THE ORIGIN OF ORGANIZATIONAL SPECIES

ESRC Centre for Business Research, University of Cambridge
Working Paper No. 118

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March 1999

This Working Paper relates to the CBR Research Programme on Industrial Organisation, Competitive Strategy and Business Performance

Abstract

The paper argues that some of the limitations and problems examined by Darwin and modern biologists in relation to the working of natural selection in the case of speciation may be one aspect of more general rules which have some counterpart in the competitive selection of organisational species in capitalist economic development. In biology the laws of structure and change that characterise the selection among species are very different from those that characterise the selection of the member of the same species. These ideas are applied to understanding the "Second Industrial Revolution" and the development of the new species of "managerial capitalism" in the United States and Germany, in contrast to Britain, whose firms and entrepreneurs failed to keep pace with organisational change.

Acknowledgements

I am grateful for useful comments from Antonio Nicita, John Earle, Frank Hahn, the participants to the Siena Summer School on Economic and Evolution, and an anonymous referee of the CBR Working Paper Series. The support from the ACE-PHARE Research Project P96-6053-R is gratefully acknowledged. The paper was submitted while the author was Visiting Fellow in the ESRC Centre for Business Research.

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1. Introduction

Commenting on the analogy between his own Panda's thumb evolutionary story and the Economics of QWERTY analysed by Paul David (1985), Gould has observed that:

> "My main point, in other words, is not that typewriters are like biological evolution (for such an argument would fall right into the nonsense of false analogy), but that both keyboards and the panda's thumb, as product of history, must be subject to some regularities governing the nature of temporal connections. As scientists, we must believe that general principles underlie structurally related systems that proceed by different overt rules. The proper unity lies not in the false applications of these overt rules (like natural selection) to alien domains (like technological change) but in seeking the more general rules of structure and change themselves" (Gould 1992 p. 66).

The purpose of this paper is to argue that some of the limitations and problems that arise with the working of natural selection in the case of speciation may be one aspect of the more general rules of structure and change and may have some counterpart on the competitive selection of organisational species in human history. In biology the laws of structure and change that characterise the selection among species are very different from those that characterise the selection of the member of the same species. This may be relevant also in economics where one may want to distinguish the laws of structure and change that govern the selection of the members of a given organisational species from those that govern the emergence of new organisational species. Or, in other words, the working hypothesis of this paper is that the problem of the "origin of organizational species" in economics may share some of the complicated intellectual challenges that characterise the "origin of natural species" in biology.

The first section considers the struggle of Charles Darwin with the concept of species. From the viewpoint of the modern definition of species, that is not based "on degree of difference" but on "absence of interbreeding" (Mayr, 1988 p. 318), Darwin's struggle was unsuccessful. In order to explain the origin of species as the result of a gradual adaptations Darwin ended up denying any fundamental distinction between species and varieties.

The second and third sections of this paper consider the modern biological debate on speciation. The purpose of these sections is to show that, in this respect, modern biology has substantially departed from Darwin's theory of speciation. Competition among many members of the same species favours the emergence and the selection of fitter one-mutant variants that favour the adaptation to the environment. However, the pressure of natural selection may inhibit the formation of new species requiring a set of "complementary" mutations characterised by the fact that "hybrid combinations" between the two species are either inferior or, even, impossible. In these cases, that involve that hybrids between the old and new species are inferior to both species, speciation may require "allopatric" conditions or, in other words, some initial protection from the competition from the members of the old species. In other words while the pressure of natural selection favours the adaptation of each species to the environment and its co-evolution with other species, it may inhibit the formation of new species. The pressure of natural selection may even contribute to a stasis of the evolutionary process. A "punctuation" of this stasis is more likely to occur in "allopatric conditions" in a relatively protected periphery. By contrast, natural selection may have a stabilising role "freezing" some parts of the genotype.

In the third section we argue that the evolution of economic organisations may be characterised by similar rules of structure and change. Organisational species are characterised by rights and technologies that fit each other and define "organisational equilibria" superior to hybrid combinations with rights and technologies of other species. Competition among the members of the same organisational species may improve its average efficiency but, because of the complementarities between rights and technology, it may also inhibit the emergence of new potentially more efficient "organisational equilibria". Thus, while the pressure of competition favours the adaptation of each organisation to the environment and its co-evolution with the other organisations, it may inhibit the "speciation" of new organisational species; as in the case of natural species, speciation may again require "allopatric conditions".

In the last section we consider the "Second Industrial Revolution" and the coming of the new species of "managerial capitalism" in United States and Germany. We argue that Britain's failure to keep pace in organisational change was paradoxically due to the fact that it had been the main actor in the First Industrial Revolution developing a robust species of "personal capitalism". The speciation of managerial capitalism required the "allopatric conditions" offered by Germany and the United States.

2. The Concepts and Origin of Species in Darwin

Helena Cronin concludes her book *The Ant and the Peacock* observing that:

"The two fundamental problems that Darwin's theory was designed to solve were adaptation and diversity. The riddle of adaptation he solved superbly. As for diversity, on certain aspects he was equally successful. The patterns of geographical distribution, the fossil record, the taxonomic hierarchy, and comparative embryology all fell into place under his incisive analysis. But in the mist of such success, there was one problem that remained just outside his grasp. It was poignantly the problem of the origin of species". Cronin H. (1991, p. 430).

In some ways, Darwin's failure was made more striking by the fact that he failed to give a satisfactory definition of species. The concept of species was somehow blurred with the concept of variety within a given species. Indeed, Darwin concludes his chapter on hybrids arguing that:

"Laying aside the question of fertility and sterility, in all other respects there seems to be a general and close similarity in the offspring of crossed species, and of crossed varieties. If we look at species as having been specially created, and at varieties as having been produced by secondary laws, this similarity would be an astonishing fact. But it harmonises perfectly with the view that there is no essential distinction between species and varieties" (Darwin 1859 p. 288).

This conclusion shows an adherence to a "phenetic species concept" defining species as a set of organisms that resemble one another and are, in this sense, distinct from other organisms. In terms of this definition the distinction between species and varieties becomes a matter of degree. Indeed, a great weakness of the phenetic species concept is that the distinction between varieties and species becomes inevitably subjective and arbitrary. Different phenetic measures may group into different ways different clusters of individuals attributing to one or to another characteristic the role of defining a border line among different species.

Darwin does not seem to be aware of the fact that "laying aside the question of fertility and sterility" is tantamount to ignoring the very essence of the "biological species concept" that defines species as groups of interbreeding natural populations that are reproductively isolated from other such groups.

The "biological species concept" has the advantage "that it places the taxonomy of natural species within the conceptual scheme of population genetics. A community of interbreeding organisms is, in population genetic terms, a gene pool" (Ridley p. 403). Moreover, the biological concept of species provides an explanation for the similarities[1] that are the main ingredient of the "phenetic concept of species": the gene flow among the members of the species gives a species its phenetic coherence while the absence of this flow among the members of different species causes more pronounced differences in their appearances.

According to Mayr (1982, p. 265), the discovery of Darwin notebooks shows that he was well aware of the "modern" concept of "biological species". Mayr observes how "No author reflects the struggle with the species concept more vividly than Darwin". Before the publication of the "Origin of the Species" his notebooks contained "a clear description of reproductive isolation, maintained by ethological isolating mechanisms" and moreover "Darwin emphasised repeatedly that species status had little if anything to do with degree of difference" (Mayr, 1982 p. 266).

Thus, according to Mayr, when one reads what Darwin says about species in the Origin "one cannot help but feel that one is dealing with an altogether different author" claiming that varieties have the same general characters as species "for they cannot be distinguished from species" (Mayr, 1982 pp. 266-7).

