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Coevolution of economic behaviour and institutions: towards a theory of institutional change

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Abstract. Traditionally, economics has regarded institutions, notably norms and regulations, as fixed or exogenous. Surprisingly few insights on institutional evolution from natural and social sciences have made their way into economics. This article gives an overview of evolutionary theories of institutions in biology, sociology, anthropology and economics. These theories are subsequently compared with non-evolutionary theories of institutions. Next, the insights and approaches are integrated into a framework for analysis of institutions based on the notion of coevolution.

Key words: Altruism – Cooperation – Culture – Dual inheritance – Evolutionary psychology – Group selection – Norms – Social psychology – Sociobiology

JEL Classification: B52, D10, D70, D64, Z13

1 Introduction

By definition, an institution or a norm is constant during a certain period of time.¹ In this way it contributes to the stability of the social system to which it belongs. Yet sooner or later it changes, in response to the decisions and actions of individuals. The current pace of institutional change in the world illustrates this, as it is characterised by new governance structures (EU), new communication technologies (the Internet and mobile phones), new policies and instruments, and shifting norms and preferences.

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¹ According to Ostrom (2000), norms are shared understandings about actions that are obligatory, permitted, or forbidden.

Economists have for long regarded most institutions as constant or at best as changed by factors exogenous to the economy, notably public policy. As a consequence, they have shown very little interest in the patterns and causes of institutional change and the endogenous mechanisms underlying them. Whenever economists recognise that regulatory institutions can change, they tend to apply normative economic policy analysis, which is aimed at proposals as to the way in which institutions should be directed and managed, typically to realise efficient levels of scarce resource use. This has given rise to mainly static and to a lesser extent dynamic optimisation analysis in which the range of possible policy changes is determined *ex ante* and exogenously. Orthodox economics lacks a positive theory of the manner in which institutions actually change and have changed during economic history.

This article aims to shed light precisely on such a positive theory. For this purpose, we examine the interaction between social institutions and the behaviour of individuals and groups. We build heavily upon evolutionary theories of institutional change, as in our view these offer the best – even if yet incomplete – insights, and thus provide the best starting point for developing an economic theory of institutional change. This means assigning a central role to bounded rationality, individual and group selection, dual inheritance, altruism, co-operation, social psychology and coevolution.

Evidently, the literature on cultural evolution following the older debate on human sociobiology and group selection provides a useful benchmark for our approach (Ruse, 1979; Boyd and Richerson, 1985). In fact, many of the fundamental issues in this debate, relating to individual versus group selection and selfish versus genuine altruism, have recently been revived (Sober and Wilson, 1998). Nevertheless, the gap between these approaches and economics is still very wide. Our aim is to fill this gap. The work by researchers, such as Axelrod, Ben-Ner and Putterman, Bowles and Gintis, Fehr, Nelson and Winter, Ostrom and others, is closely related, but has not been able to benefit fully from insights in evolutionary biology, behavioural ecology, evolutionary psychology, and human genetics.

We propose to use a new framework for analysis that is developed around the notion of coevolution. This is motivated by two considerations. First, it can take into account the diversity of institutions, which is subject to selection and innovation. Second, it can address the fact that institutional change does not occur in a vacuum, but that the underlying selection and innovation of institutions are affected by economic, social and environmental forces.

While a coherent theory of the coevolution of individual behaviour and social institutions is still missing, there are building blocks of such a framework available. At the level of culture-gene interactions, coevolution allows us to move beyond one-dimensional cultural theories as well as narrow sociobiological (genetic) theories by combining the best of both. Within a purely cultural or economic context, coevolution stresses that the system considered – the society or economy – consists of multiple subsystems, such as regions, groups, institutions and organisations that are part of a joint, interactive evolutionary process. Only by taking into account diversity within relevant subsystems, and interactions between these, can one devise a truly endogenous theory of institutions that sheds light on institutional change.

The essay is organised as follows. Section 2 provides a background for the discussion, by exploring the notion of coevolution. In Section 3, we survey relevant ideas on the relationship between individual or group behaviour and institutional change in various evolutionary theories, dealing with: sociobiology, evolutionary psychology, group selection, social-cultural evolution, economic evolution, and gene-culture coevolution. Section 4 discusses the essential differences between evolutionary and other theories of institutional change. Next, Section 5 develops a framework for studying institutional change, based on an integration of individual and group selection mechanisms, and distinguishing interactions between five layers of change. Section 6 presents conclusions.

2 Coevolution = evolution + ecology

Coevolution was originally proposed in ecology to refer to the joint evolution of butterflies and flowering plants (Ehrlich and Raven, 1964). Coevolution denotes the fact that evolutionary changes in one species are a response to changes in other species with which it ecologically interacts, i.e. in the same community (Strickberger, 1990). This definition reflects an integration of elements from ecology and evolutionary biology. Initially, coevolution was used at the level of species interactions, primarily to explain the evolutionary adaptation of parasites and their hosts, predators and their prey, and herbivores and plants. More recently, coevolution has been invoked to denote very different types of interactions: biological-cultural, ecological-economic, production-consumption, technology-preferences, behaviour-institutional, and human genetic-cultural (Lumsden and Wilson, 1981; Norgaard, 1984, 1994; Durham, 1991; Gowdy, 1994; Feldman and Laland, 1996; Wilson, 1998). Coevolution should not be confused with the biological concept of 'coadaptation'. The latter denotes changes in alleles at multiple gene loci due to selection. In other words, it refers to a kind of coevolution of different features (morphological, physiological and behavioural) within a single species.

Evolution in an ecological context means ecological adaptation. Two basic 'bionomic' strategies relate to the r and K parameters in the logistic population growth model:

- *The r-strategy*: produce many offspring and apply little parental care. This is typical for insects and amphibians, which are small, mature rapidly, and have a relatively short life span. Annual plants also belong to this type.
- *The K-strategy*: produce few offspring and apply much parental care. This is typical for birds and especially mammals, which are larger, mature more slowly, and have a longer life span. Forest trees also belong to this type.

Because of these dynamics, growth curves differ between r - and K -strategists. Population of r -strategists can overshoot and then collapse, possibly creating cycles around the equilibrium under unstable environmental conditions. K -strategists instead follow the logistic growth curve, except that often, for low (viable) levels, extinction results. This tends to result in very stable populations.

Typically K -strategist animals evolved later in natural history, due to the fact that they require a more developed brain for performing care functions, a particular

type of social interaction. Similarly, young ecosystems in early succession stages are dominated by r-strategists, which due to their features are perfect colonizers. K-strategists are found typically in older climax ecosystems, which have a more stable environment, allowing for more complex food web structures that are needed to support the larger K-strategists. Evidently, the r- and K-strategy distinction is a caricature, and they should best be considered as relative concepts. More and less extreme forms exist, both among and within groups of species. Nevertheless, evolution seems to promote a movement towards one or the other extreme once initial selection pressure has pushed a species in one direction (Putman and Wratten, 1984, Ch. 10). This in fact is an example of path-dependence.

The environment of organisms consists of abiotic and biotic elements. The biotic ones include other species, such as prey (food), predators, competitors, and other organisms of own species. Due to these various species relationships, evolution shapes species in interactions with other evolving species. This leads to our notion of coevolution, as the interactions affect the dynamics, structure and functions of ecosystems. While no theory makes claims as to the selection and adaptation of ecosystems, the notion of coevolution goes a long way in this direction, offering a theory for the evolution of communities. It sees multi-species relationships as a coadapted system of interactive species.

