

Pre-print version of:

Serrelli E (2016). Evolutionary genetics and cultural traits in a ‘body of theory’ perspective. In Panebianco F, Serrelli E, eds. *Understanding cultural traits. A multidisciplinary perspective on cultural diversity*. Springer, Switzerland, Chapter 11. ISBN 978-3-319-24347-4

**DOI**

10.1007/978-3-319-24349-8\_11

**Print ISBN**

978-3-319-24347-4

**Online ISBN**

978-3-319-24349-8

## Chapter 11

# Evolutionary Genetics and Cultural Traits in a ‘Body of Theory’ Perspective

*Emanuele Serrelli*

The fact that methods of evolutionary genetics can deal with culture and cultural traits has recently become one argument to some hyper-enthusiastic claims that the social sciences could be unified by an evolutionary approach.<sup>1</sup> In this paper, while I try to explain how culture is indeed tractable by evolutionary genetics, I adopt a less pretentious attitude. The basis of this attitude are the well-defined accumulations of scientific knowledge I call *bodies of theory*, made of mathematical methods, mathematical models and painfully achieved knowledge about these models. Bodies of theory are deposited in the traditions of the sciences along with notions and achievements about particular topics. Bodies of theory, whose usefulness depends on generality, get expanded over time, and sometimes get modified to study new problems, new domains, where, in turn, they promote definite ways of constructing problems and understanding things. I treat evolutionary genetics as a body of theory that had inherited and radically transformed Darwin’s way of thinking of characters. The ‘body’ still includes long-lasting mathematical tools that were invented by statisticians and people such as Francis Galton in the nineteenth century, but the real boost was the mathematical theory of Mendelian populations elaborated since the late 1910s. In the 1970s, evolutionary genetics was pushed by some empirical problems towards incorporating learned – or “cultural” – behaviors into its mathematical models, generating a way of describing culture in terms of traits.

---

<sup>1</sup> **Connection:** Note that, in almost every discipline, evolution has nothing to do with the concept of progress. Refer to the introduction of Chapter 3 for a commentary and further links. The separation of evolution and progress is discussed at length, in Section 13.3, with particular reference to ‘cultural evolution’.

Before telling this story from the beginning, I introduce, with a minimum of technicalities, the encounter of evolutionary genetics with cultural transmission. In the end, I will argue for a humbler view of the relationship between evolutionary genetics and culture, and, accordingly, for a less demanding epistemology of cultural traits.

## 11.1 What would you Like for Breakfast? Cultural Transmission and Evolutionary Genetics

The following example aims to illustrate why, in the 1970s, a scientific discourse started to emerge that treated things like the lactase gene and things like Italian-style breakfast in a unified way, that is, as genetic and cultural traits. The discourse, scaffolded by mathematical modeling, updated the notion of ‘characters’ that was present in the tradition of biology since Darwin.

Food customs are one of the most celebrated kinds of cultural differences. Breakfast, for example, is highly variable across countries. Italians are known for their cult of coffee, cappuccino, and various combinations of coffee and milk. It is not rare that people from different ethnic, linguistic, or national groups praise or disapprove each other for the kind of food or cooking method. Fortunately, food is also a matter of curiosity and happy exchange and cultural hybridization. In sum, feeding customs are culture. But what if human organisms, more specifically adult people, were definitely partitioned into milk-digesting and non-milk-digesting people? And what if milk-digesting people were very unevenly distributed in different regions of the world? Could breakfast habits in different “cultures” be affected by people’s varying capacity to digest milk?

Young mammals synthesize an enzyme called *lactase* that hydrolyzes the main carbohydrate of milk, lactose, into glucose and galactose. In this way they process their diet which is essentially composed by milk. After the weaning, mammals usually reduce lactase production. In humans, instead, many individuals continue to express lactase throughout adult life, and are thus able to digest the lactose contained in fresh milk. This capacity – as reported in a recent survey, Gerbault et al. (2011) – is called LP, standing for lactose-persistence. LP is not ubiquitous in humans: it varies widely in human populations, both between and within continents (Figure 11.1). As Gerbault et al. explain, “in lactase non-persistent individuals, the fermentation by colonic bacteria and osmotic effects of undigested lactose often cause symptoms such as abdominal pain, bloating, flatulence and diarrhoea” (Gerbault et al. 2011: 864). The exact genetic basis of the LP trait is certainly more complex than a single gene, and is still not fully known.<sup>2</sup> In fact, it has been shown that some individuals who aren’t able to synthesize lactase can in fact consume lactose-containing products without any obvious ill effects, and changes in the composition of the gut flora – a non-genetic trait – may be as important as the active enzyme. Nonetheless, for simplicity, I will talk about the “lactase gene”. One of the amazing features of the evolutionary genetics

---

<sup>2</sup> In recent years, a number of single nucleotide polymorphisms (SNPs) have been found in association with the LP trait in different populations. The first to be identified, -13910\*T, is found not in the LCT gene (the lactase gene) but within an intron of a neighbouring gene, MCM6. This nucleotide change affects lactase promoter activity, and the allele explains only partly the distribution of LP (its frequency map does not completely overlap that of LP).

body of theory is just its relative independence from the genetic details of the considered trait, up to traits like lactose digestion that are not reducible to any genetic character.

**Figure 11.1. HERE.**

Can the lactase gene be an example of genes influencing the differential probability of assuming and keeping cultural habits? Lactose intolerants who are able to blame milk for their morning nausea, and who lack access to chemical remedies or lactose-free alternatives (e.g., soy milk), may be reluctant to adopt the breakfast pattern from their family or colleagues. Therefore, their genotype will influence the probability distribution of different cultural alternatives. On the other hand, there is the issue of social pressure towards having breakfast in a certain way. In Italy, going for coffee and pastry is a very important social activity, so it might turn out difficult to avoid milk. Furthermore, family habits may be highly important in conditioning individual behavior, making you feel like you would never start your day without a cup of fresh milk and your favorite butter biscuits from back when you were teen. Personal aversion and social pressure to milk consumption, with their respective strengths, will influence the probability distribution of consuming milk, and many factors will eventually settle individuals on a landscape of alternative behavior types. Settling on one alternative doesn't necessarily mean a life choice. Of course, it is possible for the individual to choose a definitive stand on the matter, and to drink always and only orange juice instead of cappuccino, but maybe the individual will choose from time to time whether to have latte or not, or she will switch from time to time to stable solutions that are adequate to the various periods of life. The probability distribution of different cultural alternatives aims to subsume and synthesize all those individual life solutions, making them comparable and allowing scientists (for instance, medical researchers) to make general considerations on breakfast behavior.