"What could have brought about this complete turn around in Darwin's species concept?" asks Mayr (1982 p. 267).

The botanical literature had, perhaps, made Darwin aware of one genuine problem related to the biological concept of species: the difficulty and often the impossibility to rank geographically isolated populations that might (or might not) interbreed if they lived in sympatry (i. e. in the same area). However this difficulty does imply that species are purely arbitrary or invented for the convenience of taxonomists as Darwin seemed to maintain in the Origin.

Thus, according to Mayr the explanation has to be found in "a strong, even though perhaps unconscious, motivation for Darwin to demonstrate that species lack the constancy and the distinctiveness claimed by them by creationists" (Mayr 1982, p. 262). Creationists pointed at these characteristics of species to challenge the claim that such discontinuities could be the results of the gradual adaptation due the working of natural selection. Thus, Darwin "solved" the species problem defining them by degree of difference rather than by reproductive isolation and by denying their qualitative distinctness from varieties of the same species.

Mayr concludes his analysis observing that when species are reduced to varieties it is possible to provide a relatively simple explanation of their origin "by the means of natural selection"[2]. Thus, in some ways, "it was a good strategy to deny the distinctness of species". "But the switch from Darwin's species concept of the 1830s to that of 1850s laid the foundation for controversies that lasted for a century" (Mayr 1982 p. 269). One may add that it also laid the ground for the type of influence that Darwinism was to have on the social sciences: the fitness of organisational and cultural species was to be related to the strength of the competitive struggle while no inquiry was made on the conditions under which new "fitter" species could ever come about.

3. Natural Selection and Speciation

If the biological definition of species is accepted how can natural selection favour the formation of new species?

If one follows the Darwinian approach, the answer should necessarily be based on the argument that natural selection should be able to discriminate against the hybrids between the old and new populations and favour the reproductive isolation necessary to give them the status of distinct species. "This process by which selection increases reproductive isolation, independently of the history of the populations is simply called *reinforcement*. Reinforcement may occur when two forms coexist, and the hybrids between them have lower fitness than crosses within each form" (Ridley 1996 p. 431).

Reinforcement would act by discriminating against those that mate with members of the other form favouring a process of pre-zygotic isolation or, in other words, favouring those members that develop a mating preference for the individuals of their own form. When these preferences are selected the two population are completely separated and become two different species.

Reinforcement can be an important mechanism to isolate two populations living in sympatry (i. e. without being separated by geographic barriers). If they can mate and the hybrids are as fit or fitter than the two original forms, then selection will not reinforce isolation but will rather tend to decrease any pre-existing partial reproductive isolation.

Thus, reinforcement may be necessary to keep isolated in sympatry two populations that are able to produce hybrids. However, this does not imply that reinforcement favours speciation when a new genotype is emerging. By contrast, it can be easily shown that, even when hybrids are inferior, the pressure of natural selection may inhibit rather than favour speciation.

Ridley considers a simple case that illustrates the nature of this important problem. If we have two alleles A and *a* at a locus, the inferiority of hybrids implies that AA and *aa* have higher fitness while A*a* is selected against. In this condition the working of reinforcement means that natural selection favors AA types that have a preference to mate only with AA types and *aa* types that have a preference to mate only with *aa* types. Thus natural selection could cause the formation of two different species. However, the force of natural selection will also act against the heterozygotes (i. e. the hybrids). Assume that *a* is a much rarer allele associated with a recent mutation. Then, *a* is likely to be eliminated by natural selection because it will tend to find itself more often in the hybrid combinations A*a*. Thus the very same natural selection forces causing reinforcement cause the loss of the rarer allele. Ridley argues that the evolutionary race between these two effects of natural selection is likely to be won by the loss of the allele. This latter effect will often be faster because it does not require any new genetic variation, whereas speciation cannot happen without genetic variation for mating preferences.

Thus, when species are not defined by the "degree of difference" but by the "absence of interbreeding", it is difficult to see how natural selection may bring about the isolation of the two species: selecting against hybrids involves selecting against the rarer allele and may bring about greater uniformity instead of new species.

Besides these theoretical difficulties, evidence does not always favour the theory of reinforcement. "A theory of speciation, therefore, can avoid a theoretical and empirical minefield if, while not excluding the possibility of reinforcement, it nevertheless does not depend on it" (Ridley p. 433).

If the "biological species concept" is adopted Darwin's theory of the "Origin of the Species by means of natural selection" must, in fact, rely on the fact that reinforcement can act in situations of sympatry. The theoretical conditions under which *sympatric speciation*[3] is possible turn out to be rather special. Sympatric speciation is possible if a species first evolves a stable polymorphism and the different types are best adapted to different niches. The stability of the polymorphism rules out the possibility that reinforcement acting to eliminate the hybrids eliminates also the less common type. Once the most difficult step - the establishment of a stable polymorphism of types best adapted to different niches - is achieved, then natural selection will favour the evolution of reproductive isolation between the two types and hence speciation (Hall, 1993). In order for this process to occur "habitat selection" is crucial in two respects. In the first place habitat selection is crucial to establish the initial polymorphism whose fitness is due to the fact that different forms are best adapted to different habitats. In the second place, habitat (or host) selection is important to evolve reproductive isolation. It may be in principle possible that reproductive isolation arises as a result of a "double" (pleiotropic) effect of the gene causing the adaptation to the particular niche: the same gene also happens to cause frequent mating between individuals of the same type. However, reproductive isolation is more likely to arise because the individuals that live in the different habitats tend to mate with the other individuals living in the same habitat and are likely to evolve different mating times and habitats that may isolate their reproduction from that of the other individuals.

In *parapatric speciation*, the new species emerges in a territory contiguous to the pre-existing population. In this theory we assume that a population initially existed in an area to which it was well adapted, and that it then started to expand in a contiguous area in which the environment favoured a different form. Suppose that the transition between the two environments is sudden. We will have a graded series of forms (a stepped cline) at the border while a new population adapted to the new environment will tend to evolve in the new area. If the new population will diverge almost to become different species, the border will be recognised as a hybrid zone. Because of the sudden change, existing between the two environments, a stable cline will be indefinitely maintained by natural selection at their border. The stability of the cline implies that reinforcement has a long time to operate against the hybrids and allow speciation to take place.

In the case of parapatric speciation the stability of the stepped cline has the same role that the stability of the polymorphism has in the case of sympatric speciation. Both the stability of the polymorphism and that of the cline imply that natural selection will not eliminate the less numerous genes and that gene flow will be unable to merge the two populations.

The conditions under which parapatric and sympatric speciation occur are rather special. In both cases speciation must rely on a mechanism such as reinforcement that we have seen to have, in general, the tendency to eliminate the less numerous new group of individuals that should eventually speciate. It is a virtue of the theory of *allopatric speciation* that it does not depend on any of the special circumstances under which reinforcement can operate. According to this theory reproductive isolation evolves in allopatry, that is after that the two populations have been separated by some geographical barrier. The Darwinian natural selection mechanism against hybrids is not a (necessary) part of the theory even if it may operate in the case in which, after having evolved only partial reproductive isolation in allopatry, the two species meet again: only in this case reinforcement may be useful to complete the partial isolation initiated in allopatric conditions (otherwise partial isolation may not be completed in sympatry).

Allopatric speciation may occur in two ways. According to the "dumb-bell" model the ancestral species may be divided into two roughly equal halves, each of which forms a new species. This model must be distinguished from another model developed by Mayr where the new species emerges in a small population isolated at the edge of the ancestral species range. This process, that is obviously a form of allopatric speciation, is now denominated by Mayr *peripatric speciation,* meaning that it happens at the periphery of the ancestral population.

