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Evolutionary Biology in Economics: A Review

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As human traits and preferences were shaped by natural selection, there is substantial potential for the use of evolutionary biology in economic analysis. In this paper, we review the extent to which evolutionary theory has been incorporated into economic research. We examine work in four areas: the evolution of preferences, the molecular genetic basis of economic traits, the interaction of evolutionary and economic dynamics, and the genetic foundations of economic development. These fields comprise a thriving body of research, but have significant scope for further investigation. In particular, the growing accessibility of low-cost molecular data will create more opportunities for research on the relationship between molecular genetic information and economic traits.

> The Mecca of the economist lies in economic biology rather than in economic dynamics. (Marshall, 1920)

> Nothing in biology makes sense except in the light of evolution. (Dobzhansky, 1973)

I Introduction

Human traits and preferences were shaped by natural selection. In that context, economics and evolutionary biology have been intertwined since the work of Malthus (1798) prepared the ground for Charles Darwin's revolutionary development of the theory of evolution by natural selection (Darwin, 1892).[1] Central contributors to the development of modern economics, such as Alfred Marshall (1920), recognised the relevance of biology and other natural sciences for economic analysis.[2] However, despite this early recognition, the use of evolutionary theory as a tool to analyse human preferences, economic growth and economic policy is a recent phenomenon.

In this paper we review the research at the interface between economics and evolutionary biology and the extent to which evolutionary thinking is influencing economic research. Evolutionary biology has been used in four areas in economics: the evolution of preferences, the genetic basis of economic traits, the interaction of evolutionary and economic dynamics, and the genetic foundations of economic development. These four areas of interdisciplinary research are shown in the cells of Table 1. The left margin of the table indicates that one strand of research is

JEL classifications: A12, B52, D01, O12

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[1] Hirshleifer (1977) noted that while Malthus's influence on Darwin represents the influence of economics on biology, Malthus in turn had drawn his ideas from a biological generalisation of Benjamin Franklin.

[2] Marshall (1920) also wrote in the margin of Appendix C of *Principles of Economics*: 'But economics has no near kinship with any physical science. It is a branch of biology broadly interpreted.'

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TABLE 1
Fields of Research Integrating Economics and Evolutionary Biology

	Individual preferences and traits	Macroeconomic outcomes
Theoretical	Evolution of preferences (Section II)	Interaction of evolutionary and economic dynamics (Section IV)
Empirical	Genetic basis of economic traits (Section III)	Genetic foundations of economic development (Section V)

mostly theoretical, exploring the structure of models with genetic foundations, whereas a second strand is more empirical, focusing on observable genetic and economic data. The top margin of the table shows that this research has been applied at the level of individual preferences in microeconomics and at the population level in macroeconomics and economic development. The cells in Table 1 provide the structure for the review that follows in the next four sections.

The research on the evolution of preferences (Section II) and the genetic basis of economic traits (Section III) has been subject to previous reviews by Robson and Samuelson (2011a) and Benjamin *et al.* (2012a). Accordingly, we focus on the incorporation of these two fields into broader economic thought and the future opportunities in these areas. For our review of evolutionary economic dynamics (Section IV) and the genetic foundations of economic development (Section V) we present a more thorough analysis.

The subject matter of this paper needs to be distinguished from what is commonly called ‘evolutionary economics’. Evolutionary economics uses biological concepts, such as natural selection, and applies them to the dynamics of firms, business processes and institutions. The economy is seen as a complex adaptive system in which innovation and change are central considerations. The origin of evolutionary economics is often traced to Veblen (1898), and was revived by Alchian (1950) and later Nelson and Winter (1982), whose seminal work inspired a vast literature; see, for example, the *Journal of Evolutionary Economics*. The subject matter of this paper differs from evolutionary economics in that we focus on human biology rather than seeking to apply a biological analogy to higher levels such as firms. This paper is about the application of evolutionary biology to economic processes at the level of humans and their genes and their interactions at the population level.

II The Evolution of Preferences

Human preferences play a central role in economic analysis. By understanding preferences, the response of individuals to economic incentives and the aggregate phenomena emerging in the population can be studied. Two early advocates of examining the evolutionary foundations of preferences were Becker (1976) and Hirshleifer (1977). Motivated by the publication of *Sociobiology* by E.O. Wilson (1975), Becker and Hirshleifer saw the benefits of biological thinking in economics and parallels between the economic and biological ways of thought.

Becker (1976) argued that preferences could be explained by selection of traits with higher fitness. By way of illustration, he provided an explanation of the existence of altruistic behaviour, which by the usual definition of altruism harms the fitness of the altruist. Extending his ‘rotten kid theorem’ beyond the family, Becker argued that an altruist’s fitness may actually be strengthened if the altruist’s threat to transfer resources to harmed parties at a cost to the transgressor prevents the latter from harming people, including the altruist. This contrasts with explanations developed by biologists to explain the preference for altruism, such as inclusive fitness (Hamilton, 1964a,b), reciprocal altruism (Trivers, 1971), or group selection (Wynne-Edwards, 1963).[3] Becker’s model explains why altruism is not selected against, but it does not address how a preference for altruism could have evolved and spread through the population. Besides the evolution of preferences such as altruism, Hirshleifer (1977) saw sociobiological analysis as useful in examining the evolution of preferences, as well as understanding exchange

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[3] The usefulness of group selection arguments remains a subject of debate (see, for example, West *et al.*, 2008; Eldakar & Wilson, 2011).

and the division of labour, and in examining evolving as opposed to equilibrium socioeconomic systems.

In this section, we review the work that has followed Becker and Hirshleifer's initial advocacy of an evolutionary analysis of human preferences. In Section II.i we deal with the objective of the economic agent, and in Section II.ii the shape of the agent's utility function.

(i) Choosing the Objective: Consumption versus Fitness

In evolutionary biology, 'inclusive fitness' is an individual's ultimate 'objective'. Inclusive fitness, which is measured as the individual's contribution of genes to the next generation through its own reproduction and indirectly through related carriers of the same genes (Hamilton, 1964a,b), may be maximised by pursuing proximate objectives, with those proximate objectives shaped by evolution.[4] By contrast, in economic models agents typically maximise utility from the consumption of a basket of goods and services. To reconcile the economic and evolutionary objectives, we need to ask if the proximate objective shaped by evolution is reflected in the utility function in economic models. In other words, does consumption maximise fitness? If it does not, consumption maximisation would not be selected for and other proximate objectives should be included in utility functions.