Population genetics – a field explained below – began to consider these issues as relevant when it was already a mature, 60-years-old field, thanks to the work of important innovators such as Marcus Feldman and Luca Cavalli-Sforza. Population genetics is a fundamental part of evolutionary biology. As the name says, it deals with questions about populations and their genetics: why does the lactase gene occur at particular frequencies across populations of the world? What populations' characteristics are relevant to this issue?

Population genetics considers a gene as something that spreads and remains in a population by means of reproduction through generations. More precisely, population genetics studies the fate of particular *forms* of genes, called *alleles*, with respect to alternative forms of the same genes. In the case we are considering, LP (lactose-persistence) is an allele, while its alternative is lactose intolerance. The expansion or decline of the LP allele in the population depends on how often and how luckily the allele ends up into the offspring. LP has been a lucky allele in some populations. If we analyze a particular population, say, Italians, and we find that LP is almost omnipresent (while less frequent in other populations), population genetics will guide us to some historical factors that may explain why. If lactose intolerance has been unlucky in Italy, for example, the reason might be that for millennia Italians had been farming and consuming milk as a primary element in their diet. In a milk-consuming population, the lactose intolerance allele is unlucky because it finds itself in individuals that, on average, are slightly sicker than the

population mean. Therefore, lactose intolerance gets transmitted less frequently due to health problems of its bearers. In technical terms, in a milk-consuming population, lactose intolerance has a lower *fitness* than LP. Population genetics calculates, for example, how long must a population sustain milk consumption in order to erase the influence of initial frequencies of milk tolerance and intolerance on the current amount of lactose tolerance; as time goes by, in fact, the influence of those initial frequencies will decay. Other dynamics such as rates of emigration and immigration may be very important, and are considered and quantified in population genetics.

In the 1970s, mathematicians such as Cavalli-Sforza and Feldman found out and understood that to explain or predict the frequency of an allele such as LP it is absolutely insufficient to characterize the population as milk-consuming or not. Rather, the individual bearer's behavior will be crucial to determine how lucky the gene is. If a lactose intolerant person is, on average, also milk-averse, then lactose intolerance will be pretty as much fit as milk tolerance: the allele will be lucky to end up in a person that, being intolerant, decides to refrain from consuming milk. In other words, while the fate of the allele still depends on how frequently the allele ends up in a combination rather than another, it is the gene-behavior combination that has a fitness. And, as we have seen in talking about breakfast, when you know whether a person has a certain gene, you still don't know what her behavior will be. Social and cultural pressures will play a role. In a milk consuming population, for example, for various reasons and through all kinds of particular cases that are not even visible at the population level, the social pressure towards drinking cappuccino for breakfast might be very low. This would allow for relative well-being of lactose intolerance: people will choose only with their bellyache. Cavalli-Sforza and Feldman demonstrated in this prototypic case that the strength of cultural transmission in a population is a crucial measure to establish sound relationships between genes (lactose persistence and intolerance), behavior (milk consumption), their frequencies and their change through time. They also demonstrated that social and cultural pressures are needed to explain the observed frequencies of LP.

We will get back to the issue of lactose absorption later, to show how powerful a body of mathematical theory can be in resolving historical scenarios. But first we are going to see how the body of theory of evolutionary genetics came about in the first place, to appreciate that the value of a body of theory lays not only in its modeling power, but also in the amount of work that has been necessary to build it and accrue knowledge around it.

## 11.2 The Historical Growth of a Body of Theory: Evolutionary Genetics

Charles Darwin's idea of a character was foundational to evolutionary biology. In Darwin's *Origin of Species* (1859), the character got early and tightly related to inheritance.<sup>3</sup> Darwin made the strong statement that "Any variation which is not inherited is unimportant for us" (ivi: 12), and wrote: "Perhaps the correct way of viewing the whole subject [of characters], would be, to look at the inheritance of every character whatever as the rule, and non-

---

<sup>3</sup> **Connection:** Darwin's thoughts, as expressed in his writings, are protagonist also of Sections 13.3, 16.2, 18.2, 20.3 and 20.4.

inheritance as the anomaly” (ivi: 13). Due to the “law” of natural selection, characters are so important that they become almost autonomous phenomena in the evolutionary process:

Although natural selection can act only through and for the good of each being, yet *characters and structures*, which we are apt to consider as of very trifling importance, *may thus be acted on*. When we see leaf-eating insects green, and bark-feeders mottled-grey; the alpine ptarmigan white in winter, the red-grouse the colour of heather, and the black-grouse that of peaty earth, we must believe that *these tints are of service to these birds and insects* in preserving them from danger (Darwin 1859: 84, emphasis added).

Natural selection ‘acts upon’ characters only in an utterly metaphorical way, but characters, inheritance, and natural selection, along with individual organisms, are inseparable faces of the same phenomenon. Color is a real thing: a certain shade of green *protects* a species of leaf-eating animals, and in this way *it* prevails on other shades of green and on other hues. A character in Darwin has the crucial features of being *inherited* and *variable*. We see also the foreshadow of the population genetics idea that a character has a *fitness*. Darwin wrote:

I can see no reason to doubt that an accidental deviation in the size and form of the body, or in the curvature and length of the proboscis, &c., far too slight to be appreciated by us, might profit a bee or other insect, so that an individual so characterised would be able to obtain its food more quickly, and so have a better chance of living and leaving descendants (Darwin 1859: 94).

We see here that Darwin had a more mechanistic view of fitness than the more probabilistic one that would emerge later. Yet, the idea that one of the crucial dimensions of a character in evolution is ‘inter-generational transmission’ was already clear. Work on inheritance and evolution was carried out after Darwin, way into the twentieth century, and resulted in the construction of a powerful mathematical, statistical body of theory that is still with us today, centered on a mathematical object called Mendelian population.