Since the two populations are geographically isolated genetic drift is by itself able to differentiate the two populations. Natural selection may also lead to differentiation as long as the two populations will follow two different evolutionary paths. Stabilising selection may be a weaker force especially in peripherally isolated small populations where a small number of founder individuals spread a considerable amount of genes that would have been eliminated by natural selection in conditions of sympatry. Because of the elimination of the force of natural selection (acting in sympatry against the less numerous forms) allopatric conditions may favour a new type of "protected" natural selection of the population leading to speciation.

The irrelevance of the "origin of species by means of natural selection" argument is reinforced by the fact that even the "protected" natural selection occurring in allopatry may be a much less important cause of speciation than "sexual selection". This argument may be better understood by elaborating on the "biological concept of species" and introducing the "recognition species concept" introduced in the literature by Hugh Paterson.

According to the classical definition introduced by Mayr "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr, 1988 p. 318). According to Elredge, while this definition established the primacy of reproduction as the *sine qua non* of species, it was left to Paterson to refine the conceptualisation of the nature of those reproductive communities (Elredge, 1995 p. 466). Paterson defines a species as an inclusive community of individual biparental organisms which share a common fertilisation system. The fertilisation system includes all the components, such as courtship behaviour, genital structure, or attractiveness of the ovum to the sperm or pollen, that contribute to the ultimate function of bringing about fertilisation with another individual having the same fertilisation system.

Paterson's definition of species allows us to understand more precisely when speciation occurs. The two species become reproductively isolated when a different fertilisation system evolves. Thus, reproductive isolation does not evolve because the two species have developed two incompatible "economic relationships"[4] to the environment but is rather a mere by-product of a change in fertilisation systems. A modification of the fertilisation system is both necessary and sufficient for speciation to occur. "In other words, a great deal of economic change can accrue within a polytypic species (whether through selection, genetic drift, or other mechanism of genetic change) without reproductive isolation necessarily following. The converse is also true as we know from numerous examples of "sibling" species, reproductive isolation can exist between two closely related species that are hardly to be distinguished on the basis of external, economic phenotypic attributes" (Elredge, 1995 pp.467-468).

Sexual selection involves such striking runaway effects as the growth of the peacock tail that has no, or even a negative, "economic" value for the species in terms of its successful adaptation to the environment. This selection for continued mate recognition can lead to a divergence of the fertilisation system - such divergence having nothing to do with successful adaptations to the environment. At the same time it has been argued that "the function of courtship in sexually reproducing animals is to facilitate syngamy, and hence the male-female communication system is subject to strong stabilising selection. Unusual or fussy individuals (whether male or female) will be at a disadvantage, because they reject suitable mates or are themselves rejected" (Spencer, Masters p. 301).

It remains an open issue whether different sexual preferences develop as a consequence of "protected" natural or sexual selection. What is relevant for our argument is simply that in both cases the differentiation of sexual preferences and, in general, reproductive isolation, is likely to require allopatric conditions or, in other words, a protection from rather than the working of selection.

4. Stasis and Epistatic Interactions

Chapter nine of the "Origin was "On the Imperfection of the Geological Record". Ever since Darwin this "imperfection" has been used to conciliate the missing steps of phylogeny with the gradual nature of the adaptation predicted by the Darwinian theory.

The allopatric theory of speciation has also the virtue that it can explain the incompleteness of the fossil records without justifying the absence of intermediate populations with the fact that some intermediate populations were not able to leave a fossil for our paleontological research.

What looks in the main territory of the ancestral species an incompleteness of the fossil record and could be interpreted as a "saltation" of intermediate evolutionary events, may be due to the fact that the evolutionary process leading to speciation has occurred far away in an isolated periphery. The new species has only later re-penetrated the main territory of the ancestral species and, for this reason, this appears to be substituted by a population showing a substantial phenetic jump.

In other words, the theory of allopatric speciation seems to provide an explanation for the long period of stasis and the "apparent jumps"- or in one word the "punctuated equilibria"- that characterise natural history.

The theory of punctuated equilibria developed by Elredge and Gould (1972) implies that most evolutionary change is associated with speciation events. However, the argument is not incompatible with the idea that gradual intra-specific events may take place while the members of a species try to adapt to environmental change and co-evolve with other species In this sense according to Turner (1995, p. 65) "Efforts to demonstrate that evolution is gradual by producing evidence for slow change in one or other character of a species in the fossil record simply say nothing about the deployment of speciation". In this sense "phyletic gradualism" does not make sense for the simple fact that speciation involves always a moment of discontinuity related to the break-down of a common fertilisation system between two populations. The crucial distinction is not between the evolutionary speeds of speciation and within-species change but between the different mechanisms entailed by these two types of changes. By contrast the hypothesis that within-species events do also characterise evolution can be easily compromised with the hypothesis of punctuated equilibria. In this last respect punctuated equilibrium and phyletic gradualism can be seen as extremes of a continuum as it is shown in Figure 1 taken from Ridley (1996, p. 562).

Even if gradual intra-specific events are not incompatible with the theory of punctuated equilibria, one important aim of the theory is to explain why, after rapid changes related to speciation events, long period of stasis characterise the history of species. This explanation is related to an "holistic"[5] view of the genotype that claims that "much of macroevolution cannot be explained by atomistic genes replacements or by selection pressures on single genes, but only by a more drastic reorganisation, made possible by loosening the tight genetic cohesion of the genotype found throughout widespread populous species" (Mayr,1988 p. 471).

The "holistic" view of the gene focuses its attention on the epistatic interactions characterising the genotype. Epistatic interactions are the synergistic effect on the phenotype of two or more gene loci, whereby their joint effect differs from the sum of the loci taken separately. Or, to use a term familiar to economists, the holistic view focuses on the "complementarities" existing between different gene loci implying that each part makes a fitness contribution depending upon that part and the other parts with which it has epistatic interactions.

Even when "complementary" mutations could improve the fitness of the genotype, the epistatic interactions among the gene loci imply that the genotype is characterised by a built in inertia[6]. Evolution is characterised by a succession of single mutations and natural selection eliminates those genotypes that make only one of the two complementary changes required to improve the outcome of epistatic relations.

If natural selection has been acting for sufficient time each allele is likely to be optimally adjusted to the other alleles with whom it has epistatic relations. Thus, in these conditions, single mutations are likely to lower fitness and be eliminated by "normalising" (stabilising) selection that acts to keep the species at a "local" fitness peak. Thus, because of epistatic relations, long period of stasis may characterise evolution.

Allopatric conditions sterilise the forces of natural selection that, together with gene flow, act to keep the "integrity" of the species. In allopatric theory speciation may occur in small isolated populations[7]. In this situation the genes of isolated founders, who change only one of the two "complementary" alleles, are not promptly eliminated by natural selection. Thus, the "exploration" of a new fitness peak, characterised by different epistatic relations, becomes possible: the "founder effect", that is typical of isolated peripheries, may break previously existing "epistatic relations" and allow the formation of a new population. When and if the two population meet again reproductive isolation may result from the fact that hybrids have inferior epistatic interactions that may imply the impossibility or the gradual elimination of hybrids. The new species may, then, co-exist with the ancestral population. Alternatively, if it occupies the same ecological niche, the new species may displace and replace its ancestor.

The role that allopatric conditions have in punctuating long periods of stasis and favouring speciation implies that the evolution of life has required some balance between the forces of natural selection and the "temporary" protection of mutants to allow them to explore new fitness peaks. A similar conclusion is reached by Stuart A. Kauffman who develops the intuition that epistatic interactions are the crucial factor for the understanding of the evolution and the co-evolution of the different species.