A particular type of coevolution that has received much attention is known as the “arms race”: characteristics of species respond positively to one another. For instance, predation will select prey that run faster, which in turn will select predators that run faster, and so on. Another example is the immense size of many dinosaurs, which is explained by prey dinosaurs increasing in size due to selection – as larger size offered a better protection against predators – which in turn selected for larger dinosaur predators. Somewhat later in natural history, mutual selection for larger cerebral brain size occurred between prey and predator mammals, due to the fact that brain size is related to skill in avoiding predators as well as capturing prey (Strickberger, 1990, pp. 399 and 429).

The end result of coevolution is likely to be a stable regime of sub-optimised species. The coevolution of parasites and hosts can lead to commensalism, where the parasite inflicts minimal damage to the host. Whereas commensalism occurs at an individual level – parasites do not kill the host – a stable predator-prey relationship can be regarded as commensalism on the population level – where the predator population does not ‘kill’ the prey population, even though individual predators kill individual prey. Another coevolutionary path may be seen in the case of parasites as beneficial to the host, i.e. the case of mutualism. This illustrates that the different multi-species relationships can be linked to one another through coevolution: one type of interaction can over time change in another type.

Norgaard (1984, 1994) was the first to use the concept of coevolution explicitly in a socio-economic context. He regards it as reflecting long-term feedbacks that occur between five main subsystems, namely knowledge, values, organisation, technology and environment. Variation within each subsystem is strongly influenced by selection conditions provided by the other subsystems, which act as the total environment of the respective subsystem. He illustrates this view with the interaction – during the last century – between pests, the use and production of pes-

ticides, policies and institutions to regulate pesticides, and knowledge and valuation of pesticides and pests. Campbell (1996, p. 569) notes that the human invention of agriculture, the domestication of animals and especially plants, and the subsequent cultural-economic developments can be regarded as special cases of coevolution among animals and plants. Humans depend on the cultivated and selectively bred plants, and the plants depend on human control, i.e. either could not survive without the other.

History shows that, due to coevolution, humans do not control and change their environment to meet predetermined goals, but nature and human society are formed in a joint, interactive development. This sometimes works out beneficially to both, sometimes only to one, and sometimes to none. Notions of progress and planning lose credibility in the face of coevolution, as they are replaced by change and adaptation, and experimentation and selection, respectively.

Biologists have also studied cultural processes from a coevolutionary perspective. This is sometimes referred to as gene-culture coevolutionary theory (e.g., Cavalli-Sforza and Feldman, 1973, 1981; Durham, 1991; Feldman and Laland, 1996), and emphasises the joint evolution of human genes and human culture, which offers a perspective that differs from Norgaard's. One can even question whether it represents coevolution in a strict sense, despite its name, because it is not concerned with the interaction among different species, but rather among different *characteristics* of a single (human) species, i.e. coadaptation. On the other hand, if culture is regarded as a species separate from humans – much as language is a parasite thriving on human hosts – then human gene-culture interactions can well be regarded as coevolution in a strict sense.

This has led to a theory of dual inheritance, genetic and cultural (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985). The empirical support for it has been focused on the influence of cultural traits – in particular behavioural strategies which are studied by anthropologists – on the frequency of certain genetic traits. Examples include (Durham, 1991; Boyd and Richerson, 1985; Galor and Moav, 2002):

- The frequency of sickle cell anaemia among populations in West Africa has been shown to depend on their means of subsistence. Cutting trees allows the cultivation of yams, which in turn causes pools of standing water that promote an increase in the mosquito population. The latter transmit malaria against which sickle cell anaemia provides protection.
- The rise of agriculture, notably of dairy farming, has created a selection environment in which the proportion of individuals with genes allowing lactose absorption could increase.
- Living in densely populated societies with domesticated animals, such as cows, pigs, and sheep, has resulted in contagious diseases, and ultimately resistance against them.
- Culture may have selected genetically determined behaviours that support cooperation.
- Culture may have elicited and selected genetically codetermined, competitive and innovative, behaviour that has stimulated growth.

Additional examples include such diverse issues as basic colour terms, skin depigmentation, plural marriage, incest taboos, excess female mortality, headhunting and cannibalism.

These examples show that the nature-nurture opposition is simplistic, and should be replaced by nature-nurture coevolution. Feldman and Laland (1996, p. 456) note that “The clear conclusion of gene-culture coevolutionary analyses is that cultural transmission can transform evolutionary dynamics in numerous ways, implying that, for many questions related to human evolution or human behaviour genetics, traditional methods and models are no longer appropriate.” Similarly, the motivation for this paper is that models of singular evolution are inappropriate as a general approach in the evolutionary analysis of institutional change. Instead, a coevolutionary perspective is required in which interactions at multiple levels – behaviour, institutions, technology, etc. – is examined. The next section discusses a number of evolutionary approaches in literature that provide relevant concepts and insights for studying such coevolution.

3 Institutions in evolutionary theories

3.1 Human sociobiology and evolutionary psychology

Based on the groundbreaking work of William Hamilton, Robert Trivers and John Maynard Smith, Wilson (1975) presented a genetic-biological perspective on the social behaviour and organisation of animals, including (in a final chapter) human beings. The theme of human behaviour was continued, partly in response to critiques, in Wilson (1978) and Lumsden and Wilson (1981). Sociobiology is a powerful theory with surprising insights, which has caused much debate (see Ruse, 1979). The argumentation used in sociobiology is mainly theoretical (genetics, logic), while definite empirical-genetic statements have been provided for social insects. For higher animals, and certainly mammals, primates and humans, such irrefutable empirical evidence is missing (De Waal, 1996). Nevertheless, many writers now agree that the criticism of sociobiology was unfair, because it is not so much a theory as a field of research. Durham (1991) notes that a coevolutionary view in which the genetic evolutionary perspective is matched by a serious cultural evolutionary one overcomes much of the criticism which suggests that sociobiology overemphasises genetic factors. Durham (1991) and Boyd and Richerson (1985) have undertaken such a matching using anthropological and social-psychological factors, respectively.

Essential to sociobiological explanations of altruism are kin selection, reciprocal altruism, and inclusive fitness. Kin selection means that altruistic behaviour is genetically based because altruists are actually protecting their own genes by helping close relatives survive. Reciprocal altruism refers to behaviour based on the expectation that favours will be returned. Inclusive fitness of a gene not only reflects the performance (survival and replication) of the individual by which it is carried, but also of relatives of the individual who carry the same gene. An individual can thus be altruistic towards his relatives and at the same time maximise the inclusive fitness of a certain gene - without even being aware of it.

Although social science as the study of 'culture' or 'nurture' in social relationships is often regarded as the antithesis of sociobiology as the study of 'genetic constraints' or 'nature' underlying social relationships, they support the same insight; namely, that individual behaviour can only be understood completely within a social context. While sociobiology has focused on the commonality of human nature (i.e., a unity of genetic basis) rather than genetic differences, the debate between its supporters and opponents has been – confusingly – largely about the degree of biological or genetic determinism assumed by the theory (see Ruse, 1979). It should therefore be concluded that sociobiology is not providing support to racism, as some have tried to argue (e.g., Rosenthal, 1998). It rather focuses the attention on similarities of behaviour among groups within a certain species, and to a lesser extent between species due to genetic overlap and historical constraints. Behavioural differences among individuals and groups within a single species are regarded as mainly due to different environments. For humans this is consistent with the main conclusion following from an analysis of the ultimate causes of differences among current human cultures and the domination of the Eurasian culture by Diamond (1997). Important for the study of institutions is that, according to sociobiology, higher culture and social organisation have their historical origin in co-operation based on kinship.