### 11.2.1 Galton

William Provine in his classic book *The Origins of Theoretical Population Genetics* (1971) tells the story of how the issue of inheritance was addressed after Darwin. The story begins with Francis Galton, who was not at all convinced of Darwin’s theory of inheritance, i.e. ‘pangenesis’ (1869). Galton, in trying to demonstrate his own theory of inheritance, invented *regression analysis*, a mathematical method that became perhaps the first tool in the evolutionary genetics body of theory. Galton’s methods are still used today (Hartl & Clark 2007), although interestingly disconnected by most of his ideas. For example, Galton’s saw his own methods as endorsing his anti-Darwinian idea of evolution ‘by jumps’; moreover, his hypothesis that “genius was a hereditary trait” (1869) fell squarely in the context of the foundation of human eugenics, an extremely controversial idea (and later, a practice) entangled with ideologies and tragedies in history.<sup>4</sup> Still, as Provine says, if some of Galton’s derivations and positions were questionable on empirical as well as on philosophical grounds, “he nevertheless opened the door to a

---

<sup>4</sup> **Connection:** see Chapter 4 for some more hints on eugenics.

statistical analysis of correlations of characters, an analysis which was to have immense influence upon evolutionary thought” (Provine 1971: 22-23).

Galton’s problem was to model the transgenerational dynamics of traits such as size in sweet peas, and stature, eye color, temper, artistic faculty, and disease in humans. These were ‘quantitative’, as opposed to discrete, traits. Stature is inheritable – tall parents generally have tall children – but is not copied identically from one parent, nor is it simply the parental mean. How are parents’ and offspring’s stature correlated? Galton measured that the stature of the adult offspring is, on the whole, “more mediocre” than the stature of their parents, that is to say, nearer to the general population’s median (Galton 1869: 95; cit. in Provine 1971: 20; see Figure 11.2). This phenomenon, valid for all continuous characters studied by Galton, is named *regression*, and implies, for example, that offspring of extreme individuals are quickly brought back towards the median of the population, more so the larger the parental deviance. For Galton this implied that natural selection acting on variation can “be of no permanent value for evolution, because there is a constant tendency in the offspring to ‘regress’ towards the parental type” (Galton 1869: 34; cit. in Provine 1971: 23). No cumulative change through selection was possible for Galton, who thought that new characters in evolution only emerge as as new complexes in equilibrium – called ‘sports’ – not subject to regression. “Types of intelligence”, for example, were explained in this way (Galton 1869).

**Figure 11.2. HERE.**

### **11.2.2 Statistics, Biometrics, and Mendelism**

Provine’s famous reconstruction proceeds, after Darwin and Galton, with the rediscovery of Mendel’s work in 1900, and with the consequent, all-British intellectual battle between so-called Mendelians and Biometricians, featuring scientists such as Karl Pearson, W.F.R. Weldon and William Bateson. The parties were linked by “the study of variation as the key to unresolved problems in evolution” (Provine 1971: 38). From several aspects of the story, one is tempted to frame the conflict as one between scientists who knew mathematics and others who didn’t know or value it. Whether this is the case or not, views and methods provided by biometricians were to survive, suitably incorporated into the later mathematized theory of evolutionary genetics.

Weldon, a prominent biometrician, wrote this telling aphorism: “It cannot be too strongly urged that the problem of animal evolution is essentially a statistical problem” (Weldon 1893: 329; cit. in Provine 1971: 31). And later, he wrote that “the questions raised by the Darwinian hypothesis are purely statistical, and the statistical method is the only one at present obvious by which that hypothesis can be experimentally checked” (Weldon 1895: 380-1, cit. in Provine 1971: 49). Weldon, working directly with Galton, developed Galton’s methods to address the amount of interrelation between characters *within* an individual, thus introducing the *correlation coefficient*, a fundamental feature of evolution. Weldon also had Pearson working on a problem of characters distribution in the shore crab. In such animal, all characters had normal distributions except one: the relative frontal breadth. With the *method of moments* for fitting a theoretical curve to observational data, Pearson uncovered dimorphism of frontal breadth, signaling the presence of two distinct races in the crab. The statistical methods used by Pearson and Weldon, although developed from Galton’s, countered his view of

evolution: they were particularly suited for the study of continuous variation and its evolution, whereas Galton had emphasized sports. According to Provine, for Pearson and Weldon Galton had “simply misinterpreted his own valid methods” (Provine 1971: 34). This story illustrates several epistemological peculiarities of mathematized science. For example, sometimes a law can get to be interpreted in a radically new way, while remaining mathematically the same. This happened in 1898, when Pearson corrected and revised Galton’s “law of ancestral heredity” (Galton 1897) quantifying the contribution of each past generation to the heritage of the current one. Pearson made the law consistent with Darwinian selection, and was even praised by Galton for doing that. These statisticians and statistically-inclined biologists like Weldon and Pearson were “Darwinists” as well as continuists, for their belief in the effectiveness of natural selection. Opposite positions were held and strongly defended by the Mendelian, William Bateson, who was convinced of Galton’s dichotomous view of variation, combined with the discrete nature of the characters studied by Mendel: although continuous variation was actually there, the major source of novelties in evolution had to be something else. For Bateson, the source of innovation was hybridization between distinct variants. Bateson provided biological arguments, and it is true that the issues brought out by this controversy have persisted under different forms and still are important in evolutionary biology. However, as Provine notices, “Bateson never became competent in mathematics – a sore point in his later controversy with the biometricians” (Provine 1971: 36). Mendelians worked under Mendel’s idea that characters depend on “factors” that are somehow transmitted from parents to offspring. A pea plant has white flowers because it carries a certain two-factors combination. Wilhelm Johannsen coined the distinction between phenotype (the type of flowers, e.g., “white”) and genotype (the particular combination of factors). Factors from the parents will “segregate” in the offspring and their recombinations will result in the observed variability among siblings. We see that by the time Mendel’s work on heredity was rediscovered by Hugo De Vries, Carl Correns and Erich von Tschermak, “the situation was already tense” (Provine 1971: 55). The theoretical dispute on whether evolution is continuous and driven by natural selection, or discontinuous and realized through sports or macro-mutations, surrounded the subsequent period of intense experimental researches on heredity.