Kauffman's (1993) NK model of rugged fitness landscapes considers a model of epistatic interactions where N is the total number of parts and the fitness of each part depends upon that part and upon K parts of the N. The relatively rugged or smooth nature of fitness landscapes is defined by its "correlation structure" or the degree of similarity of the fitness value of one-mutant neighbour. In a smooth landscape knowing the fitness value of one point carries a lot of information about the other points because neighbouring points in the space have nearly the same fitness value. By contrast in a maximally rugged landscape it carries no information about the fitness of neighbouring points because fitness values are entirely uncorrelated. Kauffman shows that in the NK model tuning the K parameter from 0 to N-1 increases the ruggedness of the landscape in a controlled manner. In other words, increasing the richness of epistatic interactions among the components of the system changes the landscape from the K=O case where it is single-peaked and smooth to the K = N -1 case where it becomes fully random.

When K = 0 and there are no epistatic interactions, the fitness of a mutant neighbour can only differ by the amount of the independent fitness contribution of an allele in a different locus. This implies that the landscape is smooth carrying maximum information about neighbouring point. Any genotype can be sequentially changed via fitter one-mutant variants to the global optimum and no local optimum exists.

When K= N-1 and the richness of epistatic interactions is maximum, the fitness of a mutant neighbour does not only differ by fitness contribution of the altered allele but affects also the fitness contribution of all the other genes. For this reason the fitness value of a genotype is entirely uncorrelated with that of a mutant neighbour. The landscape is maximally rugged carrying no information about neighbouring points and sequential changes via fitter one-mutant variants can only lead to one of the many local optima.

In general as K increases from 0 to N-1, fitness landscapes change from smooth to fully uncorrelated landscapes through a family of rugged landscapes. In rugged landscapes many local optima exist and this poses the problem of the existence of a trade-off between evolvability and sustained fitness. At sufficient low mutation rates natural selection will induce the population to climb the nearest fitness peaks and remain clustered about one or the other of these peaks; thus sustained fitness will be sacrificed. By contrast at sufficient high mutation rates the low fitness valleys will be passed and new peaks be explored but natural selection will be unable to accumulate heritable information beyond the coherence of walks due to founder effects; thus in this case evolvability is sacrificed. In other words at low mutation rates population becomes trapped on poor local peaks while at high mutation rates populations are driven far below the peaks in fitness lowlands. A delicate intermediate rate of mutation where populations are just beginning to "melt" and come down from the peaks could allow natural selection to optimise both evolvability and sustained fitness.

However stasis at a local peak is likely to be a normal state for parts of organisms characterised by complex epistatic interactions. These parts of the genotype are somehow "frozen" by epistatic interactions and provide an explanation for one important puzzle about stasis: while it is normally accounted for as stabilising selection which holds a phenotype at the optimum in a stable environment, the latter cannot be stable if other species are co-evolving in the same niche. Kauffman's solution of the puzzle is that frozen components imply that "species within or on the boundaries of such components have an unchanging optimal genotype and phenotype, despite changes in some of their coevolutionary partners. Thus familiar stabilising selection *can* sustain the phenotype in stasis despite changes in the niche" (Kauffman 1993 p. 270).

Kauffman's contribution clarifies how natural selection may contribute to the stasis of species by inhibiting the exploration of new peaks. Natural selection helps adaptation when improvements only require one by one sequential changes but may well inhibit those changes that are such that involve that a single change lowers fitness if it is not accompanied by a complementary changes. If speciation is characterised by the inferiority of hybrids with the ancestral species, the (future) hybrid combination is a fitness valley that is hard to overcome in the presence of tight natural selection.

Even if a fast rate of mutations allows some genotypes to survive the fitness valley between the old and new peak, the selection against hybrids (or reinforcement) may not separate the two species. It may rather imply the elimination of the few mutant alleles that are likely to find themselves more often in the inferior hybrid combinations.

While selection may stabilise the parts of the genotype frozen by epistatic interactions, it can help the diffusion of those fitter one-mutant variants that characterise intra-specific events. However, this may help to stabilise even more the "frozen parts" of those species that happen to be more numerous and can have a higher number of one-mutant variations in the "non-frozen" parts of the genotype. Darwin himself pointed out how more numerous species would not only show greater fitness because they were less liable to accidental extermination but also because "these from existing in greater numbers will, in the aggregate, present more variation, and thus be improved through natural selection and gain further advantages" (Darwin, 1968 p. 211).

5. The Speciation of Organisational Models

Are the biological debates concerning stasis and speciation relevant to the understanding of the origin of organisational species?

A positive answer to these question might be based on the observation that the history of organisational species also seems to be characterised by those long period of stasis and allopatric speciations that characterise natural history. I will try to develop these points in the following section whereas in this section I will be concerned with some particular theoretical reasons for which organisational species may share the same laws of "structure and change" that characterise natural species.

A simple definition of an organization of production can be based on two factors. The first is its technology and, in particular, the technological characteristics of the resources used in production. The second is the set of rights (which may be legal rights and/or customary rights supported by social norms) on the resources employed in the organization and on the organization itself.

The relationship between these two factors has traditionally been a controversial issue in social sciences: if causation exists, it can go both ways. On the one hand property rights can be seen as factors shaping the nature and the characteristics of the resources used in production. On the other hand, the technological characteristics of resources employed in production can be considered to be the cause of changes in the system of property rights.

This double way relationship was at the very root of the Marxian theory of history and of his view of the firm. It was the source of interesting problems and contradictions within this theory. Marxist analysis has often oscillated between "technological determinism" (technology invariably gives rise to a unique set of property rights) and "property rights romanticism" (alternative property rights can invariably bring about an alternative technology)[8]. Moreover, as Hirschman (1981) observes, Marx "oscillated between the grand generalisation with which to characterise an entire epoch or process and the discriminating analysis of events which made differences between countries and subperiods stand out in richly textured detail".

In spite of these contradictions and limitations the two way relationship considered by Marx has not ceased to be an important key for the understanding of alternative organisations and it is difficult to disagree with John Hicks when he maintains that when we come to "theories of history" "there is so little in the way of an alternative vision which is available" (Hicks 1969 p. 3).

The relationship between property rights and the characteristics of productive forces, which created so many interesting problems and contradictions (as well as so many wrong "predictions") in the Marxian approach, became a non-issue in neo-classical theory. In a market economy workers' or capitalists' ownership would have had no effect on the characteristics of the resources (or of the productive forces) employed by the firm. At the same time, the characteristics of the resources employed in the firm had no implication whatever for the form of ownership which was going to characterise the firm.

This point of view was well expressed by Samuelson when he argued that "In a perfectly competitive economy it doesn't really matter who hires whom...." (1975 p. 894) - a statement that contained the double implication that, while the nature of property rights has no implication on the choice of "optimal" technology, the latter does not involve that particular owners are better suited to its management.

Recently, both New Institutional and Radical Economists have reconsidered the interaction between rights and technology. However, the relationship between rights and technology is still very controversial. In these two streams of literature the direction of causality runs in opposite directions. In New Institutional economics rights are endogenously and efficiently determined by the characteristics of the resources employed by the organisations[9]: namely their degree of specificity and their monitoring requirements. By contrast, in the Radical Literature the characteristics of the resources employed in the firm are in turn determined by the rights which owners of different factors have on the organization[10].

In spite of their differences the lines of inquiries of New Institutional and Radicals are not necessarily incompatible and they can be integrated in a framework that considers the two-way relationship between property rights and technology.

The "Radical direction"[11] of causation runs from property rights to technology. It is argued that the specificity and monitoring characteristics of the resources are due to the nature of property rights under which they are employed. For instance, individuals working in organisations where they do not have rights are likely to be characterised by a relative underinvestment in organisation specific skills and by an unfavourable distribution of asymmetric information attributes that makes them "easy to monitor". Specific and difficult to monitor workers are high-agency-cost resources that are expensive for the present owner who has an incentive to substitute them with low-agency-cost resources. By contrast, no similar substitution occurs for the individuals having rights on the organisation: the alignment of their objectives with that of the organisation allows a considerable saving of the high agency costs that would have been paid if they were employed by other agents.