Sociobiology and economics have been shown to share a starting point, namely competition for scarce resources (e.g. Witt, 1991). This has stimulated some economists (Hirshleifer, 1985; Becker, 1976; Tullock, 1979) to argue that altruism and social behaviour can be entirely explained on the basis of utilitarian altruism as an equivalent of sociobiological selection and fitness. This has been operationalised by including the welfare or consumption of relatives in an individual's utility function. Some economic implications of sociobiology are then that the welfare of near relatives is more important than that of distant ones, and that altruism, co-operation and solidarity can be consistent with self-interest. The analogy is incorrect, however, in that the utilitarian approach based on utility maximising behaviour adopts the Spencerian (and not the sociobiological-Darwinian) notion of 'selection of the fittest', which should in fact be replaced by 'selection of the fitter and luckier' or "selection of the fitting" (Boulding, 1981), suggesting consistency with bounded rationality. This relates to the well-known Alchian (1950) thesis: individuals seeking profits dominate due to a selective advantage under the pressure of competitive markets. It incorrectly supposes, however, that selection pressure from markets is perfect, and that profit maximising ("profit seeking" in Alchian's words) can be perfectly imitated by others (Winter, 1964).

Elements of human sociobiology have recently been adopted in a field known as evolutionary psychology. Here human psychology is studied on the basis of evolutionary insights about human individuals, societies and their environments (Barkow et al., 1992; Buss, 1995; Crawford and Krebs, 1998). In particular, it is hoped that constraints to human behaviour can be identified on the basis of an understanding of the social and environmental conditions that prevailed during the Pleistocene Era. In other words, the belief is that genetically we are still Pleistocene beings. By focusing on evolutionary roots, ultimate rather than direct or proximate causes of behaviour are traced. The main line of reasoning is Darwinian selection, but

evolutionary psychology links up with group selection (see next section), as human hunter-gatherer groups showed a large degree of co-operation and altruism, which probably cannot be entirely explained on the basis of kin and reciprocal selection. The presence of mechanisms of punishment and reward in a context of social learning seems to be crucial. The topics addressed by evolutionary psychology include general ones, such as information processing, the role of emotions, time allocation, problem solving, co-operation, and the role of language, along with more specific topics, such as aggression and violence, sexual behaviour, the formation of relationships, jealousy, parental strategies, and the preference for status and power. One general insight is that human behaviour is predominantly automatic and characterised by heuristics and biases instead of being rational. This is very much in line with the Nobel Prize-winning work of Simon (1957) and Kahneman (with Tversky, 1979).

As expected, evolutionary psychology, like human sociobiology, has been subject to strong criticism (see, e.g., Rose and Rose, 2000). Opponents tend to emphasise that evolutionary logic in terms of adaptation to environmental circumstances often sounds convincing, but can lead to 'just-so-stories' without any factual evidence. They further argue that genes work in combination and at different levels, taking away the basis for ultra-Darwinian 'selfish gene' theories in the spirit of Dawkins (1976). Nevertheless, support is increasing for the idea that as long as the results of sociobiology and evolutionary psychology are judged critically, they can provide interesting hypotheses for empirical testing and generally provide a useful biological starting point for thinking about social behaviour (see also Cosmides and Tooby, 1994; Ben-Ner, 2000; Jackson, 2000). Indeed, psychological research comparing identical and non-identical twins has provided support for the idea that genes have a significant and identifiable influence on human behaviour. This should of course not be confused with genetic determinism. Also, evolutionary psychologists themselves have argued that 'adaptation stories' should be built on firm ground, involving multiple sources of evidence: theory, history, experiments and empirical facts. This implies an integration of insights from evolutionary and social psychology. De Waal (2002) emphasises the "dilemma of the rarely exercised option". This means that an evolutionary, adaptive explanation of atypical behaviour should be consistent with explanations of the typical, dominant behaviour found in reality. In the case of exceptional acts such as rape of women by men, and child abuse by stepfathers, this is not the case (the dominant behaviour is no rape and no abuse), which causes related adaptive stories to be suspect.

Sociobiology and its modern counterpart, evolutionary psychology, try to identify the genetic evolutionary foundations of the range of possible human behaviours. The simple idea here is that culture is bounded, not determined, by genes and natural history.² While the similarity of human cultures around the world is the result of genes, this does not deny the variation of cultures. Sociobiology can explain the general similarity rather than the variations in behaviour, which are not inconsistent with it. Moreover, the general similarity of human behaviour and cultures in differ-

² A reviewer noted that this can be interpreted in two ways: (1) boundaries are closed; and (2) boundaries are open. Only in the second case are there sufficient degrees of freedom for cultural evolution to occur.

ent parts of the world is consistent with the fact that the genetic differences between human groups are very small. This is in fact the main argument against misusing sociobiology to support ideologies of racial discrimination and class domination.

3.2 Group selection

One of the hottest debates in evolutionary biology since the 1960s has been over group selection (Wynne-Edwards, 1962; Wilson, 1975; Ruse, 1979; Sober, 1981; Boyd and Richerson, 1985; Trivers, 1985; Alexander, 1987; Wynne-Edwards, 1991; Wilson, 1997; Sober and Wilson, 1998). This denotes that the fitness of every member of a group depends on a group characteristic that is not isolated in an individual. In particular, it is suggested that groups characterised by non-kin and non-reciprocal altruism out-compete groups composed of selfish individuals or individuals showing only kin and reciprocal altruism.

Williams (1966) presented an influential early critique of group selection that supported the opinion that group selection was based on incorrect reasoning. Sociobiology provided opposition to ideas about group selection by offering an alternative according to which social behaviour is the result of individual selection (Wilson, 1975). An extreme version is Dawkins' (1976) selfish gene interpretation (see also Ruse, 1979).

The important criticism raised against group selection theory is that there is no clear mechanism to ensure that an advantageous pattern of change for the group will be replicated by the actions of the individuals in the group. In other words, a basis for group inheritance is missing. The reasoning is that if a characteristic valuable to the group is not also of value to the individual or the 'gene' – directly or indirectly – then it will not be passed on. An important element in the discussion of group selection and altruism is free rider behaviour. Free riders will profit from the benefits of being part of the group with genuine altruism and social institutions, without contributing to either. When the relative proportion of free riders in the group increases, the benefits of the group and the characteristics of group selection will slowly disappear. In other words, group selection may work as long as free riders do not dominate the group. Suppression of free rider behaviour is most likely to occur when resource scarcity and competition are low, i.e. when it is relatively easy to be altruistic. But altruism is less common when scarcity and competition are high, i.e. when it implies a serious sacrifice. Typically, selective pressure is higher in the second case, so that individual selection will usually have more of an impact than group selection.

Following an argument in favour of group selection by Edwards (1962), Maynard Smith (1964) presented an early model in support of it, known as the "haystack model". It describes nonassortative random group formation as leading to distinct groups, some with more altruistic cooperators than others. Although within an 'altruistic group' cooperators have fewer offspring than defectors, the group as a whole produces more offspring than 'less altruistic groups'. Altruistic cooperation can evolve because groups exist for some time – several periods – before being mixed with other groups. This allows groups with relatively many altruists to grow

relatively fast, causing the proportion of altruistic cooperators in the whole population to increase. This result is conditional upon the interaction among individuals not being equated to a prisoner's dilemma but to a "stag hunt" type of game. This type of game is characterised by defection being the best response to defection (as in prisoner's dilemma games) and cooperation being the best response to cooperation (unlike the prisoner's game, where defection is the best response to cooperation). In a generalised model, Cohen and Eshel (1976) show that an equilibrium with only altruists is also possible if the game between individuals is a prisoner's dilemma, as long as groups remain intact for a minimum amount of time. The reason is that the latter results in an intertemporal game that is not a prisoner's dilemma.