A seminal paper that illustrates this point is Rubin and Paul (1979) on the evolution of risk preferences. In their model, they defined utility as fitness, which depends on the number of females that a male attracts. This utility formulation explains changes in risk preferences of males as they age and gain additional income and resources. A male with a level of income below that required to attract a female will be risk seeking with respect to income, as a loss in income does not reduce his utility. A male with a level of income slightly above that required to attract a female will be risk averse, as a small drop in income will materially reduce his utility. This pattern would be repeated at higher levels of income wherever a threshold for additional mates is approached.

In another attempt to reconcile utility and fitness, Gandolfi *et al.* (2002) considered a framework in which a person maximises fitness by maximising long-term intergenerational wealth, which can be spent on children and their education as required. This model explains the low fertility in modern societies as a long-term fitness-maximising strategy. It is not the number of children and their genes in the next generation that matter but the number of children over the entire future. However, the positive correlation between numbers of children across generations in developed countries (Rodgers *et al.*, 2001; Murphy & Knudsen, 2002) suggests that people with more children have higher fitness. More direct evidence that parents overinvest in the education of children to the detriment of their number comes from Kaplan *et al.* (1995), who found that men were not maximising their number of grandchildren.

This low fertility at the cost of fitness may be caused by the fact that today humans live in an environment that has changed dramatically, offering little time for selection to act on relevant traits.[5] As evolution shapes traits through proximate mechanisms, a change in environment can result in pursuit of a proximate objective failing to maximise fitness (Bowlby, 1969; Tooby & Cosmides, 1992; Irons, 1998). That is, the pursuit of the proximate objective is maladaptive. For example, the taste for fat and sweetness, which increased fitness when calories were scarce in the Malthusian environment, is leading to overconsumption of high-calorie foods in modern times (Breslin, 2013). Brooks *et al.* (2010) proposed that this preference for high-calorie foods, the evolved mechanism to regulate protein intake more strongly than calories from non-protein sources and a fall in the price of carbohydrates relative to proteins have together contributed to the spread of obesity. Therefore, the traits and preferences under selection in past environments need to be considered in determining those to be used in economic analysis, as proposed by Jones (2000), Miller (2003) and Burnham (2013). Alternatively, an evolutionary analysis may allow people to adapt to the new environment and for utility-maximising behaviour to move towards maximisation of fitness over time.

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[4] The distinction between proximate and ultimate evolutionary objectives was made by Mayr (1961) and Tinbergen (1963).

[5] In Galor and Moav's (2002) model, the lower fitness of quality-preferring types in the modern growth era is due to this type of overinvestment.

It is also possible that consumption is fitness maximising through its role as a signal of quality.[6] De Fraja (2009) showed that if male conspicuous consumption serves as a signal that females prefer when choosing mates, a utility function in which a male maximises consumption is equivalent to fitness maximisation. Other papers make an implicit assumption that consumption maximises fitness (for example, Hansson & Stuart, 1990), without stating how the agents allocate resources between consumption and reproduction. This approach may be justifiable as consumption could include allocation of resources to the production of children. Alternatively, the findings of De Fraja could be used to justify this assumption.

As the effect of an individual's actions on others affects its own inclusive fitness, we must also ask whether the proximate objective relates purely to private interests or is other-regarding. Accordingly, some economists have examined the problem addressed by Becker (1976), the evolution of altruistic behaviour. Much of this research has been directed to the evolution of 'strong reciprocity' (Gintis *et al.*, 2003; Bowles & Gintis, 2004), which is the predisposition to cooperate and punish those who violate the cooperative norms; and 'parochial altruism' (Bowles *et al.*, 2003; Bowles, 2006), which is a combination of within-group cooperation and inter-group competition (for a review, see Rusch, 2014). This work has also included examination of the preference for moral behaviour, which is a preference for 'doing the right thing' (Alger & Weibull, 2013; Newton, 2014).

Much of the work on strong reciprocity and parochial altruism focuses on group interactions, often described as 'group selection' and as an alternative or exception to an inclusive fitness approach (Gintis *et al.*, 2003; Bowles & Gintis, 2004; Bowles, 2006). However, inclusive fitness is the more common approach in biology,[7] and the research in strong reciprocity and parochial altruism can be reconstructed using an inclusive fitness approach (West *et al.*, 2008). This has led some biologists to argue that advances in evolutionary theory have been communicated poorly to the social sciences, leading to confusion in terminology and methodology, and a proliferation of explanations for the same phenomena (West *et al.*, 2011).

(ii) The Shape of the Utility Function: Time Preference and Risk Preference

Utility functions may have different shapes, with two properties – time preference and risk preference – attracting special attention. Time preference, the relative valuation that people place on goods based on the time they are consumed, has received significant analysis from an evolutionary perspective (Hansson & Stuart, 1990; Rogers, 1994; Sozou, 1998; Dasgupta & Maskin, 2005; Robson & Samuelson, 2007, 2009; Robson & Szentes, 2008; Netzer, 2009). Time preference has strong parallels with life-history theory, which examines the effect of natural selection on the timing of the stages of life of an organism, such as development, maturation, reproduction, investment in offspring, senescence and death.

The evolution of time preference was considered as early as Fisher (1930), who pointed out that it should approximate the rate of population increase, although he noted that this would yield a rate of time preference below that observed. Hansson and Stuart (1990) agreed that the intergenerational discount rate would reflect long-term population growth. Rogers (1994) studied the optimal transfer of resources from a mother to her daughter. He concluded that the discount factor is one half per generation and the long-term real interest rate should equal approximately 2 per cent per year. Robson and Szentes (2008), however, argued that Rogers's analysis was based on the assumptions of identical offspring and a single same-age transfer between mother and daughter. Without these assumptions, the rate of time preference would depend upon the survival function faced at each age, and thus no particular rate of time preference could be derived. While

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[6] Veblen (1899) coined the term 'conspicuous consumption' for the wasteful signalling of wealth or other qualities. Zahavi (1975) argued that waste makes a signal reliable as only a high-quality individual can carry the 'handicap' imposed by the waste. Biologists debated whether Zahavi's concept was plausible – Maynard Smith (1976) concluded it was not – until Grafen (1990a,b) showed that the condition for a handicap to be a reliable signal was that high- and low-quality agents must face different marginal costs of signalling. This mechanism is the same as that in Spence's (1973) job market signalling model.

[7] Another potential approach is multi-level selection, a group-based perspective that is mathematically equivalent to the inclusive fitness approach (D.S. Wilson, 1975; Queller, 1992).

these approaches generate a low rate of time preference, Robson and Samuelson (2009) proposed that aggregate risk that affects the viability of the entire population gives rise to a higher optimal discount rate than agent-specific risk. Ultimately, however, evolutionary theory has provided little guidance for parametric improvement of existing utility functions, such as determining what is the appropriate rate of time preference or level of risk aversion. This may be because experimental evidence relating to risk or time preference is a better source.