As Provine says, “by 1918, primarily as a result of the analysis of successful selection experiments, many geneticists had realized that Mendelian heredity and Darwinian selection were complementary” (Provine 1971: 130) and that Mendelian characters, mostly very small and preserved throughout crossings, provided the variability for selection. While experimental data and findings piled up, along with interpretations thereof, mathematical methods were laid down into the toolbox that was taking shape and that was to become evolutionary genetics.<sup>5</sup> Udney Yule (1903) and Pearson (1904) had outlined mathematically the possibility already grasped by Mendel that if two or more pairs of factors are involved in a phenotypic character, the result might be an apparently continuous array of variations. Natural selection operating through continuous variation might thus provoke sorting of the involved

---

<sup>5</sup> Case studies surely played a role as well, as exemplars, in the toolbox, used by scientists through the epistemological strategy of abduction. But my focus here is on mathematical generalizations rather than on case studies.

alleles. Assuming random breeding populations, Yule, Godfrey Hardy and German Wilhelm Weinberg had independently studied the equilibrium frequencies, i.e. those frequencies that, once reached, are conserved due to the mechanism of segregation alone. In the U.S., H.S. Jennings and Raymond Pearl tried to derive formulas to calculate the genetic composition of a population. H.T.J. Norton and Howard C. Warren had quantified the effect of selection on a gene under different conditions. With the celebrated systematic work by Ronald Alymer Fisher, Sewall Wright, and J.B.S. Haldane, along with the progressive demonstration that Mendelian inheritance *could* account for observed correlations (parent-offspring, fraternal...) and for observed responses to artificial selection, we see the gradual emergence of a logical-mathematical object – the Mendelian space – to which all quantitative considerations would apply. Evolutionary genetics was born.

### 11.2.3 The Mendelian Combination Space

The Mendelian space is probably the most important object of evolutionary genetics.<sup>6</sup> It is a mathematical object. It is the space of all possible individual combinations given a number of loci with their correspondent sets of alleles. It is thus a combination space: an ordered collection of individuals, where each individual consists in a combination, i.e. an array of alleles, in the number of two for each genetic locus. Genetic loci are the same, in number and identity, all over the space: all individuals share the very same loci, but each individual is a unique combination of coupled alleles occupying each locus. Conversely, for every genetic locus a number of different alleles are available, and any combination of them is allowed in the space, including the homozygous combination (i.e., two copies of the same allele in a locus). At any time, only a number of individuals – conventionally designated with the letter  $N$  – are considered existent, and  $N$  is exceedingly small compared to the number of possible combinations in the space. These  $N$  individuals are one population at a particular moment, a subset of the Mendelian space. Individuals are sexually reproducing, and reproduction consists in the production of novel individual

---

<sup>6</sup> This statement is a simplification and is exposed to several criticisms. For example, it could be argued that the Mendelian space is central to only one tradition of population genetics. For Lewontin (1980), population genetics was actually split into two fundamental “research traditions”, each of which based on a “theoretical structure” or “scheme” with deep roots in the history we have told so far. Lewontin viewed the two traditions as dating back to, respectively, Sewall Wright and Ronald A. Fisher. In the latter – a continuation of “biometrical genetics” (see 11.2.2) – everything is dealt with in terms of phenotype, while genes “get lost in the shuffle”, (Lewontin 1980: 63). It was Fisher (1918) who showed compatibility – or even mathematical entailment – between the kind of continuous variation which is found in phenotypic traits and the distribution of discrete Mendelian genetic variation with a number of independent loci (Hartl & Clark 2007: 12). In this way, however, Fisher legitimated the two traditions in pursuing *autonomous* research strategies, each through equations that handled the continuity of variation and change in different ways. Today, one of the most used handbooks of evolutionary genetics, by Hartl and Clark (2007), avails Lewontin’s idea of the two traditions, and shows a flourishing development of the part Lewontin called Mendelian genetics (chps. 1-7). Only chapter 8 deals with “evolutionary quantitative genetics”. In this theoretical structure, the variance of a quantitative trait is partitioned into various components representing different causes of variation. Reminiscent of Galton’s work, quantitative genetics describes systematic relationships between traits, across parents and offspring or also within an organism. However, the most promising results come from *merging* the two theoretical traditions. For example, the response of a trait to selection is necessarily tied to genetic variation affecting the trait (ivi: 397). Therefore, while, e.g., heritability can be interpreted in purely statistical terms, with no genetic contents, “if we postulate that there are Mendelian genes underlying the phenotypes, then the genetic underpinning allows us to do more” (ivi: 403).



combinations in the space by random recombination between parents. Every new generation replaces the previous one, as generations are conventionally non-overlapping in the Mendelian space, but the composition of the new generation depends on the previous. How does a population of  $N$  individuals explore this space over generations? This became the central question – definitely, a non-trivial question – of the new evolutionary genetics body of theory.

The establishment of a research community and tradition around the Mendelian space allowed, on the one hand, for the accumulation of a large and precious knowledge base. Modifications to the space were introduced to reflect both advancements in computational tools and empirical discoveries (e.g., linkage disequilibrium, namely the non-complete independence of segregation between physically contiguous loci). On the other hand, one can safely say that the Mendelian space was now known in full, as all methods are partial and require several layers of theorization and statistical summarization. As Sewall Wright had noted already in 1932, a Mendelian space with a realistic number of loci contains a number of combinations that is greater than the number of protons in the universe. How can we know what happens in such an astronomically huge space?