Group selection can also result from assortative interaction or group formation. Special cases are families subject to kin selection. Other cases require a minimal degree of (social) intelligence – notably altruists (or egoists) recognising and associating with their own kind. The degree of kinship (biological relatedness) can be regarded as a proxy for the probability of assortative interaction. In an economic context, however, the variety of assortative characteristics among groups will depend on group-specific institutions that promote cooperation and altruism. Examples of these are schooling, religion, political features (voting systems), free press and democratic history. Roughgarden (1979), Sober and Wilson (1998), Gintis (2000) and Bergstrom (2002) present an overview of other, related models that suggest that group selection can work.³

Although for many years group selection as a factor in evolution was considered unscientific – in spite of the aforementioned model-based support for it –, the 1980s and 1990s have witnessed a renewed interest in-group selection, in biology (Wilson, 1997) as well as social science (Boyd and Richerson, 1985; White, 1998; van den Bergh and Gowdy, 2002). The existence of group behaviour relates to the recently much referred to notion of 'strong reciprocity' in human behaviour (Fehr and Gächter, 1998; Ostrom, 1998). The experimental and empirical finding that reciprocity applies in a positive and negative sense, that is, subjects co-operate if others co-operate and punish if they do not, is consistent with the tit-for-tat strategy made famous by Axelrod (1984). Bowles and Gintis (1999a,b) used findings of experiments and case studies of hunter and gatherer societies to argue that sharing is as much 'normal' human behaviour as is selfishness. This has recently also been confirmed in a comparative study of fifteen hunter-gatherer, nomadic herding and other small-scale societies, which show much cultural diversity (Henrich et al., 2001). The general lesson therefore is that 'Homo reciprocans' is more human than 'Homo economicus'.

The criticism of group selection is too general, and the truth seems to be more subtle. Non-reciprocal and non-kin altruism are rare in animals, causing group selection effects to be weak. The social organisation of insects is entirely genetically determined. Group selection requires individuals with extended memory and intelligence, found in social mammals as diverse as wolves, dolphins and apes (De Waal, 1996). According to Wilson (1975) all extended social behaviour and organisation

³ Surprisingly, in a review of the biological basis of economic behaviour, Robson (2001, 2002) does not pay any attention to group selection issues.

starts with the strong tie between mother and child, which explains why it is most common and well-developed in mammals.

The existence of social cognition among humans suggests that group selection in human populations and thus in economic systems may be more significant. One reason for this is assortative matching supported by intelligence and perception of characteristics – notably degree of selfishness or altruism – in others, which leads to groups with relatively many altruists. In addition, a wide range of possible individual behavioural strategies can be elicited or suppressed. In human hunter-gatherer societies, co-operation, recognition of trustworthy or cheating individuals as well as of potential reciprocators meant a selective advantage. Nowadays, culture fosters and reinforces this kind of co-operative behaviour. As a result, one can find that many individuals behave automatically as co-operators and ‘punishers’. It is, therefore, not surprising to find increasing attention for group selection issues in economics (Bergstrom, 2002).

Group selection based on real (pure, genuine) altruism (self-sacrificing) would mean that individuals who sacrifice themselves while contributing to increase group benefits would by definition have a negative impact on their own individual fitness. Group selection theories argue that, even if such individuals and their genes disappeared, so that their genes were less proportionally represented in the next generation, real altruism can be still be maintained and the number of free riders can be kept low. The following mechanisms are responsible for this:

- Social institutions leading to norms, punishment and rewards stimulate or even force individuals to behave genuinely altruistically. In other words, the replication of real altruism is a *social* and not a *genetic* process. Therefore, the disappearance of individuals behaving genuinely altruistic in the next generation can be compensated by the social capacity to replicate pure altruism in subsequent generations through existing social institutions. Genetic factors do not play any direct role. Of course, indirectly they do, if only because evolution has determined the human capacity for institutions.
- Pure altruism can also be based on a combination of socially-acquiring and genetically-supported kin and reciprocal altruism. In this case, pure altruism is more stable, because selfish altruism will stabilise the social institutions supporting and eliciting pure altruism.

The first mechanism is reinforced by the existence of a meta-norm. This is the willingness to punish a person who did not enforce a particular norm. Note that this is different from not following a norm. The idea is that a norm system is more stable under certain meta-norms, or if it generates such meta-norms. Other mechanisms to support a norm system are dominance, internalisation, deterrence, social proof, membership, law and reputation (Axelrod, 1986).

Feldman and Laland (1996) state that the popular arguments against group selection are false because they recognise only genetic inheritance, instead of dual inheritance – cultural and genetic (see next section), which explains the enlargement of differences among groups. This is further discussed in the next section.

3.3 *Dual inheritance*

The previous sections indicate that co-operation and social institutions can have several sources: (a) selfish or egoistic ones (mutual benefits), (b) kin altruism, (c) reciprocal altruism, and (d) social learning and group selection. Here we will elaborate upon the last type. This will be done in the context of theories of cultural evolution, also known as dual inheritance theory, cultural Darwinism and evolutionary anthropology (Boyd and Richerson, 1985).

Theories of cultural evolution make ample use of both sociobiological and group selection concepts and mechanisms. According to the dual inheritance theory of Boyd and Richerson (1992), evolution is the basis of all human behaviour, but should be extended with cultural acquiring or learning. This means that elements of individual behaviour are subject to cultural transmission (Cavalli-Sforza and Feldman, 1981). Culture is thus regarded as a system of inheritance analogous to genetic inheritance. The core question in the context of culture and evolution is: why is there so much diversity of human behaviour at the level of individuals and cultures? Genetic selection and cultural selection interact. Cultural selection can, for example, weaken natural selection pressure: e.g., a social welfare state creates a less harsh environment, in which physically and mentally weaker individuals can survive more easily. Dual inheritance theory and its formal models of combined genetic and cultural transmission account for this interaction of genetic and cultural selection and therefore go beyond sociobiology. These models show that the mean and distribution of features of human individuals can shift away from the phenotype favoured by genetic selection toward that favoured by cultural selection, as long as cultural selection forces are relatively strong.

The forces of cultural evolution are shaped by the transmission of behaviour modified by a number of mechanisms. One can classify these as follows (see Cavalli-Sforza and Feldman, 1981; and Boyd and Richerson, 1985):

1. *Random cultural variation.* Cultural transmission involves 'errors' of various kinds. In fact, the rate of culturally transmitted errors seems much higher than that of genetic mutation.
2. *Institutional drift.* In small groups, cultural and institutional mutations may have a large impact, causing the respective culture to be less stable. Small, isolated human societies provide examples of this. Note the similarity with the biological notion of genetic or molecular drift.
3. *Biased social transmission.* Individuals are predisposed to adopt certain pre-existing cultural variants, and so these will increase in frequency. Boyd and Richerson distinguish between three types: (a) direct bias, where the adoption of cultural variants depends on the properties (attractiveness) of the variants (e.g., food characteristics); (b) indirect bias, the imitation of certain characteristics (e.g., style of dressing) that are perceived to be associated with others that are regarded as attractive (e.g., fame, wealth, happiness); and (c) frequency dependent bias, where imitation of the majority is dominant. Direct bias is more effective but involves more time and costs than the other two transmission mechanisms.

4. *Guided (Lamarckian) variation.* Humans can consciously and purposefully change their behaviour, rules and norms through learning by doing (trial-and-error) and communication. This involves self-generation of alternatives, distinguishing it from 3a, although involving possibly the same or similar cognitive capabilities. It is often referred to as the Lamarckian aspect of cultural evolution, because it is a source of purposeful creation of variety.
5. *Genetic-cultural (Darwinian) coevolution.* Cultural traits have an impact on the survival and reproduction, or the fitness of individuals, and in turn are influenced by these. For instance, certain food habits include tastes that are not easily learned but must have been selected, as they are related to toxicity. Another example is the evolution of co-operation, possibly involving group selection. Boyd and Richerson refer to this as “natural selection of cultural variants” (see further Sect. 3.5).