The dominant approach behind these results is to derive the utility function that would maximise fitness in a given environment. This generally results in a pattern of exponential discounting that may be considered 'rational' in the sense that it leads to consistent choices over time. One notable exception is work by Sozou (1998), who provided an evolutionary argument for hyperbolic discounting, which generates inconsistent choices over time (Strotz, 1955; Ainslie, 1975). Sozou showed that people can update their estimate of the probability of an underlying hazard, with the induced reduction in the discount rate generating a hyperbolic pattern of discounting. Where time-inconsistent behaviour is observed in experimental settings that do not involve a hazard (such as in Tversky *et al.*, 1990), the hyperbolic behaviour may be an evolutionary relic from more hazardous times. Robson and Samuelson (2007) also demonstrated an evolutionary basis to hyperbolic discounting using life-history theory.

Alternative evolutionary approaches provide scope for other behaviour such as loss aversion (Kahneman & Tversky, 1984) and preference reversals (Lichtenstein & Slovic, 1971) that do not relate to intertemporal choice. The remainder of this section will consider these types of behaviour.

The first step is to understand the agent's evolutionary objective. For example, in Rubin and Paul (1979), agents appear risk averse above certain incomes and risk seeking below them only through misspecification of the agents' objectives, for in the domain of attracting mates or fitness, the behaviour is risk neutral.

These evolutionary objectives can vary with context. The modular theory of intelligence is based on the concept that the human mind does not act as a single, centralised processing unit, but rather is comprised of relatively independent modules that solve problems in different domains (Cosmides & Tooby, 1992). Accordingly, different decision rules will be applied in different contexts, such as whether the decision relates to mating, child rearing, status or social interaction. Kenrick *et al.* (2009) proposed that this modularity can be used to explain many of the departures from rationality reported in the behavioural economics literature. Such decision rules would have had positive fitness consequences for most of human history, and Kenrick *et al.* describe them as 'deeply rational'.

Another approach deals with bounded rationality or the use of heuristics (rules of thumb).[8] Rayo and Becker (2007a,b) demonstrated how peer comparison and habit formation could arise by considering happiness as an imperfect gauge by which economic agents make decisions. If agents had superior sensory capabilities and their happiness response was perfectly attuned to their choices, the evolved utility function would simply map happiness onto fitness. But if agents are constrained in the way they feel happiness, such direct mapping may not be possible.

Rayo and Becker (2007a,b) considered agents who cannot tell close-together choices apart due to limits to the sensitivity and bounds of happiness.[9] These physiological constraints might be likened to a voltmeter, which must first be calibrated to the problem at hand to give an accurate reading (Robson, 2001), or the human eye, which adjusts to the general luminosity of the surroundings (Frederick & Loewenstein, 1999). If an agent cannot discriminate between choices, it may be possible to achieve greater sensitivity through evolving an amplified happiness response. But if there is a bound on happiness, amplification may push certain choices outside of the viable range. Rayo and Becker showed that under these constraints, agents will maximise the strength of the signal where it matters most, considering currently available opportunities. Hence, utility will depend on the relative outcome of decisions, with information conveyed to the brain in terms of contrast between outcomes. Their approach captures the empirical observations of the short-lived effect of a change in income on happiness, and people's strong positional concerns. A general

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[8] One excellent analysis of decision-making in this framework is by Gigerenzer (2000).

[9] Similar constraints were used by Robson and Samuelson (2011b) in providing an evolutionary explanation of why people's decision utilities and experienced utilities vary.

increase in income across society does not increase happiness (consistent with Easterlin, 1974). This formulation is also consistent with a positive correlation between income and happiness in cross-sectional data as people with a higher income are more likely to have received a recent positive income shock.

Evolutionary theory may also provide insight into the heterogeneity of preferences, such as variation in time preference (Warner & Pleeter, 2001; Frederick *et al.*, 2002) and risk aversion (Cohen & Einav, 2007; Barseghyan *et al.*, 2011). The heritability of economic traits points to the influence of genetic factors (for example, as demonstrated by Cesarini *et al.*, 2009). Saint-Paul (2007) considered the interaction of genetically heterogeneous agents in a trading situation. He found that genetic heterogeneity could be maintained where trade allowed for comparative advantage.

A further extension of research in this area examines a broader range of economic preferences, particularly those that are not features of typical utility functions. Time preference and risk preference have attracted much attention, whereas preferences such as the human desire to cooperate, innovate or signal have received less interest, particularly in the economic literature. As a striking example, the propensity to exchange among non-kin (an area of analysis suggested by Hirshleifer, 1977), a hallmark of humans when compared to other species (Kaplan *et al.*, 2012), is the foundation to much economic activity and to concepts such as comparative advantage. Yet despite the 'propensity to truck, barter, and exchange one thing for another' being noted by Adam Smith (2003), the evolutionary examination of this propensity is rarely considered in the analysis of economic preferences. Equally, the evolution of economically relevant traits such as human cognition and intelligence has received limited attention from economists, although the genetic foundations of these traits have increasingly been a subject of research. That research is the subject of the next section.

III The Genetic Basis of Economic Traits

An important empirical finding of behavioural genetics is that all human behaviour is heritable (Turkheimer, 2000); that is, a proportion of the variation in phenotypic (observable) behavioural traits can be attributed to genetic variation among individuals. This finding also applies to economic behaviour, with a genetic basis to economic behaviour demonstrated across a range of studies (Benjamin *et al.*, 2012a,b). The empirical analysis of molecular genetic information as it relates to economic traits has become known as 'genoeconomics' (Benjamin *et al.*, 2008).

The recent growth of genoeconomics builds on past work on the heritability of economic traits, particularly through twin and adoption studies. In twin studies, a higher correlation in traits between identical twins than for fraternal ones provides an estimate of heritability. In adoption studies traits of adopted children are compared with those of their adoptive and natural parents. These studies have produced estimates of heritability of savings behaviour of 0.33 (that is, 33 per cent of the variation in savings behaviour is attributable to variation in additive genetic factors; Cronqvist & Siegel, 2015), of risk preference of 0.2–0.57 (Cesarini *et al.*, 2009; Le *et al.*, 2012; Zhong *et al.*, 2012) and of intelligence of 0.5–0.8 (Johnson *et al.*, 2010). Estimates of the heritability of income include those from Taubman (1976), who estimated a heritability of 0.18–0.41 in white male twins, and Benjamin *et al.* (2012a), who found heritability of permanent income of 0.37–0.58 for men and 0.28–0.46 for women. Sacerdote (2007) produced a series of estimates of the heritability of several measures of educational attainment, which ranged between 0.34 and 0.46.

