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Reviews

Genetic ecology: A new interdisciplinary science, fundamental for evolution, biodiversity and biosafety evaluations

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Abstract. Genetic ecology is the extension of our modern knowledge in molecular genetics to studies of viability, gene expression and gene movements in natural environments like soils, aquifers and digestive tracts. In such milieux, the horizontal transfer of plasmid-borne genes between phylogenetically distant species has already been found to be much more frequent than had been expected from laboratory experience. For the study of exchanges involving chromosomally-located genes, more has to be learned about the behaviour of transposons in such environments. The results expected from studies in genetic ecology are relevant for considerations of evolution, biodiversity and biosafety. The role of this new field of research in restoring popular confidence in science and in its biotechnological applications is stressed.

Key words. Genetics; ecology; DNA-transfer; conjugation; transformation; transduction; transposons; dormant cells; epilithon; microbial colonisation; symbiosis; virus resistance; biosafety; release of genes; insults to humanity; evolution; biodiversity.

I. Introduction: What is genetic ecology?

When knowledge of microbial and molecular genetics reached a peak in the late sixties, nearly all scientists preeminent in this field turned their interest towards the eukaryotic world, particularly to the problems of cell differentiation and thus also to the causes of cancer. With the discovery of the "in vitro recombination of DNA", a new quantum jump was achieved, because it offered extremely efficient methodologies for opening up new avenues for fundamental and biomedical research. With this technique, selected genes could be introduced into microorganisms ('cloned') and their structure and function thus studied. Later, the same procedures were extended to produce transgenic animals and plants. The medical and agricultural applications of this genetic engineering ('gene technology') that we can see today, and those that are already planned for the future, could be seen partly as the unintended consequences of ideas which were expressed strongly in the 1960s, especially by the 1968 movement. There was a demand for science to be 'societally relevant' – without, however, too much questioning of what is really good for society, and even less about what will be good in the future. We will have to come back to these considerations in the last part of this essay.

In the sixties and seventies, fundamental knowledge of a number of mechanisms of gene transfer in some bacteria under laboratory conditions was available: (i) transformation by added free DNA, (ii) conjugation mediating cell to cell transfers and (iii) transduction of genes by bacteriophages as vectors. However, virtually none of the successful microbial geneticists extended their studies towards what we now call 'genetic ecology' – in particular, to the movements of genetic material within and between species and even kingdoms in natural environments. We should point out here that events involving gene transfer between bacteria in the laboratory appeared to be confined to a very few species, so that in the scientific community the dominant belief was that in natural environments these exchanges were virtually absent, and certainly did not exist outside bacteria. Only in the past decade have increasing numbers of investigations demonstrated this belief to be false. According to my first, still very subjective, impressions after entering this field, horizontal gene transfer is actually much more frequent than we generally assume when extrapolating from laboratory experience.

It is a fact that, besides the transformations with free DNA, most of the recent observations and experiments in nature are concerned with the transfer of genes located on plasmids and not of those of the genome. For biosafety considerations this emphasis is clearly understandable, because in the transgenic bacteria used industrially, the foreign, artificially introduced genes are located on plasmids. Nevertheless, the transposable elements could, in principle, allow for the jumping of genes from the genome to the plasmid and vice versa. In consequence very much more emphasis is given today to the study of the behaviour of these mobile elements in natural environments, as will be further discussed below. Only recently has the transduction of genes by viruses in natural environments become the object of

thorough investigations. When one considers the continuous flow of genetic material, the genetic stability of species is in fact rather astonishing, and also deserves increased research efforts. In order to understand evolution and biodiversity, much more knowledge is needed in the field of genetic ecology. The modern methods of gene technology, born of research in molecular genetics, now allow for significantly better experiments to be carried out than were possible hitherto.