Mechanisms 3 and 4 are especially important in explaining the rapid pace of change in social organisation, subcultures and institutions in our modern world. Mechanism 3 involves social learning, traditionally the domain of social psychology. Social learning occurs through various mechanisms. Vertical cultural transmission (parent to child) dominates at young ages. Horizontal (from peers) and oblique (from non-parental adults, such as teachers) cultural transmission become more important as children get older. It should be noted that an empirical distinction between vertical cultural transmission and genetic transmission is difficult, as the majority of parents are biological parents. The combination and synergy of both transmission types supports the empirically assessed high parent-offspring correlation for many cultural traits, such as for religion, political preferences, and food habits. The effectiveness of horizontal and oblique cultural transmission is indicated by various other empirical regularities.

Genetic and cultural inheritance have some important differences (Boyd and Richerson, 1985, pp. 7–8). ‘Cultural mating’ is different from biological or genetic mating. First of all, an individual (‘cultural offspring’) has more ‘cultural parents’ than genetic parents. In the ‘cultural mating family,’ not only the nuclear family but also the extended family, leaders, and prestigious individuals may be influential in the cultural development of an individual, though generally with declining importance. Nowadays, with advanced communication and transport technologies (television, internet, travel), influences become more complex and less localised. The difference between genetic and cultural inheritance is further linked to the earlier distinction between horizontal and vertical transmission. The first of these is akin to the spreading of a disease, as in the case of fashions and technology. Not surprisingly, epidemiological models can be used to describe it. The second type of transmission is determined by genetic ties. Thus, information is flowing from parent to child, or vice versa, and from one generation to the next. Both horizontal and vertical transmission occur in cultural evolution, whereas biological evolution is dominated by vertical transmission, simply because horizontal genetic transmission is extremely rare in nature – with the exception of some types of bacteria.

The temporal characteristics of cultural evolution differ from those of genetic evolution in many respects. Cultural transmission of behaviour is faster and more

flexible than genetic transmission, implying that culture can never be subject to detailed genetic control. It also implies that sociobiology cannot provide a complete underpinning of cultural and social theory, but only can identify the boundaries of cultural evolution. Generations in cultural evolution can be longer than in biological evolution. For instance, parents are also grandparents and thus transmit culture to their children and grandchildren. Children may even influence their parents, and in general younger people can influence older ones. This illustrates that cultural evolution is more difficult and less predictable than biological evolution. In addition, cultural transmission is a slow process that takes much time. In fact, it never stops during one's life. These features are opposed to genetic transmission, which occurs in a single moment, known as conception.

Most notable and relevant in the present global-economic context is the evolution of co-operation among ever larger groups of human individuals. Ben-Ner and Putterman (2000, p. 92) note that “[t]he universality of maternal and, more broadly, of kin altruism across human cultures is an illustration of the fact that organic evolution can produce organisms that are not strictly self-interested. But more remarkable and of at least equal importance to economics and other social sciences is the phenomenon of reciprocal co-operation among *nonkin*.” Diamond (1997) identifies four main stages of social structure that humankind can be considered to have moved through over the last 13,000 years. Throughout history, non-kin relationships increased in importance.

1. Family/band: this covers 5 to 80 people; is kin-based; consists of extended families or several related ones; everyone knows one another; conflict resolution is informal; the life style is nomadic.
2. Tribe: hundreds of people: kin-based clans; everyone knows one another; informal conflict resolution; sedentary life style, restricted to one village.
3. Chiefdom: thousands of people; centralised conflict resolution; one or more villages; one ethnicity.
4. State: more than 50,000 people: many villages and cities; laws, judges and police; possibly multiple ethnicities.

Given the current process of globalisation, we could add a fifth stage in which communication and co-operation lead to the emergence of supra-national or even world institutions. This involves billions of people and multiple ethnicities, and a large number of institutions, which deal with, among other things, international trade (WTO), international agreements, military co-operation and conflict resolution (UN), economic development and poverty (IMF, World Bank), and socio-economic integration (e.g., the EU).

3.4 Economic evolution and self-organisation

In a historical context, one may see economic evolution as a process that closely follows or is even integrated with cultural evolution, depending on how one defines and demarcates the latter. Two important transitions in human history from a cultural as well as economic perspective are the transition from the hunter-gatherer to the agriculture era, and the Industrial Revolution (or industrialization). Both

involved many institutional changes, such as the emergence of markets and trade, (re)stratification of society, new types of human organisation and co-operation, new social norms and rules, and new types of public regulation. Economic evolution can occur at a very fast pace. The significant economic and institutional changes that have occurred since the Industrial Revolution, only less than 250 years ago, illustrate this.

The economic literature on evolution has focused on firms and technology rather than social and public institutions (see Nelson and Winter, 1982; Dosi et al. 1988). An exception is Nelson (1995), who presents a more encompassing view of evolution, including cultural, ethical, institutional and legal issues. The evolution of institutions has received some attention in the context of common property or common-pool resources such as fisheries (Ostrom, 1990; Bromley, 1992; Ledyard, 1995; Sethi and Somanathan, 1996). A central question is whether resource conflicts and overuse should be responded to with strict policies set by higher-level governments, or rather one should rely on the endogenous formation of use regimes. An evolutionary perspective suggests that externally imposed rules and monitoring can reduce and destabilise co-operation or even destroy it completely (Ostrom, 2000). When monitoring is imperfect, stimulating norms through communication is certainly more desirable than external regulation. The latter is only desirable if monitoring and sanctioning can be well developed. The self-organisation process underlying the emergence of norms is still not entirely understood – for instance, the influence of the size of the group and the extent of heterogeneity are still unclear.

Insights on co-operation and sanctioning behaviour in small groups are studied within a framework of evolutionary game theory by Sethi and Somanathan (1996). They consider the problem of changing norms in the context of competing users of a commonly owned renewable resource, some of which punish others who do not co-operate. Sethi and Somanathan find that their theoretical model of frequent communication among self-interested members of small informal group of resource users can describe reality satisfactorily, in particular noting that co-operative behaviour patterns are persistent. However, instability can arise when certain parameters change, for instance, the resource price, and interestingly also the implementation of other external rules (state property, open access) by an external regulator. In the latter case, norms may erode, ultimately leading to resource extinction. A spatially explicit model analysis shows that cooperative outcomes are more likely than suggested by a non-spatial analysis performed by Sethi and Somanathan (Noailly et al., 2003).

Axelrod (1997) studies the ‘emergent properties’ of locally interacting agents. An important question is the way in which independent actors sometimes co-operate to an extent that they give up most of their independence, resulting in a new level of organisation. Simple rules of punishment combined with mechanisms to increase or decrease commitments can lead to clusters of actors that co-operate as one independent agent. In another study, Axelrod (1997) applied the multi-agent based framework to investigate the process of social influence and the emergence of shared culture. By accounting for different dimensions or features that characterise people, his simulations indicate that the number of stable homogeneous regions decreases with the number of features, increases with the number of alternative traits per

feature, decreases with the range of interactions, and decreases as the geographic territory grows beyond a certain size. Unlike those models that describe culture as a continuous dimension or as one variable with a single pair of alternatives, Axelrod's model does not converge towards homogeneity. Instead, cultural variety is sustained.