Early behavioural genetic studies were candidate gene studies, where a gene of interest is hypothesised to affect an economic trait based on that gene's biological function. However, candidate gene studies have a poor record of replication. For example, Chabris *et al.* (2012) sought to replicate published associations between general intelligence and genetic variants. They found a significant relationship in only one of 32 tests, compared to the expected 10–15 given the power of the tests. Benjamin *et al.* (2012a) pointed out that the failure of candidate gene studies may be due to small sample sizes, with only one study reviewed in their paper using more than 500 people; the use of *ex post* hypotheses that are formed after discovery of a statistical relationship; and publication bias, which is the tendency that only positive findings will be published.

As genomic techniques became cheaper, genome-wide association studies (GWASs) became feasible. These studies take an array of hundreds of thousands to millions of single-nucleotide polymorphisms (SNPs) and search for associations between the sampled SNPs and a range of tested phenotypic outcomes. One limitation of GWASs is that the effect of most SNPs is low and typically explains less than 1 per cent of the phenotypic variation, even for traits with a large genetic component such as height (Lango Allen *et al.*, 2010). Consequently, large sample sizes are required so that the significance level can be set high enough to avoid false positives, but still have enough power to identify SNPs that affect the trait of interest. A significance level of 5×10^{-8} is commonly adopted, which reflects the 1 million SNPs in a typical array (Risch & Merikangas, 1996). However, even large samples may fail to produce consistent results. Beauchamp *et al.* (2011) searched for genetic variants associated with educational achievement in one sample of 7,500 people. They were unable to replicate their initial findings in a second sample using 9,500 people.

Accordingly, to this time, most of the heritability observed in twin and adoption studies has not been explained by the identification of the relevant SNPs. This has been termed the 'missing heritability problem' (McCarthy & Hirschhorn, 2008). The complexity of gene–gene and gene–environment interactions, the small effect of any particular gene and the difficulty of obtaining genotypic data across all members of the relevant sample create practical constraints on the use of genetic data.

The difficulty in finding SNPs with a significant association with a trait of interest stimulated the development of an alternative approach examining the combined contribution of the genotyped SNPs. Benjamin *et al.* (2012b) used a technique (developed in Yang *et al.*, 2010) which they called 'genomic-relatedness-matrix restricted maximum likelihood' (GREML) to estimate the proportion of variance in economic and political preferences and in educational attainment that could be explained by the combined genetic variation within an SNP array. While the GREML approach is a noisy measure that gives a lower bound estimate of heritability, genetic variation was found to explain at least 20 per cent of the variation in trust. No significant relationship was found for the other three economic traits tested: risk, patience and fairness. The analysis of political and economic preferences using GREML indicates that although the genetic effects are highly polygenic, genetic information in the form of SNP data will be able to predict a substantial proportion of phenotypic variation. This finding supports other studies that demonstrated that genotyped SNPs explain a substantial proportion of the variance in traits such as height (Yang *et al.*, 2010), intelligence (Davies *et al.*, 2011) and personality (Vinkhuyzen *et al.*, 2012). The question then becomes when datasets may become large enough to identify the SNPs that affect economic preferences.

Genoeconomics may improve economic models by providing direct measures of behavioural parameters and allowing the use of genes as control variables or instruments in empirical studies. Identification of biological pathways as the basis of economic traits would give the analysis of the evolution of preferences more substantial grounding and provide additional foundation to theoretical analysis. In particular, this may assist in the dynamic analysis of how preferences evolved. Genomic information may also benefit social programs and public health policy through identifying heterogeneity between people. Benjamin *et al.* (2012a) provided an example of targeting supplementary reading programs at those whom genetic screening has identified as being at increased risk of dyslexia. However, the use of heritability in policy development has been subject to criticism, which is also likely to be made of genoeconomic research. In an influential paper, Goldberger (1979) questioned the value of information on heritability in social policy (largely reflected in Manski, 2011). Goldberger argued that information on the heritability of poor eyesight has no effect on the policy decision of whether or not to provide eyeglasses. However, knowing the genetic cause allows a more effective targeting of screening programs and early intervention.

To reach a point where genoeconomics can make these contributions, datasets large enough to provide the requisite power for analysis are required. To achieve this, there may be value in pooling datasets, which requires consistent measurement of phenotypes across studies. The Social Science Genetic Association Consortium[10] aims to achieve this through the establishment of standardised surveys for traits such as risk and time preference, trust, education and wellbeing. In one output from this pooling, members of the consortium conducted a GWAS using a sample of 101,069 individuals, and a replication sample of

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[10] For information on the Consortium, visit http://www.ssgac.org.

25,490, and found SNPs that explained approximately 2 per cent of the variance in educational attainment and cognitive function. In the future, full genome testing may be routine and allow even larger samples as sequencing costs continue to decrease rapidly (Wetterstrand, 2016). This was illustrated in one recent analysis of height using a sample of over 250,000 people, which found 697 genetic variants that, in combination, explained 20 per cent of the heritability for adult height (Wood *et al.*, 2014). Once large enough samples are collected for economic traits and behaviours, the quantity of data will be difficult to ignore.

Until genoeconomics progresses to this point, however, there are alternative means to incorporate genetic information into economic analysis. In the absence of molecular data, family history can provide control variables relating to heritable traits and capture much of the phenotypic variation due to genotype. For example, estimates of height using a 54-locus genomic profile explained only 4–6 per cent of the sex- and age-adjusted variance in height in a population, whereas parental height explained approximately 40 per cent (Aulchenko *et al.*, 2009). Larger genetic sample sizes may eventually yield more accurate prediction than family history, but that is not yet the case.

Another area with potential for future analysis is epigenetic transmission of traits. Epigenetics is the study of heritable chemical changes in gene expression that are not caused by changes in the DNA sequence (Berger *et al.*, 2009).[11] These changes include modification of histones, which are proteins around which DNA is wrapped, DNA methylation, in which a methyl group is added to DNA nucleotides, and RNA modification.

Epigenetic changes are influenced by environmental factors such as abuse during childhood and poverty. They have been proposed to affect physical and mental health in later life (Hochberg *et al.*, 2011; Hoffmann & Spengler, 2014) and have also been proposed to affect subsequent generations. Intergenerational transmission may occur through the parents' behaviour affecting their offspring, or due to environmental effects on the embryo and its germ line. As human eggs form in the female embryo, environmental stresses on a pregnant woman can act directly on the eggs of her daughter, which will eventually develop into grandchildren. Of interest from an evolutionary perspective is the potential for intergenerational transmission of epigenetic changes beyond the people or germ lines exposed to the environmental stress. One famous example of intergenerational transmission of epigenetic changes comes from a study of three cohorts born in the Överkalix parish in northern Sweden, where diabetes mortality was higher if the paternal grandfather experienced food scarcity during certain stages of development (Kaati *et al.*, 2002). Similarly, the children of men who were prenatally undernourished in the 1944–5 Dutch famine were heavier and more obese than those in the cohort who were not undernourished (Veenendaal *et al.*, 2013).