When we leave the Neo-classical world with zero agency costs, the "Radical direction" of causation can be justified by using a fundamental principle of economic theory: that profit-maximising employers tend to replace high cost factors with low cost factors. This point becomes evident when one considers that a change in property rights from one factor to the other changes also the relative costs of employing these factors. The new owning factors will save on their own agency costs while they will pay the agency costs of employing the former owning factor (while this cost was saved in the former ownership arrangement). Thus the simple profit-maximizing principle allows us to state there is an influence of property rights on the combinations of productive forces that is going to be adopted in the precise sense that the optimal technology changes with a change in property rights.

Also the "New Institutionalist" direction[12] of causality, running from the nature of technology to property rights, can be easily understood by using another fundamental principle of economic theory: that, like other economic goods, organisations tend to be owned by those individuals in the hands of which they are more valuable. This implies that for each combination of resources employed in production property rights should go those individuals that can save the most on agency costs when they own the organisation: these are the most difficult to monitor and specific factors that is to the high-agency-cost factors that involve higher agency costs when they are employed by other people. Thus for each combination of resources employed by the organisation there is an optimal assignment of the ownership rights on the organisation.

Thus in a world of positive agency costs there is an optimal technology for given ownership rights on the organisation and an optimal set of ownership rights for a given technology that is employed by the organization. Using the biological terminology we could say that organisations are characterised by epistatic interactions between rights and technology - an observation that suggests that many of the "laws of structure and change" that characterise the origin of natural species may be also relevant for that of "organisational species".

Like the "frozen part" of a genotype the interactions between technology and property rights have a "built-in" inertia. Pagano (1991, 1992) and Pagano and Rowthorn (1994, 1996) have tried to capture this point by introducing the concept of organisational equilibrium and investigating the characteristics of "institutional stability" that characterise these equilibria in the framework of a simple two factor model.

An organisational equilibrium is defined by the fact that technology is optimal relative to property rights and property rights are optimal given the technology that is employed. The self-sustaining[13] characteristic of organisational equilibria comes from the fact that owning factors saving on their own agency costs tend to choose a technology characterised by high intensity of their own high-agency-cost factors - that is, a technology under which their ownership is optimal.

The analogy between the epistatic relations characterising natural species and the characteristics defining an organisational equilibrium have, of course, to be taken with some caution. Human learning may allow patterns that are not permitted to genes. On the other hand the concept of organisational equilibria entails already a considerable degree of rationality. The optimality of technology given property rights and that of property rights given technology defines a "Nash equilibrium"; it is tantamount to assuming that "financiers" are able to choose the optimal owners for each firm characterised by a certain given technology and that "production managers" are able to choose the optimal technology for a certain given ownership structure. Indeed, it is reasonable to assume that this equilibrium is rather achieved by an evolutionary process by which firms that have sub-optimal technologies given the ownership structure as well as those that have sub-optimal ownership structures given technology are gradually eliminated by competitive forces[14].

The analogy between organisational equilibria and natural species turns out to be useful to explore the issue of the characteristics of the organisational models that come into existence as a result of the working of competition. In particular, we may ask the following question: "Does competition entail the selection of efficient organisational models?"

Indeed, the analogy with natural species may even help to clarify the meaning of this problem. In natural selection the pressure of competition helps to select the best members of a given species; however, we have seen that the effects of natural selection on speciation are much more controversial. Our question is related to the case of speciation: we are not asking whether competition can select the best member of a given species of organisations but whether it can help the formation of a new more efficient species of organisation characterised by different technology-property rights "genotypes".

We have seen that epistatic interactions imply that each species is characterised by important "development constraints": the fitness of each mutation is constrained by the other characteristics of the species. This implies that many evolutionary paths may be blocked. Unfortunately, in the case of organisational equilibria these obstacles may work exactly against those changes that may otherwise lead to the formation of a superior species of organisation. Suppose that there are some efficient alternative potential owners that could get a higher ownership rent than the present owners. These alternative owners are efficient because their employment by the present owners involves very high agency costs that could be saved if they own the organisation. For this reason, the factors of the potential alternative owners are promptly replaced by factors that are cheaper for the present owners. In other words, an "anti-speciation" mechanism is embodied in each "species" of organisational equilibrium and it has the unfortunate characteristic that its strength is related to the efficiency of the alternative potential species[15].

However, suppose that this “anti-speciation” factor is overcome and one of the characteristics of the old species mutates into one characterising also a potential more efficient new species of organisation. For instance, some organisations are characterised by new property rights that, if they were coupled with the associated optimal new technology, could form a new more efficient organisational equilibrium. Until this new technological combination is developed and employed, we will have a situation of organisational disequilibrium or, in other words, an inferior hybrid between the new property rights and the old technology. If the pressure of competition by the members of the old species is strong, the hybrid is likely to be wiped out before it has any chance of turning into the new superior species. Or, in other words, the epistatic interactions between property rights and technology imply the existence of a rugged multi-peaked fitness landscape; in these conditions the pressure of competition will act to keep the firms at the local peaks.

However, even if speciation is successful, the survival of the new species can endangered by a strong competition by many members of the old species.

In the first place, if there are few members of the new organisational species, “interbreeding” with the many members of the old species will be very frequent and will produce numerous inferior hybrids. In these conditions “interbreeding” may lead to the extinction of both mutations. When the new technology is imitated and run under the old property rights system it turns out to be inferior and, vice versa, when the new rights are influenced by the old technology they also turn out to be inferior. Hybrid organisations that have imitated only one aspect of the new species will be doomed to fail and the new mutation may tend to disappear with them.

Secondly, in nature, the efficiency of each species depends on its frequency. Also organisations share the same characteristic. For instance, network externalities in property rights and in technologies may imply that few firms characterised by different organisational equilibria are not viable: they would be outcompeted by firms that, even if inferior when they exist with the same frequency, can better benefit from network externalities because of their present large number.

Thirdly, as Darwin pointed out more numerous species may enjoy more mutations. Also organisations that are more numerous will share this advantage for the non-frozen part of their characteristics. Even if few organisations have succeeded in speciating they may find hard to compete with the innovations of the more numerous species.

These considerations imply that, while many characteristics of organisations evolve and co-evolve with other institutions, some important aspects of property rights and technology may be characterised by long periods of stasis.

If the analogies with the origin of species may be pushed even further we should expect that while competition favours the selection of the best members of a given organisational species it may inhibit the formation of new species. In other words we should expect that the formation of new species does not happen in sympatry but is more likely to occur under allopatric conditions or, in general under conditions where the members of the new species could somehow be protected from the competition of the members of the old species. Alternatively, institutional and technological shocks should be strong enough to overcome the inertia built in the epistatic relations characterising rights and technology.

6. British Organisational Stasis and the "Allopatric Speciation" of Managerial Capitalism

In the last half of the nineteenth century "came into being a new economic institution, the managerial business enterprise, and a new subspecies of economic man, the salaried manager. With their coming, the world received a new type of capitalism - one in which the decisions about current operations, employment, output, and the allocation of resources for future operations were made by salaried managers who were not owners of the enterprise" (Chandler 1990 p. 2).