Nelson and Winter (1982) suggested that policy making is 'a continuing evolutionary process' of the formation of organisational and institutional structures. Therefore, the design of good policy is to a large degree the design of an organisational structure capable of learning and adjusting behaviour in response to what is learned. Such ideas have received some attention in the context of natural resource and ecosystem management, where the notion of adaptive management has become popular. This is based on the belief that complex, uncertain and uncontrollable systems, such as ecosystems and economies, require a certain combination of experimental research, monitoring and policy learning (e.g., Holling et al., 1978; Walters, 1986; Gunderson et al., 1995). Adaptive management is based on a participation of relevant stakeholders and is supported by relevant disciplines, such that learning can occur through both experts and stakeholders.

3.5 Cultural-genetic coevolution

A correct long-term perspective on institutions should acknowledge that genetic evolution of humans and cultural evolution are, ultimately, interactive. Indeed, all evolution is coevolution, because it is virtually impossible that one species evolves over a long period of time in the absence of any evolution in species and ecosystems with which it interacts. Nevertheless, biological evolution is generally much slower than cultural, social and economic evolution. As a result, cultural-genetic coevolution is difficult to observe. This does not mean, however, that it does not exist. There is both theoretical and empirical support – for instance, in human genetics, behavioural ecology, primatology and evolutionary psychology – for the idea that a joint and interactive evolution of the genetic composition of humans, their behaviour, their culture and their environment has occurred. Different phases of this coevolutionary history are the hunter-gatherer era, the agricultural era, and the industrial era. For a complete picture of developments in the very long term, the categorisation of Durham (1991) offers a good starting point. It includes two interactive and three non-interactive relationships between genes and culture:

- *Genetic mediation*: genetic changes affect cultural evolution. One can regard this as suggesting that biological limits are critical or operative. The ability to talk, for instance, allowed for more subtle forms of communication and co-operation among humans, ultimately leading to advanced and cumulative social learning.
- *Cultural mediation*: cultural changes affect genetic evolution. This can be considered as culture changing the biological limits. For example, domestication of animals and our close proximity to them led to the spread of contagious diseases, and ultimately to human genetic resistance against these diseases (Diamond, 1997). Domestication of animals and dairying ultimately also led to a larger proportion of individuals capable of adult lactose absorption.

- *Enhancement*: cultural change reinforces natural evolution. This means that cultural and biological factors or effects add up. For example, a taboo on incest reduced the chance of unfavourable combinations of alleles. Another example is the spread of agriculture due to the intrinsic growth of the population of farmers (natural selection: higher survival and offspring due to more food) and the transformation of hunter-gatherers into farmers (cultural selection: imitation of successful strategy).
- *Opposition*: cultural change goes against natural evolution, i.e. they are negatively additive. For example, the direction of progress in health care allows individuals who may have perished under ‘natural conditions’ to survive and reproduce.
- *Neutrality*: cultural change is independent of biological evolution or selection. One can regard the biological limits as non-critical or non-effective. Perhaps a major and increasing part of (higher) culture falls into this category.

Whether the latter relationship is dominant has divided biologists and social scientists most strongly. Wilson (1978, p. 167) has made a clear statement of it: “The genes hold culture on a leash. The leash is very long, but inevitably values will be constrained in accordance with their effect on the human gene pool”. Durham (1991, p. 35) links three questions to this statement: Is the leash the same length at all times and places? The answer is probably no. Can the causal chain of the leash be reversed, so that culture leads genetic evolution? The answer is yes in the case of the cultural mediation mode. Is the leash ever so long as to be ineffective, providing no boundaries to cultural evolution? Perhaps it is safe to say that, in the long run, culture cannot escape the genetic leash. Of course, this just shifts the question to what is the relevant time scale.

An understanding of the neutral mode can be enhanced by examining the role of positive feedbacks that lead to more complex systems. In this context, concepts such as meta-system transitions (Heylighen, 1996) and autocatalytic cycles (Kauffman, 1993) have been proposed. The beginning of the Agricultural and Industrial Revolutions show many such positive feedbacks. More recently, the advent of computers and information technology has created a growth cycle involving positive feedback through the incorporation of more and more individuals in a global network of communication and co-operation.

An interesting example with far-reaching implications of the “enhancement mode” has been proposed by Galor and Moav (2002). Their thesis is that the struggle for survival that characterised most of human existence generated an evolutionary advantage to human traits that was complementary to the growth process, which in turn triggered the take-off from an epoch of stagnation to sustained economic growth. At first sight, one might think that, unlike genetic evolution of certain physical features that depend on variations of a single or few genes (lactose and gluten tolerance, sickle cell trait), the interaction between human genetic evolution and economic growth finds little support in evolutionary biology and theories of cultural evolution. The reason is that human behaviour involves so many genes that its evolutionary timescale does not match that of economic growth. In particular, Galor and Moav’s view seems to overlook the fact that economic growth is a phe-

nomenon that arose long after *Homo sapiens* had evolved (at least several hundred thousand years ago), and even much later than the rise of agriculture (about 13,000 years ago). Significant economic growth did not actually arise until the end of the Middle Ages, and sustained growth not until the Industrial Revolution was set in motion some 250 years ago.

Nevertheless, selection (and possibly recombination) effects may have changed the distribution of certain parental care characteristics, notably the trade-off between quantity of offspring and quality of parental care. In modern economic growth jargon, such quality improvements can be regarded as an early or even ancient type of investment in human capital. In particular, the gradual emergence of the smaller family since the rise of agriculture may have played an important role in this. Hitherto, larger groups, such as tribes built around one or more extended families, exerted a dominant influence on human evolution. Galor and Moav (2002) argue that human organisation by way of smaller families fostered a strategy that focused relatively much attention on parental investment in quality of offspring, such as education. Together with the sufficiently large size of the communicating human population, this led, through technological innovation, to the essential impetus for the take-off of the Industrial Revolution. This may be termed an 'endogenous evolutionary theory' of the Industrial Revolution. Note that the selection pressure was effective during the preceding "Malthusian era" because the majority of people were living at a subsistence consumption level.

One explanation that the authors cannot exclude, however, is that the change in parental care has culturally rather than genetically evolved. This implies that the theory needs to be tested empirically, which is a difficult if not impossible task. But perhaps this is not really problematic, because the theory works in a similar way for both cultural and genetic selection, and may even be formulated to include both. Finally, with the Industrial Revolution, the selection forces changed through institutionalised educational systems as well as incomes-consumption levels far exceeding subsistence levels. As a result, a new 'evolutionary regime' applies nowadays, at least in the developed part of the world.

These considerations lead to the general question as to whether current human culture – supported by advanced medical, informational and other technologies – has moved to a level that is completely independent of natural evolution. The answer to this question is a definite 'no,' since there is considerable variation in the number of offspring among individuals, groups and countries, which creates room for natural selection at a genetic level. It is, however, difficult to predict where this will lead. It is clear that, genetically and behaviourally, we are still predominantly hunter-gatherers. But in line with the previous discussion, it cannot be excluded that over thousands of years we have adopted new strategies that find support in genetic changes. This period covers several hundreds of generations, allowing for significant evolutionary (selection, recombination and mutation) effects since the Neolithic revolution. Even the industrial era, covering only about ten generations, is already sufficiently long to allow the trace of selection effects. This perspective raises interesting hypotheses and questions, which can only be tested through cooperation of economists and biologists, notably human geneticists. This should address factors such as group and family size (e.g., tribes, extended family, nuclear

family), life expectancy, parental investment (wealth and knowledge), and effects of these factors in later generations.⁴

4 A comparison with non-evolutionary theories of institutional change

Institutional economics has developed as a separate branch of economic theory (Kapp, 1976; Hodgson, 1988; Commons, 1990; Tool, 1993; Swedberg, 1994). Within institutional economics, usually a distinction is made between old (Veblen, Mitchell, Commons) and new streams (Myrdal, North, Olson, Williamson).⁵ Many institutional theories in economics emphasise dynamics of institutions, and even use the terminology ‘evolution’, although often in a non-specific and loose manner. Hodgson (1993) has argued that the frontier of evolutionary economics is not very distinct. Nevertheless, this seems to apply more to informal types of evolutionary analysis than formal approaches that explicitly describe populations, diversity, selection and innovation. In the following, we present a schematic account of the main differences between evolutionary and other theories of institutional change.