If epigenetic changes can be transmitted across multiple generations, they could provide variation for natural selection to act upon and thereby allow faster pathways for individuals to adapt to changing environments compared to rare and random DNA mutations. However, the development of the field of epigenetics does not present an alternative to classic gene-based approaches. First, epigenetic changes are likely to be induced by the organism's genes, and some instances of proposed epigenetic transmission may simply reflect unidentified genetic mutations (Heard & Martienssen, 2014). Second, there is limited evidence that epigenetic changes in humans are transmitted with high fidelity across more than a couple of generations. In mammals, the embryo and germ line undergo a round of epigenetic reprogramming in which most parental epigenetic marks are erased, although a limited number of marks escape the reprogramming (Daxinger & Whitelaw, 2012). Third, for most examples of intergenerational epigenetic transmission, no biochemical mechanism by which the epigenetic change occurred or was transmitted has been identified (Kaati *et al.*, 2002; Heard & Martienssen, 2014).

However, epigenetic changes may still be a relevant economic consideration, even if transmission is behavioural or rapidly decays across generations. The transmission of environmental stresses across a few generations is of interest for economic and social policy. But the lack of identified mechanisms means that it is not currently feasible to include epigenetic marks in any analysis. Controlling for parental and possibly even grandparental traits and experiences is one alternative to capture the effects of interest.

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[11] The definition of epigenetics is subject to debate and includes definitions that do not require the changes to be heritable (Ledford, 2008).

IV The Interaction of Economic and Evolutionary Dynamics

Given that most economic change occurs over shorter periods than human evolutionary change, taking economic preferences as fixed through time seems a reasonable assumption. However, over the longer timeframes that are relevant for economic growth and development, the evolution of traits and preferences needs to be considered. This is particularly the case given the increasing evidence of the accelerating pace of evolution and changes in gene frequencies in human populations since the spread of agriculture (Voight *et al.*, 2006; Hawks *et al.*, 2007; Cochran & Harpending, 2009; Fu *et al.*, 2013). Any economic analysis over tens or hundreds of generations should incorporate evolutionary change. Wilson (1970) argued that there could be significant alteration in intellectual and emotional traits in humans in less than 10 generations, with considerable evidence of this occurring in recent human evolutionary history (Stearns *et al.*, 2010; Milot *et al.*, 2011; Courtiol *et al.*, 2012).

(i) Human Evolution and Economic Growth

While economists such as Hansson and Stuart (1990) noted that human populations evolving in different environments may vary in their evolved economic traits, the dynamic analysis of economic preferences and economic growth received limited attention until Galor and Moav (2002) considered whether human evolution was a factor underlying the transition from Malthusian conditions to modern levels of economic growth. In a unified growth framework (Galor & Weil, 2000; Galor, 2011), Galor and Moav developed a model in which the population comprises two types that vary genetically in the relative weight they place on the 'quality' or quantity of their children. 'Quality-preferring' types invest more in the education of their children than 'quantity-preferring' types, who prefer a large number of children. As education adds to human capital, quality-preferring types earn a higher income that they can spend on more and better-educated children, but they also bear the cost of educating their children. Which group has a fitness advantage depends on the stage of economic development. In the Malthusian state, education leads to a higher level of fitness and an increase in the prevalence of the quality-preferring types. This raises the average level of education in the population, driving technological progress and economic growth.

The prevalence of the quality-preferring types is initially low in the Malthusian state. Therefore, the high level of education of the quality-preferring types translates into only a small increase in the average level of education and technological progress remains low. Nevertheless, the increasing rate of technological progress steadily increases the returns to education and eventually it becomes worthwhile for the quantity-preferring types to educate their children. This shift from an educated elite to mass education vastly enhances the average level of education in the population, initiating a leap in technological progress that sends the economy into a new high-growth state. Simulation of the Galor and Moav model by Collins *et al.* (2014) showed that the economic take-off could occur within a few generations, which reflects the nature of the take-off observed around the time of the Industrial Revolution in parts of Europe. After the take-off, the quality-preferring types decline in prevalence because they overinvest in the education of their children relative to the level that maximises fitness. The new high-growth state is maintained by the continuing investment in education by the quantity-preferring types.

One outcome of the simulation of the Galor and Moav model is that the population stabilises during the transition out of the Malthusian state. This does not conform with the historical record as high rates of population growth persisted in Great Britain and other countries beyond the economic transition during the Industrial Revolution, until the end of the nineteenth century. The simulated decline in fertility of the quality-preferring type is, however, consistent with a decline in fertility among the wealthy in Great Britain during the economic transition (Clark & Cummins, 2015).

The stability of the modern growth state is subject to the assumption of only two types of parents (Collins *et al.*, 2014). If a third strongly quantity-preferring type is present in the population – through mutation, migration or having always been present in small numbers – that type will have an evolutionary advantage in the modern growth state as it will direct all of its resources to quantity of children, with no investment in the education of their children. As the strongly quantity-preferring types increase in prevalence, it is possible that they will drive down the average level of education, ultimately halting technological progress and sending the population back into a Malthusian state. This return to a Malthusian state may be prevented if other effects such as a technological scale effect are present. However, that scale effect must not be contingent on the population members educating their children.

Galor and Michalopoulos (2012) utilised a similar framework to Galor and Moav (2002), but their trait of interest is entrepreneurial spirit, proxied by the degree of novelty or risk seeking. They proposed that in the early stages of development, risk-tolerant individuals had an evolutionary advantage. As they expanded to form a larger portion of the population, the risk-tolerant types drove technological progress through their entrepreneurial activity, ultimately triggering a take-off in economic growth. After the take-off, risk-averse individuals have a fitness advantage and increase in prevalence. Galor and Michalopoulos proposed that a reduction in the proportion of risk-tolerant individuals in developed countries might lie behind the process of convergence between developed and less developed countries. The economy may even be vulnerable to a return to the Malthusian state through the reproductive success of increasingly risk-averse people.