For comparison, take an extremely simple abstract system described by Cavalli-Sforza and Feldman in a book we will encounter again (1981: 78-84). The system is composed by some agents, each of which can be in one of only two states  $H$  or  $h$ . The agents mate in couples. Each couple necessarily finds itself in either one of four states:  $HH$ ,  $hh$ ,  $Hh$ , or  $hH$ . The couples give rise to the new generation of agents. How does this system behave over few or many generations? Don't try to answer with your intuition: even with only two agent states,  $H$  and  $h$ , the system's dynamical behavior can vary very much according to different assumptions. The graph in Figure 11.3 shows how fast or slowly  $H$  may disappear (leaving room to  $h$ ), or otherwise conquer the whole population. We see that each trait has a *trajectory* in evolutionary genetics, which is the temporal dynamics of its frequency in the population, possibly in relation with the trajectories of other traits, and certainly in dependence from many features of the population. The graph gives a sense of how many things you should know (or assume) about the system to be able to predict its dynamics: the initial frequency of  $H$ , how often the alternative types of couples are formed, as well as each kind of couple's probability to have  $H$  or  $h$  offsprings. See the Figure's caption for some details. Deposited knowledge about this abstract system will thus include at least: (1) a whole list of *parameters* that are, or can be, relevant to the dynamics of systems of this kind (for example,  $p_0$ ,  $p_1$ ,  $p_2$ ,  $p_3$ , i.e. the respective probabilities of the different couple types to be formed at each generation;  $b_0$ ,  $b_1$ ,  $b_2$ ,  $b_3$ , explained in the Figure caption); (2) *ideas* on the effects of different configurations of the parameters onto the system dynamics, with relative weights for their importance (e.g., population size has great effect); and (3) *mathematical methods*, some numerical and some probabilistic, to statistically analyze what goes on in the system.

**Figure 11.3. HERE.**

We are starting to get a sense of how much knowledge is promoted and, at the same time, required by a single simple model. Let's add that evolutionary genetics has to derive, from studies of these simple-but-complex models, the dynamics across the hundreds or thousands of loci in a realistic population

exploring the Mendelian space. In light of this complexity, the body of theory accumulated around the Mendelian space acquires a huge importance: the body of theory is a fragile and complex ensemble, full of assumptions and theorems, but it is the unescapable way of accessing what happens in determinate kinds of systems.

History teaches that one good reason to be conservative and to go with familiar mathematical systems is that knowing the behavior of even simple mathematical systems, despite the fact that they are built by us, is so laborious that it requires the establishment of a community of people that improve upon each others' work for years and decades, developing a knowledge tradition.

### **11.3 The Application of Evolutionary Genetics to Culture**

Evolutionary genetics is a mathematical body of theory with a centennial history. In the 1970s, the body began to be modified to accommodate other transmission patterns than the Mendelian one. The occasion was provided by lactose absorption, which was playfully introduced earlier in this chapter, and by other empirical case studies.

#### **11.3.1 Cavalli-Sforza, Feldman, and Gene-Culture Coevolutionary Theory**

Luca Cavalli-Sforza and Marcus Feldman kicked off a collaborative stream of work in 1973, taking cue from a debate over the genetic basis of Intelligence Quotient (IQ). They built mathematical models of a new kind, where “the phenotype of a child is determined by the phenotypes of his parents *and* the child’s genotype” (ivi: 619). Studying the mathematical systems in which these two transmission mechanisms work together – ranging from one extreme, i.e., pure cultural transmission, to the other extreme, i.e., pure biological transmission – the authors performed one of the most typical services of a mathematical body of theory: they had spelled out all the relevant statistical measures that necessarily influence the outcome, presenting them as guides to empirical investigations of problems such as the IQ heritability. They concluded that “formalization of the contribution of cultural transmission to a trait *is possible*” (Cavalli-Sforza & Feldman 1973: 636, emphasis added). A dry and useful review of what happened thereafter is provided by Feldman and Laland (1996). A new branch of evolutionary genetics was born that, “in addition to modeling the differential transmission of genes from one generation to the next, incorporates cultural traits in the analysis” (Feldman & Laland 1996: 453), where cultural traits are those traits for which, in the mathematical model, a different transmission mechanism with a whole set of parameters is set up. Cultural alleles are like  $H$  and  $h$  in the model presented above (Figure 11.3): they do not combine in pairs because there is no genotype-phenotype distinction, and they get transmitted accordingly. With respect to purely Mendelian systems, systems with the addition of one “culturally transmitted” trait are more complicated. The possible combinations (sometimes called “phenogenotypes”) are at least doubled, and the transmission mechanisms intersect. Therefore, very different trajectories and stable equilibria are possible for the system. To predict the outcomes, a remarkable extension of the evolutionary genetics body of theory is required.

I like to describe this expansion as an application of the body of theory to a new domain.<sup>7</sup>

In the “body of theory” perspective presented here, cultural traits were added into the known mathematical systems because this was elicited by some situations the body of theory ran into, and was not prepared to. Lactose absorption was studied thanks to the addition of cultural traits in the models (Aoki 1983; Feldman & Cavalli-Sforza 1989). The formalization assumed three possible genotypes for the genetic trait (*AA*, *As*, and *aa*) and two possible states for the cultural trait: milk user and non-user. Despite the fact that the genetic bases of lactose absorption were even less clear than today (Gerbault et al. 2011), the studies were able to explore – variable by variable, parameter by parameter – the conditions under which the ‘absorption allele’ does spread or does not. From the lactose absorption frequencies actually observed in populations across the world, the models were built to work backwards, evaluating the conditions for those frequencies to come about. Another interesting domain of analysis was the spread of agriculture (Aoki 1987; Aoki et al. 1996), where the researchers set up mathematical models to aid determination of the demographic composition of the “expanding wave” of farmers in the Neolithic (around 12,000 years ago): how many of them were converted hunter-gatherers, and how many were descendants of farmers? In other words: was the spread of agriculture more a demographic expansion of farmers or more a conversion of hunter-gatherers to farming? Several other case studies are reviewed in Feldman and Laland (1996), and more were carried out later. As a consequence of all this work, the evolutionary genetics body of theory became adjusted to a whole set of new systems.