Economics has generally regarded institutions as constraints, emphasising the role of markets and property rights. Transactions costs are often claimed by institutional economists to be their intellectual focal point. Institutional change is commonly framed as a control problem rather than an endogenous phenomenon. An exception is the Coase theorem, which states that, in the presence of negative externalities, negotiations among rational agents can lead to socially optimal outcomes. Applied institutional analysis has focused on the liberalisation of markets (energy, public services), the fighting against imperfect competition (anti-cartel legislation), and the taking away of barriers to market entry (property rights, international trade agreements). In addition, interest in the creation of new markets has taken flight, notably in the context of environmental policy (tradable permits) and semi-public goods (auctions to sell wavelengths for telephone communication). Essential for the optimistic tone coming out of this literature on public policy and market liberalisation and creation, has been the core assumption that individuals are rational – i.e. purely selfish and able to solve complex decision problems. This allows a predetermined optimal institutional arrangement, without the necessity of internal diversity. Evidently, all evolutionary approaches deny the validity of the assumption of unbounded or perfect rationality.

Some approaches, such as that of the Historical School, describe institutional change, but leave it unexplained, at least in terms of a general mechanism. Often, institutional change is considered as influenced by exogenous factors, or as a deliberate choice among options, such as contracts (Bromley, 1989) – which is very

⁴ Globalisation tends to ‘homogenise’ cultures, which in effect reduces diversity of human cultures and behavioural strategies that have taken centuries to millennia to evolve. Durham (1991) argues that we should try to learn about and from cultural diversity before it is too late, and that its study will probably enhance understanding of, tolerance for, and valuation of cultural diversity. It is possible that certain cultural diversity has become an outdated ‘adaptive toolbox’ because our economy has shifted the emphasis from agriculture to industry and ICT. This may elicit appropriate types of new diversity.

⁵ Space does not allow, and purpose does not require us to provide, a complete overview of the economic literature on institutions here. For a comprehensive survey, see Hodgson (1988).

close to the traditional economic optimisation perspective. Institutional economics pays much more attention to historical patterns and detailed descriptions of institutions, but generally does not succeed in translating this into a forward looking dynamic model. Hierarchical processes of learning and changing norms and rules (teleological processes) are often stressed (Stein, 1997). This can be linked to the evolutionary concept of ‘emergence’: higher-level social structures emerge, often repeatedly at different levels, from the complex interactions among individuals, their habits and accumulated knowledge. Specific anthropologically oriented theories focus on local communities and societies, which are often considered as organic and influenced by other societies (Bush, 1987; Edgren, 1996).

Evolutionary theories of institutional change try to capture the idea that there is a diversity of potential and actual institutions, which allows for their selection. Moreover, new institutions arise, often unplanned, through innovation, regrouping of individuals, or integration of different levels or scales of human organisation (local to international). Often this happens in response to changes in other areas of the economy or even the environment. This leads to the notion of coevolution. Selection and variety creation (innovation) are cornerstones of these theories, whereas path dependence and lock-in are typical implications. Non-evolutionary institutional theories are limited to mechanistic changes that assume unchanging structure below the population level. Inclusion of a changing population structure would, by definition, move them into the realm of evolutionary approaches.

Altruism is a central issue in both evolutionary and institutional theories. However, in the latter, it is often linked to social-cultural conditions, such as:

- *Wealth*: being altruistic is easier when one is relatively well off.
- *Family background*: copying the behaviour learned in a family setting when acting in relationships with non-family.
- *Education and religion*: using reward and punishment to satisfy a general, prevailing norm in one’s social group; and socially acquiring empathy through experience with reciprocal altruism.
- *Distance*: both social and geographical distances, with the ‘giver’ having an important influence on cultural bonds and altruistic actions.

Some of these elements of institutional approaches can be fruitfully combined with evolutionary approaches to address institutional change.

Finally, some of the statistical-econometric work on historical institutions (‘cliometrics’) can also be linked to the evolutionary approach. North (e.g., 1990) studied the role of institutional variation in such a way. This did not, however, give rise to evolutionary theories explaining how this variation changed over time, for instance, by identifying selection and innovation mechanisms. In recent work, North strongly argues in favour of using evolutionary approaches to deal with the path dependency of institutional change in economic history (North, 1997).

5 A coevolutionary framework for analysis of institutional change

Here we will outline a coevolutionary framework to understand and describe changing institutions. We consider it essential to include individual and group selection

mechanisms. Although both have received much criticism, evidently a description of human societies should include at least one and most likely a combination of them. A number of relationships that define the complex coevolutionary process between individuals and institutions can be identified. The impact of institutions on individuals includes the following mechanisms:

- Institutions influence, enable or constrain behaviour of individuals.
- Institutions select among the diversity of individual behaviours and preferences.
- Alternative institutions compete in different stages: conception, design, implementation, and ex post evaluation.
- Enforcing of norms occurs through rewarding or punishing of individuals that do (not) follow the norms.
- Meta-norms may be present, which means that (non-)enforcers of a norm are rewarded (punished).

The impact in the opposite direction includes the following mechanisms:

- Interactions among individuals influence institutions: altruism, co-operation.
- Individuals form groups, depending on the size of the population. Note that groups and institutions are tightly connected, as isolated individuals do not need to co-operate or avoid conflicts through institutional arrangements.
- Groups influence individuals and institutions.
- Altruism can benefit (selfish) or harm (genuine) the respective individual.
- Co-operation between individuals can be voluntary (spontaneous) or enforced (regulation, norms).
- Co-operation can be beneficial, disadvantageous or neutral to the participating individuals.

Table 1 shows different views on the factors of influence on human behaviour and their social institutions. The ‘pure environment’ view covers various types of learning, including guided variation and biased transmission. According to this view, all diversity of cultures is due to diversity of environmental conditions. The ‘pure genes’ view reflects an ultra-sociobiological view. The ‘genes + culture’ view states that cultural transmission dominates in the short run and genetic transmission in the long run. According to Boyd and Richerson (1985) these latter transmission mechanisms are, however, so indirect that the genetic influence on culture is implicit and difficult to prove. Nevertheless, some cultural habits are directly related to survival and reproduction – think of the role division and interaction among men and women, and food habits. Others, however, such as fine arts, have a less evident impact. Feldman and Laland (1996) argue that cultural evolution is most effective in environments that change slowly relative to the lifetime of individual generations. In rapidly changing environments, social learning has no adaptive value, as information becomes outdated – differs too much between parents and offspring. Only very rapid evolution, such as certain types of current technological evolution, could accommodate such rapid environmental changes. In static or very slowly changing environments, cultural transmission has no adaptive advantage over genetic transmission, since genetic adaptations are capable of keeping up with, and accommodating, environmental changes.

Table 1. Possible factors of influence on behavioural variation in humans

	Heritable cultural variation unimportant	Heritable cultural variation important
Genetic variation unimportant	Pure environment	Environment + culture
Genetic variation important	Pure genes	Genes + culture

Source: Boyd and Richerson (1985, Table 5.5, p. 158).

