The result is increased productivity.

On the other hand, a pest that is specialized to this particular genotype can destroy the whole population, while a heterogeneous one contains only a small fraction of sensitives. Thus a homogeneous population (inbred lines, F_1 heterosis hybrids, or asexually-propagated clones), has to be protected, and this increases the price of the ultimate product. On the other hand, consumers' demand and technology frequently change. Yet creation of new types to meet such changes is almost impossible in the absence of a large gene-pool with considerable genetic diversity. Mutational breeding cannot substitute for this, because the natural genetic diversity is made up of adapted allelic variants—which have been naturally selected for many thousands of years—and is not just a collection of random mutants.

The replacement of natural ecosystems by modern forestry and agriculture is also profitable at first. But climatic (Gribbin, 1975), biogeochemical, and other troubles, are known to be caused by the large-scale removal of the original, relatively stable ecosystems (Holdgate & White, 1977). Of this insidious danger as a potential global ecodisaster we must beware (Vida, 1977).

Long-term Effects

An obvious effect of diminished genetic diversity is the reduction of species number. Several plant and animal species which have already become extinct in historical times died out not because Man actually killed the very last specimens but simply because the

* *See* footnote on page 129.

† In answer to our questions about this astonishing and alarming figure, Professor Vida replied (*in litt.* 3 February 1978) that 'it is shocking indeed' but he 'meant it as a possible upper value' though 'at present it is impossible to calculate the percentage precisely': at least such contentions should stimulate research!—Ed.

enormously reduced population-size and genetic diversity could not adapt itself to the often altered environment. With some knowledge of population biology it can be predicted that, for similar reasons, several large mammals (especially marine ones), and also some plants, will probably follow them in the near future. (It should be realized that, because of inbreeding troubles, botanical and zoological gardens cannot maintain species indefinitely.)

The following problem cannot be solved by population biologists and geneticists alone, and ecologists are still in dispute on the ecosystem complexity–stability question (Smith, 1974). By complexity they usually consider the degree of species-richness and disregard genetic diversity in each population representing any species. Furthermore, on a global scale, not only is the ecosystem's own stability important but also that of the entire biosphere. This sort of stability is indeed great, almost suggesting some self-maintaining ability for the whole Earth (Lovelock & Margulis, 1974). But can this homeostatic system function without sufficient genetic diversity?

Life has survived the most dramatic environmental changes during its history of more than three thousand million years. All the previous troubles, however—including the whole transformation of our atmosphere to the present oxidizing one—were basically different in two aspects: (i) they were 'rapid' only on the geological time-scale affecting at least thousands of generations, and (ii) the troubles have always been overcome by the enormous genetic diversity which the majority of species possessed. *None of these conditions holds for the present environmental problems.*

The global change of the terrestrial land-surface from natural communities to agriculture, urban areas, etc.—together with other man-made effects—will inevitably modify our climate. Accordingly, plants and animals will have to adapt themselves to changed and often new environments. If genetic diversity of a population is small, it cannot evolve new adaptive gene-combinations in a short time, and will consequently disappear. The complexity of each ecosystem is expected to decrease in this way. In some heavily-degraded ecosystems, vacant positions can be filled in by certain weeds and other *r* selectionists, but *r* selectionists cannot make complex ecosystems.

All the key processes in our environment are maintained or influenced by ecosystems. The further fate of our biosphere depends substantially on whether or not the remaining semi-natural ecosystems, plus the man-made agricultural and forest systems, can also fulfil this all-important function. If the man-modified systems should happen to fail, a self-amplifying, runaway process might be generated which could eventually make the entire Earth as uninhabitable as our apparently lifeless fellow-planets Mars and Venus.

CONCLUSIONS

The study of the interrelationship of genetic diversity and environmental stability covers several biological, mathematical, and environmental, disciplines. Some of the basic processes involved are not yet understood quantitatively. In addition, major gaps exist in those common areas of knowledge where different systems interact. Until a reliable estimate of risk is available, *the loss in genetic diversity of the whole biosphere ought to be minimized* in order to avoid the possibility of an irreversible catastrophic biospheric degradation (Vida, 1977).

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SUMMARY

Increasing evidence indicates that a major portion of the enormous amount of polymorphism present in natural populations is maintained by natural selection. This polymorphism is necessary for adaptation. In the absence of a suitable amount of genetic diversity, a species will tend to die out in a changing environment.

The genetic diversity of most species has been considerably reduced in historical times. Breeding for uniformity, and reduction in the number and size of wild populations, are largely responsible for this loss. Replacement of a natural forest ecosystem by modern agriculture reduces the genetic diversity by three orders of magnitude at the very least. A comparison of the estimated prehistoric and present amount of genetic diversity leads to the alarming conclusion that we may already have lost as much as 90% of the total genetic diversity of the biosphere.* Further loss is expected because of the rapid growth of human population.

* A leading specialist Referee comments that he is 'not as pessimistic as [this Author] regarding the loss of the world's gene-pools', as (i) 'Varieties of crop-plants used in commercial one-crop agriculture differ considerably according to the region where they are grown...', (ii) 'In many parts of the world, the subclimax communities that now exist are richer in species than the climax communities that preceded them... Species have, of course, been lost, but among plants this loss has been more than made up by the evolution of new species of weeds and semi-weedy species such as those of *Rubus* and *Crataegus* that flourish in disturbed habitats created by Man' †, while (iii) 'The broad, flat plains most suitable for agriculture contained mostly species with wide distributions ... represented by many thousands or millions of individuals at present. Most of the genera to which they belong have centers of species diversity in surrounding mountainous regions, where relatively little elimination of the original species-cover has taken place. My guess for California's native flora is that the total gene diversity has been reduced by only about 10 to 20%, while for more sparsely populated regions, such as Australia, it is much less than that—certainly not more than 5% of the original gene-pool. These

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The outcome of such diminished gene-diversity could be beneficial in the short-term, troublesome in the mid-term, and potentially catastrophic in its long-term effects. Decreased genetic diversity might lead to decreased complexity of ecosystems in changing environments. If complex ecosystems are responsible for biospheric stability, such processes on a global scale might have the gravest possible consequences for the future of our biosphere—even conceivably leading to its ultimate destruction.

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considerations lead me to believe that the figure of 90% loss of total genetic variability stated by [this Author] is a gross overestimate. My guess would be in the neighbourhood of 25% to 35%. Now that the world is becoming conservation conscious, further reduction could be kept down to 5% or at most 10% if rules of conservation established by UNESCO and IUCN are observed and enforced.'—Ed.

† To item (ii) in the above footnote the Author responds (*in litt.* 3 February 1978): 'Species richness is not a good indication of genetic diversity. A weedy community may well be richer in species than a stable climax one, yet in the climax community genetic diversity could be greater, because all the species are 'K-selectionists' and therefore highly polymorphic, while the weedy plants are uniform as most '*r*-strategists' are. *Rubus* and *Crataegus* species are particularly good examples of this problem, many species being apomicts forming uniform local populations although species diversity is generally great in these genera.'—Ed.

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Lament

If I could walk through those green hills
I trod so long ago,
To stand once more beside the stream—
The one that flows no more—
And breathe the air that springtime brought
On that day long ago,
I'd give all I could—doubt not!
And I could give a lot!

But there's no wealth in all this Earth
To buy back what is lost:
The sad brown hills and grey, dark sky
Are mute, and do not answer why
The life that once was there is gone,
And cannot render its reply.

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