According to Chandler, the advent of the new institutions and the "new subspecies" of economic man were strictly related to the building and operating of the rail and telegraph systems. The complexities of their operations required firm-specific organisational capabilities that could not have been developed within the members of the family owning the firm nor efficiently monitored and controlled by them. The new firms required a managerial hierarchy where to a great extent salaried managers controlled other managers. In other words the new technology required the employment of "high-agency-cost" managerial skills. In turn, this required that rights, incentives and safeguards were to be given to these managers. In particular it was vitally important for managerial effort as well as for the efficiency of the firm to know that promotions from the low to the high positions of the managerial hierarchy would be related to their achievements and unrelated to family and other social ties.

The new system came first into being in the rail and telegraph industry but it showed greater efficiency in many of the industries characterised by economies and scale and scope that could be efficiently exploited by the use of managerial hierarchies. Indeed, the diffusion of the new organisational model characterised the coming of a new species of capitalism: "managerial capitalism". The new species had two local varieties "Competitive Managerial Capitalism" in the USA and

"Cooperative Managerial Capitalism" in Germany. While in German industries family control lasted longer that in the United States, in both countries salaried managers with little or no equity in the enterprises for which they worked participated in making decisions concerning current production and distribution, as well as in planning and allocating resources for future production. "The greatest difference, however, came in interfirm and intrafirm relationships" (Chandler 1990 p. 395). In the United States the new managerial firms competed aggressively for market share and profits and the anti-monopolist legislation reflected a shared belief in the value of competition. By contrast, in Germany many firms preferred to cooperate and trade associations played a much larger role in the Germany than in United States.

While the coming of these two sub-species of managerial capitalism made the USA and Germany the two most important actors of the Second Industrial Revolution, Britain - the main actor of the First Industrial Revolution - became a late industrializer in many of the new industries. In Britain the commitment to the "species" of personal capitalism that had been so successful at the time of the first industrial revolution continued. While long-term profits based on long-term growth were a goal on which the managers and the major investors of the American and German managerial firms could agree, the families owning the British firms often preferred to pay out earnings in dividends rather than using them to make the extensive investments required to move into foreign markets or to develop new products in related industries. "Because their firms grew slowly and because they hired only a small numbers of managers, the founders and their families remained influential in the affairs of the enterprise and so affected dividend policy" (Chandler, 1990 p. 595). By contrast, the long-term growth of American firms helped the managers to gain strong job rights in their firms. "Such a goal not only helped to assure tenure for the senior executives, but it also enhanced the opportunity for advancement for the more junior managers" (Chandler, 1990 p. 595). British firms did not provide similar opportunities to non-owning managers. The key managerial positions were usually reserved for the owning family. Social and family ties were more important than competence to advance up the managerial ladder. There were few opportunities for junior managers while no job security similar to those of German and American firms could be given to senior executives. It is hardly surprising that organisational capabilities that were so important for the firms of the second industrial revolution stagnated. As a result, Britain lost the world economic leadership to the countries that had "speciated" the new form of managerial capitalism.

Using the terminology of the preceding sections the coming of competitive and cooperative managerial capitalism can be seen as a form of "allopatric" speciation. The speciation did not occur in Britain where the competition and strength of personal capitalism was the strongest but in countries that had not participated in the first industrial revolution and had not built any form of personal capitalism as well developed as that which characterised Britain. In the USA and Germany the nature of productive forces required by the railways and telegraph changed first the structure of rights that characterised these sectors and after a few years that of the other industries where the growth of productive forces could benefit from the change. Soon, the new rights favoured the widespread employment of "specific" "difficult to monitor" (and, therefore, high-agency-cost) managers while their employment had a self-reinforcement feed-back making the new rights of managerial capitalism an irreversible choice.

U. S. and Germany saw the speciation of new organisational equilibria where the managerial rights and managerial skills were a fundamental characteristic of new "epistatic interactions" between relations of production and productive forces. On the one hand, given tenure rights for senior executives and fair promotion opportunities for junior managers, productive forces were best characterised by a relative high intensity of high-agency-cost managerial skills. On the other hand, given the employment of these skills, only a system of strong managerial rights could ensure the commitment of managers to the organisations and save the high agency costs that should have otherwise been paid in case of a pronounced incongruence of their goals with those of the organisation.

By contrast, in Britain the "epistatic relations" between the structure of rights and the nature of productive forces were not broken by the Second Industrial Revolution. By that time the managerial skills accumulated by the British families had already made some of their members high-agency-cost factors. This reinforced the stability of their ownership rights: only under their ownership could their own high agency costs be saved. In turn these ownership arrangements had a feed-back on technology involving the continuation of the intensive employment of the high-agency-cost skills of the owning family members. In this framework, in spite of the environmental changes no tendency to "sympatric" speciation of managerial capitalism came about. In fact the vicious circle characterising managerial skills and rights mirrored the self-reinforcing interactions that we have just considered. Since managers were not involved in the organisation their agency costs could not be saved like those of the committed family members; for this reason the former were often substituted by the latter; but this damaged even more managers' commitment to the organisation and their accumulation of organisational skills. At the same time, the low intensity of high-agency-cost managerial skills implied that the (partial) saving of these agency costs (that would have occurred under managerial capitalism) could not favourably compare with the saving of agency costs of family members (that characterised British personal capitalism).

Thus, in spite of the technological shocks induced by the Second Industrial Revolution, the "frozen part" of the genotype of the British firms did not melt. The fairly strong competition that characterised the British environment had not the effect of favouring a new species of capitalism but acted as a normalising selection that favoured the organisational "stasis" of British capitalism. Organisational change was inhibited by the same laws of structure and change that make so difficult sympatric speciation in natural history. The inferiority of hybrids was, perhaps, again, the crucial problem: a high intensity of high-agency-cost managerial skills coupled with the property rights of personal capitalism lay in a "fitness valley" that was too difficult to overcome under strong competitive pressure. The forces of competition favoured the selection of the best members of the British species of personal capitalism but inhibited the speciation of managerial capitalism. Allopatric conditions, where the competitive pressure of "personal capitalism" was weaker, were required for the coming of the new species of capitalism[16]. In this respect the glorious contributions of Britain to the achievement of the First Industrial Revolution became a paradoxical disadvantage for the further development of its economy.

7. Conclusion

Sidney Winter has observed how biological analogies have been often used to justify the efficiency claims of neo-classical economics.

"Under competitive conditions a business firm must maximise profit if it is to survive - or so it is often claimed. This purported analogue of biological natural selection has had substantial influence in economic thinking, and the proposition remains influential today. In general, its role has been to serve as informal auxiliary defence, or crutch, for standard theoretical approaches based on optimisation and equilibrium" (Winter, 1987 p. 545).

With reference to New Institutional Economics a similar point has been made by Geoff Hodgson (1996) who has shown how often Williamson uses evolutionary thinking to justify the use of efficiency as a positive principle.

These uses of biological analogies are hardly surprising. The traffic of metaphors between economics and biology has gone both ways since the very beginning of the two subjects and, indeed, Political Economy had a considerable influence on the early development of the theory of Evolution[17]. However, the influence of modern biology on economics should, perhaps, go in the sense of helping the understanding of some limitations of competition: while competition has a fundamental role in promoting gradual change, it may help "freezing" some relations between rights and technology and be a cause of organisational stasis. In a world that too often praises the advantages of global competition "the common rule of structure and change" would rather suggest that the allopatric protection from competition played also an important role in the formation of new and, sometimes, fitter organisational species. More generally, biological debates should help us in understanding why, in spite of some common legal forms of a market economy[18], we have a considerable diversity of species of capitalism, with histories characterised by fast changes and long periods of organisational stasis.

Notes

1. We will see that another relevant explanation of the "integrity of the species" is given by the forces of "natural selection" themselves.

2. The complete title of Darwin's masterpiece - "The Origin of Species by the Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life" synthesises the main target of his research programme.