A core feature of the papers by Galor and Moav (2002) and Galor and Michalopoulos (2012) is the manner in which the evolutionary processes operate. In the Galor and Moav model, the quality-preferring types lose their evolutionary advantage after the economic take-off. The result is that the population before and after the take-off has the same composition. In fact, the evolutionary dynamic may not be required if there is another source of technological progress, such as a scale effect (which reflects the model of Galor & Weil, 2000). Similarly, in the Galor and Michalopoulos model, the evolutionary advantage switches between risk-tolerant and risk-averse individuals at the time of the economic take-off, meaning only a temporary change in population composition.

A different approach to human evolution and economic growth was taken by Collins *et al.* (2013), who proposed a model in which the population composition changes permanently. Collins *et al.* extended Kremer's (1993) model of population growth and technological progress to incorporate the evolution of 'innovative potential', which may be thought of as research productivity per person. Kremer combined the concepts that a Malthusian population's size is constrained by its level of technology and that more people leads to more ideas, to show that population growth is proportional to its size. Collins *et al.* extended this framework by proposing that population growth is proportional to human innovative potential because more people means more mutations and greater potential for evolutionary change (Fisher, 1930). If mutations that increase innovative potential raise the fitness of the bearer, these genes will spread through the population, increase technological progress and enable further population growth. Adding the evolution of innovative potential to the analysis enhances the stability of the population, as the innovative potential of people is higher after each successive shock. Unlike in the preceding models, an increase in innovative potential is associated with a permanent change in the composition of the population, and growth of the now more innovative population eventually becomes the more important source of technological progress than further evolution of innovative potential.

Taking an empirical approach, Clark and Hamilton (2006) used wills in England dated 1585–1638 to show that wealth was strongly (and positively) predictive of reproductive success. Building on this, Clark (2007) inferred that the inheritance of fitness-enhancing traits of the wealthy such as thrift, prudence and hard work was a factor behind the emergence of the Industrial Revolution in pre-1800 Great Britain. To the extent that those traits were passed from parent to child, they would spread through the population and provide a basis for the acceleration in economic growth. Clark was equivocal as to whether the transmitted traits were cultural or genetic, although in subsequent work Clark (2008) argued for a genetic inheritance. Assuming that wealth is positively related to education, the positive association between wealth and fertility during the pre-industrial era coincides with the Galor and Moav (2002) model. Clark and Cummins (2015), however, suggest that the positive wealth–fertility relationship for households earning more than the subsistence level of income in the Malthusian era is not consistent with the Galor and Moav model. They also suggest there is limited evidence of increasing returns to human capital, as should be evidenced through increasing skills premiums, during the Industrial Revolution (Clark, 2005).

Clark's (2007) proposed mechanism contrasts with that of Galor and Moav, who argue that the heritable trait under selection is a preference for investment in education. A larger challenge for the Galor and Moav model, however, will be empirically establishing its evolutionary features: that natural selection for a preference for quality occurred during the Malthusian period (some preliminary evidence is presented in Galor & Klemp, 2014); that this selection changed the population composition sufficiently to increase technological progress, in turn inducing most of the population to educate their children; and that the selection advantage of the quality-preferring types disappeared after the transition.

Clark's thesis leaves scope for further research on why Great Britain was the site of the Industrial Revolution and the nature of the selection of traits and preferences that occurred. Clark notes that positive selection on wealth has been observed across many pre-industrial societies (see Nettle & Pollet, 2008, for a summary), but argues that different traits are associated with wealth in hunter-gather societies than in pre-industrial Great Britain. He also argues that the income–fertility link in China and Japan was weaker, although this is based on data for the nobility, with equivalent data for rich commoners not available.

The finding of higher fecundity of the rich is suggestive of the role of sexual selection in humans. Fitness depends on an individual's ability to attract a mate. Conflicts arise among males for access to females, and females become choosy and discriminate against unwanted males. Sexual selection can result in fast evolutionary changes as it has a direct impact on reproductive success and fitness (Brown *et al.*, 2009). Wade and Shuster (2004) estimated that sexual selection accounts for approximately half of total selection in *Homo sapiens*, while Miller (2001) suggested that sexual selection shaped the human mind.

Zak and Park (2002, 2006) incorporated sexual selection into an age-structured model in which agent cognitive ability and beauty [sic] are genetically determined. The agents in Zak and Park's model do not maximise biological fitness directly, as they trade off marriage, children and consumption of goods. As such, an agent with lower preference for consumption relative to children would have a fitness advantage. In Zak and Park's baseline scenario, sexual selection increases intelligence, human capital and beauty. The baseline simulation generated 1 per cent growth in human capital per generation over 40 generations, which Zak and Park suggest is a reasonable approximation of the last 800 years.

A recent application of sexual selection to the analysis of economic growth is by Collins *et al.* (2015), who hypothesised that sexual selection and the resulting propensity to engage in conspicuous consumption contribute to economic growth. Collins *et al.* posited that men who signal their quality through conspicuous consumption have higher reproductive success, as conspicuous consumption provides a signal of their quality to potential mates. The creative and productive activities required to fund conspicuous consumption generate economic growth. This analysis may provide an explanation for several phenomena, including the sudden appearance of goods associated with conspicuous consumption in the historical record, increasing rates of technological progress following the appearance of those goods, and continuing investment in work effort in modern economies where additional resources are not required for subsistence.

(ii) *Evolution of Economic Traits*

Traits may not always be determinable by a maximisation exercise of the nature undertaken in the previous analysis of the evolution of preferences. This possibility is illustrated by Frank (1988), who argued that the path dependence of evolution led to emotions playing a role in creating a credible threat of retaliation when engaging in trade. He proposed that when we are considering whether to retaliate against a party who has cheated us, we do not engage in a rational cost–benefit analysis of whether the gain in reputation in the future is worth the retaliation cost today. We instead have an emotional response to cheating, which impels us to retaliate. The mix of emotions with high discount rates applied to future reputation gains is a stable evolutionary bootstrap resulting from the path by which these respective traits evolved.