Further consequences of the results of such studies concern the so-called 'biosafety research' that has to do with the possible, real or only alleged dangers of the accidental or deliberate releases of transgenic organisms into the 'natural' environment. This aspect is particularly debated in countries in which industry is strongly fostering gene technological production lines, and where, in consequence, public acceptance is a question of immediate importance. The last part of this essay is an attempt to analyse the sociological, psychological and philosophical facets of these problems of acceptance.

The author of this interdisciplinary essay, who was already involved in molecular biology long before it got its name, has attempted to produce an overview of this new field – an enterprise made difficult by a redundancy of publications due to the surfeit of conference reports and books that have appeared as an answer to popular worries about gene technology. An attempt has been made to reduce the number of references by referring either to the first innovative approach or/and to an already more comprehensive, later treatment of the topic. The bibliography is therefore not exhaustive, but should enable the reader to find his or her way when more detailed information is required.

II. Different fields of genetic ecology

a) Microbial colonisation and symbiosis

An extremely fascinating field is the microbial ecology in the intestinal tract and in soil. In germ-free animals (mice, pigs) the colonisation of the gut by bacteria is being studied by groups in the USA and France[15,46]. The conditions under which the permanent establishment of a new strain can occur have been investigated. With the new knowledge acquired, the transfer of various plasmids can now be examined[16] and, in consequence, the transfer of genomic genes also, particularly those that are moved by transposable elements[57].

The microbial colonisation of the gut is a fairly simple type of symbiosis, yet our knowledge about it is still very rudimentary. The best known situation is that in ruminants, where microorganisms (in the broadest sense) are responsible for processing cellulose to make it available for the nutrition of the animal.

We are also at least beginning to understand the importance of symbiosis in other systems than that of the classic text book example: the lichens[45]. In the roots of plants, symbiosis with mycorrhizal fungi is of fundamental importance[9], as is that with bacterial partners, which in many cases are able to fix nitrogen, as in the well-known case of legumes with rhizobia. Recently, increasing numbers of other nitrogen-fixing bacterial species associated with non-leguminous plants have been discovered[30,59]. Another important finding is that microorganisms normally found in soil may produce antibiotics which protect plants from disease[38].

The biochemical mechanisms of nitrogen fixation by *Rhizobacteria* and other species are presently being studied in many laboratories with the tools provided by molecular genetics[13,14,32,52]. The initial incentive for this research was the hope of replacing chemical nitrogen fertilizers by making the plant capable of using dissolved gaseous nitrogen directly. The ambitious goal of directly 'grafting' the genes involved in nitrogen fixation into the plant genome is far from being achieved, and it is questionable whether it ever will be. However, by investigating symbiosis more profoundly, we shall learn more about the conditions which allow such partnerships. Fostering new symbiotic associations is probably a much more realistic and promising approach.

It is to be expected that the colonisation of the roots of plants might have many common features with the colonisation of the gut in animals. However, before detailed comparisons can be made, the microbial ecology of the soil has to be much better understood[23,67]. In this discipline progress is and will be very slow. Myriads of different types of living organisms constitute the microcosm of the soil, and even their description and taxonomy will take decades. Use of the scientifically well established approach of abstraction – or, expressed in modern, rather negative terms, of reduction – may turn out to be more efficient. Sterilised soils, or even simulated soils (only the latter are free of DNA) are being used in studies of colonisation by microorganisms, analogously to work with germ-free animals. It may be possible to establish the main components of this colonising flora or fauna fairly expeditiously. Such artificially colonised soils might also be tested for their ability to support plant growth and gene transfer. As an additional method, the study of aquacultures with a view to identifying the essential microorganisms might rapidly reveal their essential features.

b) Transformation by free DNA and conjugation in the natural environment

The fate of 'free' DNA in natural environments, which contain in general clay or quartz sand, is another very important consideration for horizontal gene transfer. Fundamental contributions have come from several groups[62], but mainly from Wackernagel and Lorenz in Germany, who simulated such natural environments in the laboratory[42,43,44]. They found that DNA adsorbs strongly to the minerals present and – once adsorbed –

is about 100 times more resistant to DNases[54]. These results suggest that genetic transformation could be more frequent than would be expected from extrapolations of our previous laboratory knowledge of microbial genetics.