3. Models of sympatric speciation have been elaborated by Maynard Smith (1966) and Seger (1985).

4. On the relationship between "economic" and "reproductive" activity see Elredge (1996).

5. This holistic view has been extended by Wilson and Sober (1994) who have argued that natural selection operates on a nested hierarchy of units and is not incompatible with group selection. As far as the fate of each gene is linked to the fate of the other genes, it cannot do anything better than maximising the fitness of phenotype or of the other relevant vehicles of selection. The selection of the genotype is one form of group selection but also "higher" forms of group selection are possible insofar as the group is the relevant vehicle of selection.

6. Comparing the genotype to a team of rowers Dawkins claims that "It is the "team" that evolves. Other teams might have done the job just as well, or even better. But once one team has started to dominate the gene pool of a species it thereby has an automatic advantage. It is difficult for a minority team to break in, even a minority team which would, in the end, have done the job more efficiently. The majority team has an automatic resistance to

being displaced, simply by virtue of being the majority. This doesn't mean that the majority team can never be displaced. If it couldn't, evolution would grind to an halt. But it does mean that there is a kind of built-in inertia" (Dawkins, 1988 pp. 171-2). Sober (1984) introduces explicitly the role of epistatic reactions in Dawkins rowing example and observes that they occur when a rower's superiority in a certain position depends on which rower is occupying another positions. However it is important to point out that in natural selection genes can also compete against themselves in different combinations because the object of selection is gene-kinds, not gene-instances. In natural selection the coach is like "a made scientist who clones his favourite rowers and makes them race against each other in all combinations" (Sober 1984 p. 307).

7. According to the Nobel Laureate John C. Eccles an important episode of our own pre-human "recent" natural history can be characterised in terms of allopatric speciation and punctuated equilibria.

   "Despite the very extensive distribution of *Dryopithecus* - Hungary, Greece, Turkey, India, Kenya - the next stages of hominid evolution were restricted to Africa, both the Australopithecines and Homo habilis. It can be asked why only the African Dryopithecines participated in the evolutionary line to *Homo*? I believe that the origin of Australopithecines represented a unique evolutionary transformation such as it is postulated by Eldredge and Gould (1972) in their punctuated equilibria. It was likely therefore to be unique to a small isolated population. The remainder of the Dryopithecines went on to eventual extinction" (Eccles, 1989 p. 12).

8. Marx contains both types of elements and is not often able to find the right balance between them. Marxists have given

different importance to the "primacy" of the productive forces or to the influence of property rights on technology. For instance Cohen (1978) defends this "primacy" whereas Brenner (1986) criticises it. Roemer (1988) offers a useful survey of both.

9. Nelson (1994, p. 28) observes that New Institutional Economics has been characterised by "a broad theoretical stance that somehow, institutions changed optimally (if perhaps with a lag) in response to changes in economic circumstances that called for those changes". However he points out how some New Institutionalists have abandoned the assumption of optimality of institutional response and analysed the interest-group conflict often involved in public responses.

10. A formalisation of the New Institutional and Radical Assumptions is contained in the Appendix.

11. See, for instance, Bowles (1985) and (1989) and Braverman (1974).

12. Alchian and Demsetz (1972) and Williamson (1985) are, perhaps, the two canonical examples.

13. This self-sustaining ability of property rights depends on their ability to shape the technology in a self-sustaining manner by inducing changes in relative agency costs. It is not surprising that the elasticity of substitution σ of factors relative to prices plays an important role in determining the robustness of organisational equilibria. A high σ acts like a good "anti-virus": it favours the rejection of the non-owning factors, that, because of the increase in their agency costs, threaten to upset the health of the existing ownership regime. Unfortunately, the "anti-virus" works particularly well with the factors that are the most efficient potential alternative owners. They are efficient potential

alternative owners because of the high agency costs that must otherwise be paid when they are employed by other factors. A high σ causes an unfortunate "preventive treatment": these factors are promptly replaced by factors that are cheaper for the present owners. Using the biological terminology a high σ can also be interpreted as an "anti-speciation" factor: by allowing adaptations of the present species it prevents major mutations that would bring about the emergence of "new species" of organisational equilibria.

A high σ implies that each ownership arrangement can define self-sustaining organisational equilibria under a wider combination of agency costs. The higher the σ the wider is ability of ownership rights to shape technology in a self-sustaining manner. For the same reason, a high σ implies that each organisational equilibrium has greater institutional stability with respect to exogenous agency cost shocks. The Appendix contains an intuitive argument relating the multiplicity and the stability of organisational equilibria to σ. A more rigorous argument can be found in Pagano and Rowthorn (1994) and (1996).

14. We are aware of the fact that the nature of learning in evolutionary environments poses very complex problems and there is no easy solution to the problem of the degree of rationality that it is proper to assume. For a discussion of this point see Dosi, Marengo, Fagiolo 1997.

15. The strength of this mechanism depends on the elasticity of substitution that also determines the multiplicity and the efficiency of organisational equilibria. For a formal intuitive argument see the Appendix to this paper. For a more complete analysis see Pagano and Rowthorn (1994) and (1996).

16. Also other cases seem to follow a similar pattern. Indeed, after the war, the "speciation" of the Japanese model was another example of allopatric speciation. In this case the war and post-war institutional shocks destroyed the epistatic interactions of the zaibatsu version of personal capitalism. The result was not an imitation of the American model but the speciation of a new form of capitalism that was going to challenge the American model itself. In this sense a new allopatric speciation took place. The new species did not come about in America where competition was strongest but in an isolated periphery where institutional shocks had irreversibly weakened the preceding epistatic interactions. In the meantime no shock has yet been able to melt the frozen parts of the genotype of Italian Family Capitalism. On this see Pagano (1996), Barca, Pagano, Trento (1997) and Iwai (1997).

17. This influence was running in both ways from the very beginning:

    In a passage of his *Autobiography* Darwin writes:

    "In October 1838, that is fifteen months after I had begun my systematic inquiry, I happened to read for amusement Malthus on *Population* and being well prepared to appreciate the struggle for the existence which everywhere goes on, from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstance favourable variations would be preserved and unfavourable ones to be destroyed. The result of this would be the formation of a new species. Here, then, I had a theory by which to work; but I was so anxious to avoid prejudice that I determined not for some time write even the briefest sketch of it" (1958 ed. p. 58).

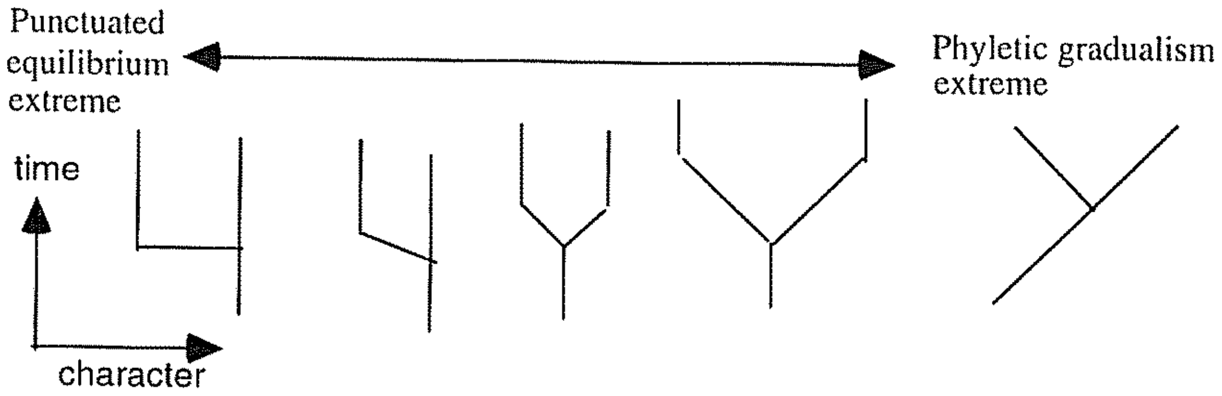
Similar passages can be found in the autobiography of Wallace who claimed to have had the inspiration of Darwin at about the same time during an attack of malaria:

"One day something brought me to my recollections Malthus Principle of Population, which I had read about twelve years before. I thought of his clear exposition of the "positive checks" to increase.... which keep down the population. It then occurred to me that these causes or their equivalents are continually acting in the case of animals also....." (My life, 1905 p. 51)

18. Iwai clarifies how the legal form of the corporation is compatible with very different organisational and property right arrangements.