Another study investigating the dynamic evolution of an economic trait was done by Saint-Paul (2007), who analysed the role of trade in human evolution. Saint-Paul describes a population that engages in two activities – fight and defence. Applying a haploid structure, each person has a gene that determines fighting productivity and a gene determining productivity in defence.[12] Each gene can be of either high

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[12] Humans are diploid with two sets of chromosomes, one from each parent, whereas a haploid organism has only one set of chromosomes. It is common to treat humans as haploid in studying the evolution of social behaviour as it avoids complications such as diploid reproduction, multi-gene traits, interactions between genes and phenotypic expression (Grafen, 1991).

productivity (H) or low productivity (L), leading to four possible genotypes: HH, HL, LH and LL. Without trade, each person must be self-reliant, and the low-productivity alleles (variants of genes) are eventually eliminated from the population. With trade, a person can specialise in a high-productivity activity. However, the specialized phenotypes HL and LH have a selective disadvantage because they may produce LL children with lower fitness if they mate. Therefore, with trade, selection will eventually produce a population consisting only of HH and HL or HH and LH phenotypes. These outcomes differ from the concept of comparative advantage in economics. The genetic analysis tells us that when there is trade, only those who have maximum productivity in at least one activity will be present in the equilibrium population. Trade may make an unproductive (LL) person better off in the short term, but over the long term their unproductive alleles will be eliminated – totally in the case of no trade and from at least one locus in the case of trade.[13]

A recent analysis of the dynamics of an economically relevant preference is by Collins and Richards (2013), who considered the evolution of fertility preferences after a fertility shock. They proposed that the genes associated with higher fertility will spread through the population after a negative fertility shock because individuals with high fertility have a fitness advantage. In fact, in most developed countries fertility has rebounded from the low rates that prevailed in the second half of the twentieth century. This recuperation in fertility is not due to the entry of immigrants whose fertility is higher than that of the local population: it is present in countries with few immigrants, such as Japan, and when immigrants are excluded from measurement (Goldstein *et al.*, 2009; Tromans *et al.*, 2009).

One area of analysis relevant to evolutionary dynamics is gene–culture coevolution (often called dual inheritance theory), as proposed by Campbell (1965) and Cavalli-Sforza and Feldman (1973). The domestication of cattle and other milk-producing livestock is often viewed as the classical example of gene–culture coevolution. The domestication of these livestock was closely tied to the development of lactose tolerance in populations that undertook this domestication, which in turn increased the incentives to maintain cattle (Simoons, 1969, 1970). However, it has been questioned whether it is appropriate to incorporate cultural change into an evolutionary or Darwinian framework (Claidière & André, 2011), with most of the gene–culture coevolution literature relying on ad hoc models with particular assumptions. El Mouden *et al.* (2014) proposed a formal framework for gene–culture coevolution that highlighted difficulties in considering culture in an evolutionary frame.

Heterogeneity of traits is often incorporated in gene–culture coevolution through the use of agent-based models, which analyse the evolution of preferences using evolutionary game theory. Gene–culture coevolution is typically path dependent, with much of the interest in the initial conditions that allow a trait to arise, in addition to the stability of the trait once it moves toward fixation in the population. For example, after examining the robustness and stability of the tit-for-tat strategy, Axelrod and Hamilton (1981) turned to its initial viability and examined how the strategy may have spread in the population. Seabright (2004) considered how traits that support cooperation and trust developed in small bands of foragers before the dawn of agriculture. He then investigates the development of the economic institutions that allow the interaction of thousands of strangers with these traits.

Spolaore and Wacziarg (2013) suggested that of three evolutionary mechanisms – biological (genetic and/or epigenetic), cultural, and gene–culture coevolution – recent research on nature versus nurture may make it meaningless to separate the first two. Yet, cultural transmission is a markedly different mechanism as it occurs horizontally as well as vertically and may occur between unrelated parties, such as through socialisation in groups. Whether the traits are transmitted genetically or culturally is important in understanding the dynamic process of development, and the policy implications that flow from the analysis are likely to vary with the nature of transmission.

What is considered genetic or cultural is subject to some ambiguity. Where the trait of interest is transmitted vertically from parent to child, the reason for the label of genetic or cultural transmission is often not provided or the author may adopt an equivocal stance as to the nature of the transmission. As an example, Brown *et al.* (1982) noted that their general model on the evolution of social behaviour by reciprocation

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[13] Ofek (2001) proposed that the evolution of the human brain was driven by trade.

could be interpreted to involve a number of vertical transmission mechanisms, including genetic, learning and cultural transmission. Galor and Moav (2002) labelled the preference for quality or quantity of children as genetic, although they note in a footnote that it may be cultural. Similarly, Clark (2007) noted that transmission of traits of the wealthy in pre-Industrial Revolution England may have been either genetic or cultural. Conversely, Fernandez and Fogli's (2009) analysis of transmission of labour force participation and fertility and Algan and Cahuc's (2010) examination of the inheritance of trust, while described as cultural, could equally have been discussed as having a genetic component.

However, examination of genetic transmission at the molecular level makes it possible to disentangle genetic and cultural pathways. For example, the gene–culture coevolution that occurred at the time of the domestication of milk-producing livestock left a genetic fingerprint in alleles that allowed the adult digestion of lactose. Much of the literature on gene–culture coevolution explicitly considers their interaction. Although many other economic traits are polygenic and likely subject to complex multi-gene and gene–environment interactions, there is some optimism that the relevant SNPs will be identified (Yang *et al.*, 2010; Davies *et al.*, 2011; Vinkhuyzen *et al.*, 2012).

One of the growing research opportunities in the area of evolutionary and economic dynamics may arise from the use of the time series data being developed by evolutionary anthropologists and economic historians. For example, the data collected by Clark and Hamilton (2006) (Clark, 2007) from their analysis of English parish wills could form the basis of a population genetic analysis of the evolution of the English population in the period leading up to the Industrial Revolution. Subsequent work by Clark *et al.* (2014) on social mobility using surnames also points to potential areas for evolutionary inquiry.

V The Genetic Foundations of Economic Development

The increasing availability of genomic data that allow comparison of gene frequencies across populations provides an opportunity to study differences in economic development. The research in this area is important in view of the persistence of technological and income differences across populations (Comin *et al.*, 2010; Putterman & Weil, 2010; Michalopoulos & Papaioannou, 2011; Easterly & Levine, 2012). To the extent that genetic factors cause these income differences, there is potential for genetic research to contribute to the understanding of economic development. To date, this research has focused on relative gene frequencies rather than directly inherited genetic traits, largely reflecting the nature of the data available for analysis at this time (see Section III).

Spolaore and Wacziarg (2009) examined the relationship between economic development and genetic distance, which is a measure of the time since two populations have had a common ancestor.[14] They used genetic data for 42 populations from Cavalli-Sforza *et al.* (1994) based on the ethnic composition of 137 countries. Spolaore and Wacziarg found that the logarithm of income was negatively correlated with average genetic distance from the United States population (the technological frontier). Genetic distance accounted for 39 per cent of the variation in income in the sample. They also calculated genetic distance between 9,316 pairs of countries in a world sample and 325 pairs in a European sample. Using these paired samples, genetic distance accounts for less variation in income than using genetic distance from the United States, although genetic distance remained significant. Similarly, Bai and Kung (2011) found that the relative genetic distance of the population of Chinese provinces from that of Taiwan was positively correlated with differences in income.