A key moment in the development of the “gene-culture” branch of the body of theory was Cavalli-Sforza and Feldman’s 1981 book, *Cultural transmission and evolution: a quantitative approach*.<sup>8</sup> The subject of the book is said to be “the dynamics of the changes within a population of the relative frequencies in the forms of a cultural trait” (ivi: 5). After a long and thoughtful Introduction that justifies the approach, the book presents an impressive and perhaps unsurpassed body of mathematical methods and results. The authors adapt techniques from all over population genetics and combine them to study problems in the framework of multiple transmission mechanisms. For example, they gather methods for both discrete and continuous characters. As Panebianco (*this volume*) demonstrates, Cavalli-Sforza and Feldman’s adapted framework would soon be noticed by modelers in economics, who would contribute and expand it with their mathematical skills. Within evolutionary genetics, the introduction of cultural transmission allowed, for example, for long-awaited new models of group selection for the origin of human cooperation. Explaining unselfish and altruistic behaviors without infringing natural selection once seemed to require group selection, i.e., selection of

---

<sup>7</sup> Many philosophers of science have reflected on this problem. I only cite one stimulating work by Ankeny and Leonelli (2011), who talk about the changing “representational scope” of a model. The representational scope is distinct from the “representational target”, i.e. the initial domain that inspired the construction of the model. The scope can stretch in unpredictable ways as science proceeds. If we take the Mendelian space as a model in the sense of a “stable target of explanation” (Keller 2002: 115), then culture will constitute an extension of its original representational scope.

<sup>8</sup> **Connection:** Several Chapters and Sections of this book rely on the way of thinking developed from Cavalli-Sforza and Feldman’s formal approach, often mediated by some informal and inspirational books written by Cavalli-Sforza. See 7.2, 7.3; 12.4; 13.3, 13.5; 15.1; 16.1, 16.2, 16.3; 18.1, 18.3.

traits because they are good for the group. But models based on genetic inheritance go against the efficacy of group selection. Robert Boyd and Peter Richerson (1982; 1985; 1989) became famous for building models with genetic *and* “conformist” cultural transmission, in which group selection became strong enough to explain the evolution of unselfish behaviors. By doing so, they also indicated a way for evolutionary theory to consider behavior as culturally transmitted, as opposed to genetically determined as in sociobiology (Wilson 1975).<sup>9</sup> Further mathematical innovations were linked to the work on cultural transmission. An example is *niche construction*, with its proposal of modifying the models of evolutionary genetics by adding selection feedbacks mediated by environmental impact: frequencies in a locus may influence the amount of a resource in the environment, affecting back genetic frequencies in other loci (Odling-Smee et al. 2003). Niche construction selective loops are particularly stimulating when they are applied to cultural traits that have a deep impact on the environment, such as farming (Kendal et al. 2011).

### 11.3.2 Tinkering and Justification

A half of the process of mutual adjustment between a body of theory and a new domain of application is thus the *mathematical tinkering* performed upon the body of theory to make it more suitable to the new domain. This tinkering will likely go through a phase of experimentation and low control, because new systems are born in the body and new knowledge needs to be built upon them. The evolutionary genetics body of theory is scientific wealth that can be invested in studying every situation that happens to turn out suitable to be modeled as a Mendelian population, or as a modified Mendelian population, or as a population of continuously varying individuals with an underlying Mendelian basis. But the application of a body of theory to a new domain is not automatically appropriate. It requires ad hoc definition of the domain. In gene-culture coevolutionary theory, as Feldman and Laland (1995) point out, “culture is treated as shared ideational phenomena (ideas, beliefs, values, knowledge) that are learned and socially transmitted between individuals” (Feldman & Laland 1995: 453, emphasis added). Treating “milk use” as a cultural trait may sound strange, but here comes the second half of the mutual adjustment between body of theory and domain: *justification*. A strong justification for the use of a body of theory is the identification of fundamental questions that will thereby have more chances to be answered. In the case of lactose persistence, the body of theory may be employed to collect data and eventually constrain the possible courses of population history, aiding historical reconstruction. Analogously, considering “farming” as a cultural trait allows for the body of theory to provide evidence for either one of two possible scenarios of the spread of agriculture (conversion of hunter-gatherers vs. demographic expansion of farmers).

Since Darwin, a candidate trait in evolutionary biology is anything of which multiple instances exist and get multiplied, and which is therefore able to be shared among an indefinite number of units. If I mean to treat “milk use” or “farming” as cultural traits, I need to make a case that this is not absurd according to what we know about culture.

---

<sup>9</sup> Boyd and Richerson’s gene-culture co-evolutionary theory was hailed as a welcome alternative to sociobiology. For an overview of criticisms to sociobiology, see Driscoll (2013).

Sometimes justification can be carried out by collecting existing studies where suitable definitions of the new domain may already be available. As seen in some essays of *this volume*, culture is a case in point. Culture scientists are not completely alien to the idea of “cultural traits”.<sup>10</sup> Philosophers and ‘evolutionary epistemologists’, *primum* Donald Campbell (1960), must be credited for early intuition and conceptual chopping, with their idea that cultural variants undergo processes of selection and drift that are analogous to, though distinct from, those that operate among organic forms and animal behaviors. Case studies from social psychology or archaeology are frequently brought to support the existence of cultural traits and their trajectories.<sup>11</sup>

Besides general justifications, there are context- and scale-sensitive justifications: while treating “milk use” as a transmitted trait might be meaningful *and* useful at the scale of population history – where it appropriately summarizes some aggregate behavior of the population – “milk use” might be an inconsistent unit at the scale of everyday life or over few generations.

### **11.3.3 The Balance between Tinkering and Justification in Cavalli-Sforza and Feldman, 1981**

According to the “body of theory” perspective presented here, evolutionary genetics is an extremely precious deposit of theoretical knowledge revolving around some mathematical systems, such as the Mendelian space. Researchers working on a body of theory are always, by essence, at work to modify the body. Often, they are inspired to do so and fueled by empirical findings and problems. Evolutionary genetics is certainly a case in point, with its constant dialogue with the variety of living beings, their reproductive systems and their ecological situations (Hartl & Clark 2007). At the same time, *any* situation where populations of combinations of traits can be identified is potentially liable to be treated by the body of theory’s mathematical methods and solutions about relevant parameters and predicted outcomes. History says *why*, since the 1970s, workers on the body of theory felt the need to *incorporate* cultural elements *into* the body of theory, yielding the creation of a specific branch named “gene-culture coevolutionary theory”. Subsequent developments exemplify that a body of theory, when applied to a new domain, must be fixed and adjusted, more than the other way around. Also, when evolutionary genetics started to deal with matters such as dietary habits, it certainly met with domains that had long been conceptualized by other approaches: culture studies, anthropology, philosophy etc. When a body of theory reaches a new domain, it has to be accepted therein, and this requires *justifications*. Some justifications may argue for the epistemic value of the body of theory. Other justifications may leverage on the presence of unanswered questions and unresolved competitions among scenarios in the domain: does the frequency of the lactose absorption allele reflect the farming history of a population? And how? Was the “wave of advance” of the spread of agriculture in the Neolithic made of expanding farmer families or converted hunter-gatherer groups? The tools from the body of theory can be proposed as solutions to long-standing debates and to open problems that cannot be