FIGURE

Figure 1


Punctuated equilibrium extreme
Phyletic gradualism extreme
time
character

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APPENDIX

Appendix

We assume the existence of a standard production function Q (k, K, l, L) such that the output Q can be produced with different combinations of low-agency-cost capital and labour (k,l) and high-agency-cost capital and labour (K,L).. Q (.) can be interpreted as a "long-run" production function. Thus, the substitution effects induced by property rights are not immediate and it is possible to have short run mismatches between property rights and the associated technology.

We assume that when workers own the organisation they pay an additional agency cost Z in order to employ a unit of difficult-to-monitor or specific capital K - a cost that is saved when K is employed under capitalist ownership· By contrast, when the capitalists own the organisation, they pay an additional agency cost H when they employ a unit of difficult-to-monitor or specific labour L - a cost that is saved when L is employed under labour ownership. No such additional costs are paid for easy-to-monitor and general purpose labour and capital k and l when they are employed by either capitalists or workers.

We denote by r and w the prices of respectively easy-to-monitor and/or general capital and labour and by R and L the prices (net of agency costs) of respectively difficult-to-monitor and/or specific capital and labour. We also set the price of output equal to 1. Thus, we can formulate our "Radical" assumption as follows:

Radical Assumption:

Under capitalist ownership firms maximise profits equal to:

$$R^C = Q(k, K, l, L) - [rk + RK + wl + (H+W)L] \quad (1)$$

Under labour ownership firms maximise profits equal to

$$R^L = Q\,(k, K, l, L) - [rk + (Z{+}R)K + wl + WL] \quad (2)$$

This way of formalising the "radical assumption" makes it very clear why property rights influence technology in a way similar to changes in relative prices: for instance, the relative prices of the high-agency-cost factors are (H+W)/R under capitalist ownership and W/(Z+R) under workers' ownership. Thus, under standard assumptions, the intensity of high-agency-cost capital relatively to the intensity of high-agency-cost labour is higher under capitalist ownership than under labour ownership. Observe that in this framework, the value of the elasticity of substitution among factors becomes a measure of the "strength" of the effects of changes of property rights on the nature of the technology.

We have seen that the "New Institutionalist assumption" runs in a direction opposite to that of the "Radical Assumption"; taking as given a certain technology the firm is supposed to be owned by that factor which can earn the highest ownership rent. This rent is equal to the difference between the cost of employing the factor in a firm that is property of the owners of the factor and the cost of employing it in a firm that is property of other owners.

New Institutional Assumption:

For any given combination of factors employed in the firm, ownership of the firm will be acquired by the factor which can get the highest ownership rent. Therefore: capitalist property rights can prevail if, given the factors currently employed, $R^C \bullet\ R^L$ or, alternatively,

$$ZK - HL \geq 0 \quad (3)$$

workers' property rights can prevail if, given the factors currently employed, $R^L \bullet R^c$, or alternatively,

$HL - ZK \geq 0$ (4)

Conditions defining organisational equilibria

There will be a capitalist organisational equilibrium (COE) if there is a technology that maximises (1) and satisfies (3) and there will be a labour organisational equilibrium (LOE) if there is a technology that maximises (2) and satisfies (4).
Let:

$(k^c, K^c, l^c, L^c) = \text{argmax}\ R^c (k, K, l, L)$ (5)

$(k^L, K^L, l^L, L^L) = \text{argmax}\ R^L (k, K, l, L)$ (6)

Then a firm will be in *a capitalist organisational equilibrium* (COE) if:

$ZK^c - HL^c \geq 0$ (7)
and in *a labour organisational equilibrium* (LOE) if:

$HL^L - ZK^L \geq 0$ (8)

Condition (7) has an immediate intuitive meaning. Suppose that a firm is under capitalist ownership and the technique of production is such as to maximise profits. Condition (7) implies that, with this technique, the ownership rent occurring to capitalists is at least as great as the rent which workers could obtain if they owned the firm. Hence, with this technique of production, the workers would have no incentive to buy out the capitalists. This is what is meant by a capitalist organisational equilibrium. Condition (8) has an analogous intuitive meaning.

The conditions for COE and LOE can also be written in the following equivalent ways:

$K^c/L^c \geq H/Z$ (7')

$K^L/L^L \leq H/Z$ (8')

Conditions (7') and (8') have also an intuitive meaning. Observe that K/L is the ratio of high-agency-cost (H-A-C) capital to H-A-C labour or the H-A-C capital intensity; observe also that H/Z is the agency cost ratio between the capitalist's extra-cost in employing H-A-C labour and labour's extra-cost in employing H-A-C capital. Thus (7') means that a COE is feasible when the intensity of H-A-C-capital is greater than the agency cost ratio and (8') means that a LOE is feasible when the intensity of H-A-C capital is lower than the agency cost ratio. For instance, high agency costs per unit of labour could be compensated by the employment of a great amount of H-A-C capital and make it feasible a COE.

Under standard assumptions, the high-agency-cost capital intensity will be higher under capitalist ownership or:

$K^c/L^c \geq K^L/L^L$ (9)

The value of the agency cost ratio H/Z either falls in the interval defined by these two values or outside it.

Let us first consider the case in which it falls in this interval. In this case H/Z is such that:

$K^c/L^c \geq H/Z \geq K^L/L^L$ (10)

Then both (7') and (8') are satisfied and we have multiple (capitalist and labour) organisational equilibria.

Consider now the cases in which H/Z does not fall in this interval.
H/Z may be smaller than the high-agency- cost capital intensities. Or:

$K^c/L^c \geq K^L/L^L > H/Z$ (11)

Then (7') is satisfied but (8') is not satisfied. In this case only a COE exists.

By contrast, if H/Z is such that:

$H/Z > K^c/L^c \geq K^L/L^L$ (15)

(8') is satisfied but (7') is not satisfied. In this case only a LOE exists.

Observe that since the ratio H/Z must necessarily fall in one of the three intervals considered above, for any H/Z ratio at least one organisational equilibrium must always exist.

We can visualise the three possibilities considered above in the following figure 8. For H/Z that goes from zero to infinity we have first unique COE equilibria, then multiple equilibria and, finally, LOE unique equilibria.

0------(COE)-----K^L/L^L-----((LOE+COE)------K^c/L^c-----(LOE)----->

- (F8)

(F4) "assumes" a certain value of the elasticity of substitution and it can give us some intuition of the effects of its changes. An increase in the elasticity of substitution widens the values of the agency cost ratio for which multiple equilibria exist. It moves K^L/L^L leftwards and

K^c/L^c towards the right widening the interval of multiple equilibria defined by them. Within this interval any initial set of property rights will induce technologies such that their interaction will define organisational equilibria. Thus, an increase of the elasticity of substitution widens the interval where property rights can shape technologies in a self-sustaining manner and increases the probability that an organisational equilibrium will stay such after an exogenous shock to agency costs (i. e. increases "institutional stability". Because of the "Radical Assumption", the higher the elasticity of substitution the more powerful the effects of ownership on technology.