Spolaore and Wacziarg (2009) emphasised that their research does not necessarily imply that differences between populations at the molecular level affect income or productivity. The measure of genetic distance is based on 120 neutral alleles that are not considered to be under natural selection.[15] Instead, Spolaore and Wacziarg believed that genetic distance captures barriers to diffusion of technology and economic development. Societies that are more closely related are able to learn from each other more easily than societies that have diverged across many generations. From this perspective, genetic distance is

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[14] Spolaore and Wacziarg use F_{ST} genetic distance, which is the probability that an allele at a given locus selected at random from two populations will be different.

[15] Neutral alleles are used in population measures such as genetic distance so that selection of the alleles does not distort attempts to track evolutionary history (Cavalli-Sforza *et al.*, 1994).

a summary statistic that captures divergence 'in the whole set of implicit beliefs, customs, habits, biases, conventions, etc. that are transmitted across generations – biologically and/or culturally – with high persistence'. Desmet *et al.* (2011), who showed that genetic distance reflects similarity in answers to questions in the World Values Survey, interpret their results in the same way.

Spolaore and Wacziarg (2009) observed that the effect of genetic distance on economic development decreases from the year 1500 through to 1820, spikes around 1870, and then resumes the decline. This is in accordance with their interpretation of the effect of genetic distance being a barrier to diffusion of technology from the world's technological frontier. The spike in the effect of genetic distance reflects the sudden growth in technology in one part of the world during the nineteenth century, followed by a decline in income differences when technology spread. Spolaore and Wacziarg (2012) extended this analysis by examining the rate of technological take-up as it relates to genetic distance. As predicted, greater genetic distance was associated with slower adoption of technology in countries of greater genetic distance from the frontier.

Guiso *et al.* (2009) investigated the relationship between genetic distance and trust. In an analysis of factors affecting trust between European countries, they found that increasing genetic distance by 1 standard deviation reduces bilateral trust by 1.8 standard deviations. In contrast, Giuliano *et al.* (2014) found that the negative correlation between genetic distance and trade flows merely reflects the common effect of geography on the two countries. The relationship between genetic distance and income identified by Spolaore and Wacziarg (2009) was, however, robust to inclusion of controls for geography and transportation costs.

Ashraf and Galor (2013a) proposed a more direct genetic relationship in their hypothesis that genetic diversity affects economic development. Genetic diversity is a measure of diversity within a population, while genetic distance reflects diversity between populations.[16] Genetic diversity within populations is affected by what is known as the serial-founder effect. As humans moved out of Africa, genetic diversity was lost along the path of migration because individuals in founder populations carry only a subset of the genetic diversity of the parent population. Thus, diversity tends to decline moving from Africa to Europe to the Americas.

Ashraf and Galor (2013a) proposed that genetic diversity promotes economic development through the wider mix of traits that can advance and implement new technologies. They showed that genetic diversity is a significant predictor for scientific output, with a 1 per cent increase in diversity linked to an increase of 0.02 scientific articles per person per year. They also suggest that genetic diversity provides for faster adaptive change. For example, populations with more genetic diversity might be better able to respond to environmental changes. This reflects the argument put forward by Saint-Paul (2007).

Conversely, Ashraf and Galor (2013a) also noted that genetic diversity may impede economic development as it increases conflict within a society and generally reduces the level of social order. They proposed that this detrimental effect occurs because genetic diversity is associated with a lower average degree of relatedness between people, which kin selection theory predicts to affect cooperation (Hamilton, 1964a). In another paper, Ashraf and Galor (2013b) suggested that ethnolinguistic heterogeneity caused by genetic diversity can be another source of distrust.

Ashraf and Galor (2013a) tested these hypotheses with genetic data from the Human Genome Diversity Cell Line Panel (Cann *et al.*, 2002), which comprises 53 ethnic groups believed to be native to an area and relatively isolated from gene flow from other groups. Using population density as the measure of economic development for the period around the year 1500, they found a hump-shaped relationship between genetic diversity and development that reflects the countervailing influences of genetic diversity on economic development.[17] Ashraf and Galor also developed an index of predicted genetic diversity based on migratory distance for 145 countries. Using this measure of diversity also produced a hump-shaped relationship between diversity and economic development for the period around the year

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[16] Ashraf and Galor use expected heterozygosity as their measure of genetic diversity, which is the probability that two randomly selected people differ with respect to a given gene, averaged over the measured genes.

[17] For certain ranges of human genetic diversity, monotonically increasing or decreasing patterns would arise.

1500. Examining the mix of ethnicities in a country, Ashraf and Galor replicated this result for the year 2000.

However, more work is required on the biological foundations of the observed relationships before they are accepted as being more than suggestive correlations. For instance, it has not yet been established that humans possess the ability to detect differences in relatedness within populations at the level required. Further, measures of genetic distance and genetic diversity are typically based on non-protein coding regions of the genome that are not phenotypically expressed. One possibility is that these non-protein coding regions proxy phenotypically expressed genetic characteristics. It has also been found that other economically relevant traits have been under selection since humans migrated from Africa. For example, the dopamine receptor gene, *DRD4*, which affects financial risk taking in men (Dreber *et al.*, 2009), has had the allele associated with greater risk tolerance under strong positive selection since its emergence 30,000–50,000 years ago (Ding *et al.*, 2002; Matthews & Butler, 2011).

Spolaore and Wacziarg (2013) recently suggested that the mechanisms by which intergenerationally transmitted traits affect development could be divided into direct effects on economic performance on the one hand, and barriers to the spread of technological on the other hand. Galor and Moav (2002), Clark (2007) and Ashraf and Galor (2013a) considered direct effects, whereas Spolaore and Wacziarg (2009) examined barrier effects. Spolaore and Wacziarg suggested that it is harder to study direct effects on economic performance than barrier effects, as an economic event such as the Industrial Revolution is a unique and complex phenomenon. In contrast, the diffusion of technology has many opportunities for comparative study. However, a failure to study the direct effects may result in misidentification of barriers. Further, if the mechanism behind barrier effects is intergenerationally transmitted traits, analysis of both dimensions will likely be required to understand how the barrier effects operate and whether policy measures may assist in overcoming them.

Research into the genetic foundations of economic development will thrive when human genomes across times and populations become available. These genomic data will provide a time series in which selection on specific genes might be observed. With information on the function of those genes, it will be possible to hypothesise as to the selective pressures faced by humans and which traits might be more conducive to technological advance and economic development. When combined with genoeconomic research that indicates how the genes under selection affect economic preferences, we may be in a better position to identify the direct and barrier effects of genetically transmitted traits and preferences affecting economic development.

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