Many groups have also studied an extended type of conjugation that is mediated by cellular contacts, and which occurs even between species[47,66] (for further refs. see 21, 27). In contrast to the well-known laboratory model of conjugation with *E. coli* this new type of transfer seems to be sensitive to nucleases, and it is not yet known whether it also involves special 'fertility' mechanisms similar to the well-known F plasmids. In most reported cases, transfers of plasmid-borne genes have been investigated. The emphasis on such situations is easy to understand in the context of biosafety research, where bacterial transgenes are always plasmid-borne. Chromosomal genes have received less attention, partly for this reason, and probably also because the experimental effort involved in such studies is not very attractive. Until recently the same was true for the study of mobile elements. However, a natural transfer of a transposon between gram-negative and gram-positive bacteria has been reported[7], and at present the 'conjugative transposons' are a new center of interest[57].

Comparing gene sequences has revealed many new cross-relations between species, strongly suggesting the occurrence of interspecies transfer. Among these, the exchanges between a coliphage and a fungus is one of the most spectacular reported, but it needs to be confirmed[49].

It is frequently claimed that gene transfer induced by free DNA ('transformations') does not occur in plants. This statement needs to be qualified. Before bacterial transformation was discovered in the laboratory, this belief was also strongly expressed for the bacterial world. This view was still upheld even after the experimental demonstration of transformation in *Hemophilus*, but – despite many efforts – not with other bacterial species. Later, other species were found to be transformable, but only if the recipient cells were 'mis' treated in order to render them 'competent'. These treatments were so specialised that nobody dared imagine that in natural environments transformations could easily, and therefore frequently occur! We have to remember that bacterial transformation had already been shown with pneumococci in 1928 – and the idea was ridiculed. A convincing experimental proof was only feasible later, when with bacteria it became possible to routinely produce and select characteristic, single gene mutants[48]. I therefore have the feeling that, in this respect, plants today may be compared with bacteria yesterday.

c) Horizontal gene transfers in aqueous habitats and the important role of the epilithon

The foregoing examination of conditions favouring DNA transfers in nature brings us now to the role and existence of the epilithon, an ecological biotope consisting of gel-like, very thin layers covering surfaces exposed to water. We find this epilithon particularly on the surface of stones exposed to aquifers of all sorts. It now seems that active life is essentially concentrated within and confined to this epilithon. Microorganisms grow there by 'attracting' and concentrating metabolites; they produce phages etc. Extremely fundamental contributions on the epilithon, studied both in situ in a small river and when transferred to the laboratory, have come from a group in Cardiff, UK[21].

Similarly surprising are the results of investigations of bacteriophages in a small lake. From laboratory studies one would predict the dilutions to be too great for there to be any chance of adsorption to a host cell and for measurable propagation to occur. Again, the reality in nature is quite different[51,58]. These studies in a lake can be readily applied to the marine environment. Examination of gene transfers under these conditions has started already[22] and, in view of the importance of marine life for the survival of life on our planet, it is to be hoped that they will be continued and intensified.

Epilithons, also frequently called 'biofilms', are by no means restricted to the external environment: they are also of medical importance[31].

d) The dormant and resting states of bacteria

The discovery of a dormant state of non-sporulating bacteria has come as a surprise to the scientific community[55]. Such cells are viable, but under the usual conditions of bacteriological culture they do not produce colonies on nutrient agar plates. Dormant pathogens can be detected by their infectivity. In most cases the conditions required for reversion to the normal 'colony forming' state are not yet known. Besides its enormous relevance for problems of public health, this dormant state clearly also has important consequences for genetic ecology – for instance if the DNA of such dormant cells, which is still intact, can nevertheless be transferred or, in the reverse direction, if cells in the dormant state are particularly competent for the uptake of DNA. As we will discuss below, several observations speak in favor of these cells being in a 'hypermutable' state, i.e. having a much higher frequency of mutations than has hitherto been determined for growing cells. One has also to keep in mind that many bacteria, for instance in soil, might not be cultivable on the growth media used at present, and thus appear to be dormant. A bacterial culture growing under optimal conditions in liquid medium reaches what is called the stationary phase when a metabolite is no longer in sufficient supply. Such cells are considered to be in a resting state, which is very comparable to the dormant state, even if, with many species, growth will resume when fresh medium is supplied. Recent studies with 'resting' cells of *E. coli* have shown that in the course of time their genes