---

<sup>10</sup> **Connection:** See Chapters 2, 3 and 13, and several other Chapters, to look for familiarity of social sciences with notions that resemble ‘cultural traits’.

<sup>11</sup> **Connection:** In this book, see Chapter 7 for psychology, and Chapters 15, 16 and 17 for archaeology.

solved by other means. Another way to justification is the adoption of a working definition of the domain that makes it suitable for the application of the body of theory. If the working definition is a pre-existing definition, all the better. In any case, general definitions of the domain are hardly sufficient justifications: more specific ones are often required relative to the particular questions and scenarios at hand. For example, concepts of various social sciences that resemble “cultural traits” can contribute to justify the employment of the body of theory, but why can “milk consumption” be considered a cultural traits at a particular scale? The possibility of talking about cultural phenomena as “traits” is, in fact, context- and scale-sensitive.

A masterful model of theoretical justification is the long Introduction of Cavalli-Sforza and Feldman’s landmark book on evolution and cultural transmission (1981: 3-76), in which the authors work hard to define the domain and circumscribe it *so that* the body of theory will be acceptably applicable. Cavalli-Sforza and Feldman “accept as the cultural unit, or trait, *the result of any cultural action* (by transmission from other individuals) *that can be clearly observed or measured on a discontinuous or continuous scale*” (p. 73, emphasis in original). Traits can be aspects of “thought, speech, action [meaning behavior], and artifacts” (ivi: 10), and their general definition is the following:

We will use the term “cultural” to apply to traits that are learned by any process of nongenetic transmission, whether by imprinting, conditioning, observation, imitation, or as a result of direct teaching (Cavalli-Sforza and Feldman 1981: 7).

Among learned traits, the applicability of the models is further restricted to those which are *irreversibly* learned by individuals:

Cultural transmission – the acquisition by one individual of a trait from another individual – may involve long and complex learning processes. These processes may in practice be wholly or partially reversible. Our models deal with traits that do not change after the process of learning is complete. This can be accomplished by studying the population at the same age in every generation – an age at which all individuals are mature for the trait under study (Cavalli-Sforza and Feldman 1981: 62).

The fidelity of transmission is also important, further restricting the candidate traits to *customs*. A custom is “any behavioral trait that is transmitted with little individual variation [...] custom is always the absence of novelty, which is avoided because it is disruptive and costly” (ivi: 64-65).

Cavalli-Sforza and Feldman also proceed by showing general, perhaps unfamiliar properties of the domain that justify employing the body of theory. An example is the issue of randomness of innovation. Since genetic innovation is the periodic origin of new alleles by random mutation, defending the plausibility of the application of genetic models to culture implies a defense of the randomness of cultural innovation, which is counterintuitive: cultural innovation is evidently intentional to an important extent. Here Cavalli-Sforza and Feldman appeal not only to the frequency of literally chance cultural innovations, but also to the limited foresight of intentional ones:

the chance that the innovations will prove truly adaptive in the long run is not 100% [...]. Because of this, and because some cultural mutation is simply copy error, a significant proportion of new cultural mutations might be truly random without any resemblance of adaptiveness (ivi: 66).

Another issue in the application of the body of theory to culture is that of conceptualizing free choice in the domain. Individuals cannot choose what genes they inherit, but they can make cultural choices. Here Cavalli-Sforza and Feldman introduce the fundamental concept of *cultural fitness*, already recognized by Campbell. In the body of theory, a cultural trait has a cultural fitness that measures its probability of acceptance, that is the *probability* for each individual to *choose* to get the trait. Only with 100% probability of acceptance it might be said that individuals have no choice. With lower probability, each individual does choose, while the overall system remains predictable in a statistical sense.<sup>12</sup> What is lacking, as admitted by the authors, is *variation* of acceptance probability across individuals: “as a first conceptual approximation we prefer to think of cases in which it is relatively constant across individuals” (p. 15). Individual differences of yet another kind – learning abilities – were deferred to another whole book which apparently was never written:

Another volume will take account of individual, inherited differences in learning abilities. The introduction of individual differences, for instance in capacity to learn, requires a quantification of some classical genetic concepts, such as “norm of reaction”, and allows us to make predictions about that elusive entity, genotype-environment covariance (ivi: vii).

Many other considerations are made in the Introduction and in the Epilogue of Cavalli-Sforza and Feldman’s book. We may say that other justificatory works that would follow in the subsequent years would retrace its encompassing blueprint.<sup>13</sup> On the other hand, justification was not at all the main part of Cavalli-Sforza and Feldman’s book. The authors, firmly centered into the body of theory, pointed out the modifications that were needed and the constraints that were in place therein. A fundamental idea to translate into the body of theory was that cultural traits undergo not only “vertical” transmission, i.e., parents to offspring, which is typical of genetic traits, but also “horizontal” and “oblique” transmission, involving peers and all people beyond genealogical bonds. Further distinctions produced 11 distinct modes of transmission (Cavalli-Sforza and Feldman 1981: 55-60). The internal structure of “nongenetic” transmission mechanisms was crucial, not as much to justify the use of mathematical models as to figure out how to build them. There were 260+ pages of mathematical studies (ivi: 77-339), divided into “Vertical Transmission”, “Oblique and Horizontal Transmission”, “Multiple State Traits” (i.e., traits with more than two alternatives available in the population), and “Cultural Transmission for a Continuous Trait”, with results that showed how, for example, sometimes “cultural transmission can simulate genetic transmission, making it difficult to separate them in careful analysis” (ivi: 9), or that vertical transmission is “more important than anticipated” (ivi: 76). Cavalli-Sforza and Feldman remarked the importance of matching the right level of analysis to the right mathematical method (ivi: 71), while maintaining tractability (ivi: 73). Different parts of the body of theory were dragged into play – for example, discrete traits vs. continuous traits – according to appropriateness and tractability.