The conditions in the rows and columns of Table 1 provide guidance for understanding which factors need to be taken into account in an analysis of institutional change. In addition, the typology is useful in a comparative analysis of institutions across cultures or countries. Siebenhüner (2000) suggests that such comparative studies can possibly shine more light on the genetic basis of human cultures and institutions. This would require co-operation among economics, sociology and anthropology. Ben-Ner and Putterman (1998, 2000) argue that evolutionary psychology opens the possibility of an important new research programme in economics, namely the influence of the environment on individual preferences. ‘Environment’ should here probably be interpreted broadly, covering physical and geographical features, environmental and natural resources, artefacts and technology, and other individuals (social-environment). Jackson (2000), Siebenhüner (2000), and Sethi and Somanathan (1996) have actually examined the role of environmental and natural resources. In particular, they have looked for an answer to the questions of why environmental problems exist, and whether human behaviour can be brought in line with the requirements for realising environmentally-sustainable long run development of the (global) economy. This line of thinking stresses that current artefacts and natural environments differ considerably from those prevailing during the period in which we evolved. In addition, consumption beyond basic needs satisfaction is found to be dominated by a striving for possession of ‘positional goods’, which in an evolutionary context can be interpreted as founded in trying to increase one’s fitness, or, more simply, finding a partner.

So far, few theoretical analyses have actually incorporated endogenous institutions and norms. One important reason may be that the analysis of norms in economics is dominated by evolutionary game theory, which employs the most aggregate type of evolutionary modelling. Moreover, it focuses the attention entirely on selection, excluding innovation. Since continuous selection exerted upon a given amount of diversity always leads to an equilibrium, the often used term ‘equilibrium selection theory’ is more appropriate here than evolutionary theory.

Incorporating changing institutions in an evolutionary context essentially means an extension of traditional evolutionary models with endogenous institutions. Doing this at an aggregate level, such as in evolutionary game theory, means that the standard replicator mechanism or any other representation of the population distribution dynamics needs to be extended, with a dynamic equation describing institutional change. If one aims to formalise the entire set of two-way interactions between individuals and institutions, then a multi-layered structure is required. This can probably only be realised with numerical multi-agent models.

Table 2. Coevolution of institutions and behaviour: layers and dimensions

Level	Components	Relationships	Processes
Genes	Population, variety	Organisational structure (network/hierarchy)	Kin selection, mutation, recombination, genetic mediation
Individuals	Population, variety, preferences, profit motive, habit/routine, altruism (kin, reciprocal, genuine), reputation	Empathy, sympathy, reciprocity (strong/weak), frequency and intensity of interactions	Competition, co-operation, communication, negotiation, imitation (direct bias, frequency dependent bias, indirect bias), horizontal and vertical transmission, enforcement (reward/punishment), retaliation
Groups	Population, variety, size, organisational structure (network/hierarchy), firms, government, NGO's, family, power distribution, emergent properties, collective goals	Isolation (geographical, cultural), distance (geographical/cultural), externalities	Organisational learning, group selection, cultural mediation, globalisation, meta-system transition (emergent properties)
Institution(s)	Contract, agreement, market, firm, government (legislation, property right), NGO's, fashion, rules (formal/informal) religion, technical standard, norm (moral value), meta-norm	Organisational structure (network/hierarchy)	Competition (design, operation), replication, regulation (rules, monitoring, enforcement), meta-system transition (emergent properties)

One can define four many layers of evolution among which interactions occur, namely genetic, individual, group and institutional. Table 2 identifies components, relationships and processes for each of these. In addition, the typology of cultural-genetic coevolution of Durham (1991), presented in Section 3.5, is relevant.

6 Conclusions

The rise of evolutionary thinking in the social sciences goes along with a sharp increase in interest in changing institutions. Various evolutionary concepts and theories have been proposed to provide a basis for thinking about institutions, norms and their dynamics: sociobiology and recently evolutionary psychology,

group selection theory, dual inheritance theory, theories of economic evolution and self-organisation, and culture-genetic coevolutionary theory. These offer complementary inputs to an evolutionary perspective on individual behaviour and social institutions. Sociobiology focuses attention on kin selection and inclusive fitness, and to some extent on reciprocal altruism. Higher culture and institutional organisation, including non-kin social relationships, are considered to originate from kin relationships. Evolutionary psychology adds a specific human dimension to this, based on the idea that genetically humans are still Pleistocene hunter-gatherers, reflected by the presence of particular automatic behavioural strategies. Group selection theory suggests that social incentive systems of punishment and reward are able to elicit true altruism, and are not necessarily founded in kinship or reciprocity. Cultural evolutionary theory emphasises the role of horizontal transmission mechanisms (through peers) in social organisation, and the fact that humans can consciously and purposefully change their rules and norms. In addition, they stress that individuals tend to adopt certain pre-existing cultural variants, so that these will increase in frequency. Various types of more or less costly imitation processes play a role in this. Finally, positive and negative interactions between cultural and biological evolution may occur, giving rise to cultural-genetic coevolution. A coevolutionary perspective in a strict sense relates to the interaction of populations of economic-cultural agents and populations of institutional arrangements. Observed institutional variation can thus be explained on the basis of genetic, environmental and purely cultural factors. It has turned out to be difficult to decompose these, especially where social and genetic transmission strongly correlate, notably due to the overlap between vertical genetic and cultural transmission and between parents and offspring.

The economic literature on evolution deals mainly with firms and technology, and to a lesser extent with social and public institutions. Social and public policy issues focus on equity arrangements, evolution of norms as a decentralised policy to deal with sustainable exploitation of public goods such as natural resources, and adaptive management as an experimental policy approach to foster learning. In addition, evolutionary economics studies the economic rationale of co-operation and altruism by assessing associated costs and benefits. Whereas economics traditionally has been interested in institutions for reasons of enhancing efficiency of production and resource use, from an evolutionary angle institutions can be regarded as contributing to stability, resilience and adaptability as well. Institutions such as education and R&D have indeed accelerated the speed of innovation through co-operation and recombination. This in turn has allowed firms to adapt more quickly to changing economic and environmental circumstances, and in general has contributed to the increasingly fast pace of cultural-economic evolution.

Many non-evolutionary theories have been proposed to study the dynamics of institutions. However, even if the frontier of evolutionary economics is not always very sharp, it seems useful to distinguish between approaches based on population-selection mechanisms and others. Most of the latter theories leave institutional change unexplained, or explain it in a mechanistic way. Both neoclassical and contractual theories regard institutional change as a control or choice problem, rather than an endogenous, historical phenomenon. Evolutionary theories present causal

explanations that open the black box of institutional change, by allowing for competition among institutions and regarding interaction among individuals, such as grouping and co-operation (coalition-formation), as leading to the emergence of institutions. The process of emergence is both difficult to understand and to model. A framework was proposed to explain the dynamics of behaviour and institutions, based on including various feedback mechanisms, resulting from multiple, interacting layers of genes, individuals, groups and institutions, as well as norms and meta-norms. The result is a multi-level system, implying that simple evolutionary game models are insufficient to formalise the entire framework, even if they could serve a useful purpose in clarifying certain features. However, numerical approaches allowing for more descriptive complexity seem unavoidable in a serious and complete theoretical study of the evolution of institutions.

Various applications of the framework can be foreseen: the dynamic interaction between business management, consumers and public regulation; the impact of globalisation on international agreements; the evolution of individual preferences in a social context; altruistic behaviour of consumers-citizens; and the impact of globalisation on 'distance' between individuals and institutions and indirectly on altruism. Evidently, this list is far from exhaustive.

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