can be rearranged very profoundly, thus giving rise to possibilities of biodiversity[2].

Another new discovery, that of selection-induced or directed mutations[20,24,25], has also been speculatively related to this 'resting' state which is supposed to be endowed with particular functions. The existence of such mutants is in flagrant contradiction to the experimentally well-established rule that mutations occur in growing cells randomly and independently of the environment, and that only afterwards are they selected by the conditions of further growth. The classical experiments were all based on growing cells; now it is believed that in the dormant or resting state completely different enzymatic and metabolic functions exist, which could possibly 'adapt' the mutations to the need of the cell to resume growth. It is also proposed that the 'hypermutated' dormant cells could be a reservoir of mutated genes, which are ready for gene exchange with growing cells[28].

e) The 'fitness' of micro- and other organisms

Finally, results more directly relevant to 'safety research' are given by studies of the 'fitness' of transgenic bacteria. We molecular geneticists have claimed in general that transgenic organisms have a decreased fitness, because of the additional burden of a gene not related to the genomically-controlled, normal activity of a microorganism. In most cases this has turned out to be true[71], but an increasing number of exceptions have become known. Lysogenic bacteria were shown to be more fit than the non-lysogenic 'parent'[17,40]. Even more surprisingly, a DNA fragment of lambda phage carrying the cohesive ends was found to enhance the fitness of the host cell[18]. It was also assumed that an unchallenged antibiotic resistance would reduce the fitness. While this is generally true, here also several exceptions have been observed[10,26], in which the antibiotic resistance was due to one or a very few gene(s), which were also involved in other important functions e.g. DNA repair[8]. Such polyvalent gene functions can be assumed in many cases. It is, however, more difficult to see how a human gene, for instance for globin or insulin, could have other favorable functions for the transgenic cell. Without a doubt, adequate tests of the physiology of transgenic bacterial strains need to be made, even in cases where the carrier hosts have previously been selected for inability to grow in natural environments[29]. Even 'dead', dormant and therefore non-growing bacteria (see Section *IId*) might transfer their DNA to other, actively growing cells.

As for microorganisms, the possibility of transgenic plants becoming more fit and therefore behaving as aggressive weeds, has been discussed intensively. The question of such 'taking-over' by plants can be indirectly addressed by studying the propagation of artificially introduced exotic plants[3,37,41] and by investigating the genetic traits which govern reversion to the wild or other invasive states.

f) Virus resistance in plants

A completely new window on fundamental research has been opened by the discovery that plants made transgenic for the capsid gene of a virus become resistant to infection by this virus[5,19,65]. This highly interesting and unexpected phenomenon shows a reaction of the plant in a manner comparable to the well-known immune response of higher animals. Before it was observed, nothing had suggested such similarities between the two kingdoms, and no immunoglobulins could be detected in plants. The way is now open for the investigation of how these newly-discovered defence mechanisms operate in plants. An important further step will be to know whether only part of the gene is already able to induce the resistance response. The risk of the well known 'phenotypic mixing', or what is now called 'transcapsidation', occurring could then be prevented by using adequately truncated capsid genes.

Transcapsidation designates the phenomenon by which any DNA can be packaged into available capsids. The host range of another virus could, for instance, be extended for one generation with the help of the 'borrowed' capsid. But also, transduction of genomic genes into other species could be promoted by these 'new' capsids. This represents a certain danger which, however, should not be overemphasised, since it appears more and more clearly that viruses have always existed in constant equilibrium with living beings; virus-mediated gene transfers may therefore occur constantly. If this is so, it adds a further dimension to the possibilities of horizontal gene transfer.

An experimental study of the above-mentioned avirulent viruses has to be considered for the time being to be an extremely difficult, if not a hopeless enterprise. Even for bacteria, among which nearly every strain is known to be lysogenic for at least one complete or defective bacteriophage[34], a systematic study of the phenomenon is virtually impossible. There are no reasons for not assuming that the cells of higher organisms are similarly virogenic.

III. Safety research in gene technology

The last example reported in (section *IId*) brings us directly to what is known as 'safety research': (i) the design of microbial vectors unable to survive in natural environments, (ii) making prescriptions about containment in fermentors in relation to the probability of gene transfers from accidentally liberated cells, (iii) the design of test experiments for transgenic plants which restrict the possibilities of gene transfer to a minimum by avoiding pollen production, transduction by viruses to other common hosts, and horizontal gene transfer mediated by soil microorganisms.

A good deal of competent research is being done to render harmless the deliberate or accidental release of transgenic microorganisms into natural environments. The host-plasmid system is chosen and/or modified so that it cannot survive in a natural environment[29]. A classical example comes from the study of the release of a genetically engineered *Bacillus* strain used for the industrial production of amylase[60]. This type of research has led to significant and reliable results thanks to the modern methods of gene technology, including the polymerase chain reaction (PCR) which allows identification of the various microorganisms involved[36,61]. These and further ad hoc studies for each individual, newly constructed transgenic organism are absolutely necessary[4,35,63]. It should not be forgotten that even in biotechnology, toxic by-products may occur, just as in organic chemical syntheses. The technology of producing transgenic organisms is not bound per se to make dangerous by-products, as is frequently stated by opponents. However, the reverse should also not be taken for granted, as was shown by the incident – which led to worldwide discussion – where a commercial preparation of tryptophane contained a noxious by-product that was generated biotechnically by the transgenic microorganism that had been manipulated so as to overproduce tryptophane[6]. Criteria for purity checks, as applied to chemical products, are equally necessary for the biotechnologically produced ones.

There is a danger that many experiments done or proposed for biosafety may be only expedients and yield no real progress in understanding. An example is the work on genetic exchanges between bacteria in natural environments. As discussed above, such exchanges are now known to occur more frequently than had been expected from laboratory experience. However; the frequencies reported in papers vary over about a 10^4-fold range. These differences could be merely consequences of inadequate experiments, but they could also represent natural variations due to hitherto incompletely known experimental parameters or even to different features of the strains employed. Extremely little is known about the transfer mechanisms themselves, especially when they involve the transfer of chromosomal genes rather than plasmids. In this context, the role of transposons is only now beginning to receive enough attention[57].

Knowledge of the frequency of transfer is vital for considerations of biosafety. For instance, if we assume it is 10^{-4}, then we can calculate that an accidental release of 10^2 bacteria entails a very low probability (10^{-3}) of genetic transfers per se, and an even lower one for a specific gene of the transgenic microorganism. The probability rises if higher frequencies of transfer are assumed. The wide range of the observed values is obviously an important obstacle to making risk evaluations. It seems that attempts are being made to standardize the experimental determination of transfer frequencies. This appears to me to be a very questionable approach. As discussed above, it might well be that some of the reported values are based on unreliable experiments, but it seems even more likely that still unknown variables might be responsible. Before standardizing the experimental set-up, it would be most valuable to do ad hoc experiments in order to understand more about the mechanisms of action that are so much affected by these natural conditions.

IV. Social, philosophical and psychological reasons that might explain some of the opposition against gene technology

Philosophers and many other representatives of human and social sciences tend to compare the social context of gene technology today with that of the peaceful uses of atomic energy in the fifties, characterised by the euphoric vision of atomic power as a very 'clean' source of energy. The problem of radioactive wastes was pushed aside, and the risk of accidents considered negligible. It is opportune to recall that at that time the medical radiologists proposed relatively high threshold doses, unconvinced as they were of the late genetic effects of ionising radiations, although biophysicists already had a considerable knowledge of them[39]. The pioneer of molecular biology, Max Delbrück, had worked long before on the hereditary consequences of exposures to such radiation[64]. Most of the half-lives of radioisotopes were then also very well known, so that the problems of disposal of radioactive wastes could have been predicted.

Radiobiology research bloomed during this same period; later, the ensuing political controversies made it much less attractive. At present it is again a focus of interest because of the now well-known repair systems, involving enzymes which have a multitude of functions, not only in the repair of radiation damage[69]. Ironically enough, the most successful results of these studies have been achieved by genetic engineering.

Scientists of all kinds, together with a large section of the public, are aware that our Western way of life with its highly developed technologies has led to very serious damage to global ecology and threatens to do even more[11]. Damage has been caused in particular by the over-use of natural resources, mainly of fossil fuels with the consequent greenhouse effect, but there are also very serious problems associated with current mainstream agricultural methods. People are now afraid that gene technology might not only play a role in perpetuating these rather disastrous courses, but make matters worse. Although this argument is only partly justified, the consequences of the 'peaceful uses' of nuclear energy are often used as an example.

The opponents of genetic engineering always emphasise the special feature that could make gene technology

even more risky than nuclear technology; namely, that living organisms are self-replicating, whereas dead matter is not.

An argument constantly used in favour of gene technology is the long practical experience derived from the breeding of plants and animals – an argument that cannot be used for radiation biology. The breeding and the subsequent domestication of plants and animals has been practised ever since men became settlers. Breeding involves random 'mixtures' of genes, whereas with transgenic organisms only one (or very few) well-defined genes are involved. The opponents of gene technology contest this argument by pointing out that breeding is restricted to the same or very closely-related species, whereas with genetic engineering we are no longer confined by these limits. It should also be pointed out that even in 15 years of laboratory practice, genetic engineering has mostly been used for the study of genes, and their products, that have been derived from microorganisms, *Drosophila* or other lower animals and not from humans.

Many people in our Western world have a religious and philosophical background which induces them to believe that not only the human being as a whole, but also the individual human genes, must be of 'better quality' than those of any other living being. As we will see later, this explains part of the prejudice against any genetic manipulations that involve human genes or mankind. However, it is not a universal view, and people with fundamentally different religious and philosophical backgrounds do not necessarily have the same feelings and fears about such manipulations.

One of the fundamental miracles of life is the fact that the same metabolic pathways occur in all organisms from the most primitive to the 'crown of creation', as humankind is called in the German culture. Enzymes have the same functions and tertiary structures, even if the primary structure is not exactly the same. It is also frequently observed that sequence homologies jump from branch to branch of the evolutionary tree.

Symbiosis had been found to be much more frequent than was assumed previously. Symbiotic bacteria are most likely to have been the source of cellular organelles such as mitochondria, plastids and kinetosomes. There is a likelihood that some of their genes, after transfer to the human nuclear genome, are still endogenously producing substances like peptidoglycan which used to be considered the exclusive hallmark of bacteria[56]. If confirmed, this would provide another indication for a much more extensive horizontal gene transfer than has hitherto been assumed!

Such new data are not well received by many people, particularly by those belonging to the Judeo-Christian tradition, as mentioned above. They are so convinced of the superiority of human genes that they are offended by these concepts, as they were and still are by the universality of the genetic code. Some offences or insults to humanity (table) were proposed by Freud, and extended by Jung[50]. I recently added to them that of genetics[33]. Besides the fear that our civilisation has taken a wrong and dangerous turning, as discussed above, a view of the world in which the human being is the supreme creation is probably among the most fundamental reasons for the non-acceptance of genetic engineering.

The insults to humanity through science

1. *The astronomical insult:*
   - the planet earth is not the centre of the universe.
2. *The genetic insult:*
   - humankind is not the centre of the living world;
   - the genetic code is universal;
   - the enzymes and biochemical pathways are universal;
   - sequence homologies exist;
   - horizontal gene transfers may take place.
3. *The psychological insult:*
   - our mind is split into the conscious and the unconscious;
   - in case of disagreement, the unconscious is always stronger than the conscious (the will).

I should like to add a last word about ethics in gene technology – a matter which now concerns everyone. When something is done for which harmful consequences (risks) are well known – and not only imagined – then this action is unethical. Many people are prepared to accept that it is unethical to use automobiles more often than is strictly required in today's society, because the greenhouse effect has been demonstrated to exist, even if all its consequences cannot be predicted. As long as beliefs substitute for facts, however, ethics cannot be involved. To exaggerate, one might speak about 'the dangerousness of unknown dangers'[53]. For the time being, the risks of creating an ecological 'super-catastrophe' by accidentally releasing transgenic organisms into nature are neither proved nor disproved. Until experimentally fully convincing facts replace beliefs we must remain vigilant. Both claims, that of the non-existence and that of the existence of very large risks, are equally matters of belief. The problem is in large part also the consequence of a philosophical attitude towards human power over nature. Most people, including engineers and also some scientists, have an extremely high opinion about our capabilities in this respect. Real experimentalists are generally much more humble.

I recently had a discussion with an intelligent person working in the field of sociology and ecology, who maintained that it is unethical to do anything which creates a possible risk of suffering. Such an attitude promotes a risk-free society, an idea which quite obviously is unrealistic. Apart from the fact that inactivity also carries large risks, humankind will always 'pro-

gress' by accepting new challenges, without knowing all the associated risks beforehand. It is a fundamental characteristic of our species. We should be grateful if ways could be found to prevent this human characteristic expressing itself in the wrong way by artificially creating very well-known, deadly risks by waging wars of all kinds. This is something which we presently see happening all over the world, and are helpless to prevent.

V. Concluding remarks

In my opinion, genetic ecology not only provides new, fundamental insights into the mechanisms operating in evolution and in the creation of biodiversity, but could also fulfil the important tasks of helping to reestablish public confidence in the natural sciences. It is, however, also clear to me that the technological applications of scientific results have to be made with a much greater sense of responsibility for the future of our world than has been current during the present century. So many errors were made, and are still uncorrected, that it becomes difficult to believe that now the public will accept without hesitation the new technological applications of part of a discipline of science that was originally the very broad area of molecular biology. People would like first to see some progress in the direction of ecology at large[11,68].

Natural scientists alone will not be able to achieve the above-mentioned goals. They need urgently the active collaboration of representatives of the humanities. From what I said in the foregoing sections it seems obvious to me that only knowledge of the basic facts of genetic ecology could convince philosophers that they should help to overcome the 'genetic insult'. Biology adds to physics in producing new philosophically relevant insights which were not foreseen explicitly by the Greek philosophers. Unfortunately, many of today's philosphers still claim that physics is responsible for the popularly predominant mechanistic, linear type of causal thinking (so-called Cartesianism), although the physicists were actually the first to overcome it with quantum mechanics and relativity theory. Genetics is another new field which philosophers should now take up rapidly and integrate into their world views and teaching.

It is somewhat symbolic that it is gene technology, with its extremely specialised and single-minded approach, that is now making it so clear that there is a pressing need for a much broader conduct of affairs. Let us hope that genetic ecology can help to reestablish popular confidence in science and scientists, and bring about a fruitful discussion and appropriate changes in policy.

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Further reading: For such a short essay, the list of references cannot be comprehensive. They have been selected either because they were among the first to treat a given topic or/and because they offer a comprehensive treatment of it. Three conference proceedings published in the last two years might be useful for a recent updating[1,12,70]. The proceedings of the fourth BAGECO conference on 'Bacterial Genetics and Ecology', edited by J. D. van Elsas, should be published shortly, cf. ref. 57.

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