---

<sup>12</sup> **Connection:** This concept of choice is fundamental to models in economics, the “science of choice”, as explained in Chapter 12.

<sup>13</sup> In fact, many major works mostly retrace Cavalli-Sforza and Feldman’s (1981) Introduction, and pile up more and more examples from the social sciences on the same blueprint.

Cavalli-Sforza and Feldman are the best example of the complex, bi-directional epistemological dynamics of dialogue between tradition and innovation, linking older and more recent literature in evolutionary genetics. This dynamics, according to the “body of theory” perspective presented here, is the right context in which to understand the mathematical studies of evolutionary genetics applied to culture.

## 11.4 Conclusion: Minding the Balance and Recalling the Body of Theory

The mutual adjustment process between a body of theory and a new domain is twofold: there is *mathematical tinkering* upon the body of theory to make it more suitable to the new domain, and there is *justification*, explaining why and to what extent the body of theory can be useful in the new domain. We have seen the balance between mathematical innovation and verbal justification in the seminal book by Cavalli-Sforza and Feldman (1981). There, justification consists in refining an acceptable definition of culture *so that* the body of theory is applicable. At the same time, justification highlights *those features* that must be taken into account for the production of new mathematical studies, and draws the *boundaries* of the sub-domain where the mathematics can be of any help.

The relative proportion between mathematical tinkering and justification may be a criterion to look at current “cultural evolution” works, too.<sup>14</sup> In some works, we may find significant imbalance in favor of justification. These works miss the challenge of modifying the body of theory to make it suitable to answer an open, pressing research question, and they just reiterate arguments for using evolutionary genetics to analyze culture. I am not claiming that mathematical innovation is necessary *per se* in each and every “cultural evolution” work, but, with mathematical tinkering, there goes awareness of the existence and nature of the mathematical body of theory, its growth and dialogue with domains. In fact, where justification is abundant and elaboration lacks, justification has an utterly new rhetoric role with respect to the function it played in Cavalli-Sforza and Feldman: it delivers a very different idea of theory, namely the idea of a theory as the faithful and exhaustive description of a domain. In fact, tools of biology are advocated as *the* right ones, and culture is presented as *having* “key Darwinian properties”; a certain definition of culture is justified, reiterated and enriched by more and more examples, *against* other ways of understanding culture that are presented as inexact and less productive (e.g., Mesoudi et al. 2006). There is a radical difference between justifying the applicability of a body of theory as a possible tool to answer open questions, and defending some “new theory of culture”. The “body of theory” perspective can be a way to describe the relationship between evolutionary genetics and culture that more properly understands

---

<sup>14</sup> I am referring here to books and papers such as Boyd & Richerson (1985), Richerson & Boyd (2005), Mesoudi (2007, 2011), Mesoudi et al. (2004, 2006). A flourishing literature in philosophy of biology builds arguments or “dual inheritance theories” to hit forms of sociobiology and evolutionary psychology that don’t take cultural transmission into sufficient account. A careful analysis is well beyond the scope of this chapter. Here, in light of the “body of theory” perspective, I just offer one possible criterion for analyzing these texts: the criterion of the proportion between justification and mathematical innovation.



the epistemological mechanism at work, and brings evolutionary genetics into healthier dialogue with other ways of studying culture.

## References

- Ankeny, R., & Leonelli, S. (2011). What's so special about model organisms? *Studies in History and Philosophy of Science Part A*, 42, 313-23.
- Aoki, K. (1986). A stochastic model of gene-culture coevolution suggested by the 'culture historical hypothesis' for the evolution of adult lactose absorption in humans. *Proceedings of the National Academy of Sciences U.S.A.*, 83, 2929-2933.
- Aoki, K. (1987). Gene-culture waves of advance. *Journal of Mathematical Biology*, 25, 453-464.
- Aoki, K., Shida, M., & Shigesada, N. (1996). Travelling wave solutions for the spread of farmers into a region occupied by hunter-gatherers. *Theoretical Population Biology*, 50(1), 1-17.
- Boyd, R., & Richerson, P.J. (1982). Cultural transmission and the evolution of cooperative behavior. *Human Ecology*, 10, 325-351.
- Boyd, R., & Richerson, P.J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- Boyd, R., & Richerson, P.J. (1989). The evolution of indirect reciprocity. *Social Networks*, 11, 213-236.
- Campbell, D.T. (1960). Blind variation and selective retention in creative thought as in other knowledge processes. *Psychological Review*, 67(6), 380-400.
- Cavalli-Sforza, L.L., & Feldman, M.W. (1973). Cultural versus biological inheritance: phenotypic transmission from parent to children (a theory of the effect of parental phenotypes on children's phenotype), *American Journal of Human Genetics*, 25, 618-637.
- Cavalli-Sforza, L.L., & Feldman, M.W. (1981). *Cultural transmission and evolution: a quantitative approach*. Princeton, NJ: Princeton University Press.
- Darwin, C.R. (1859). *On the origin of species*. 1st ed. London: John Murray.
- Driscoll, C. (2013). Sociobiology. In: E.N. Zalta (Ed.), *The Stanford Encyclopedia of Philosophy*. Winter 2013 Edition. Available at: <<http://plato.stanford.edu/archives/win2013/entries/sociobiology/>>.
- Feldman, M.W., & Cavalli-Sforza, L.L. (1989). On the theory of evolution under genetic and cultural transmission with application to the lactose absorption problem. In M.W. Feldman (Ed.), *Mathematical evolutionary theory* (pp. 145-173). Princeton, NJ: Princeton University Press.
- Feldman, M.W., & Laland, K.N. (1996). Gene-culture coevolutionary theory. *Trends in Ecology and Evolution*, 11(11), 453-457.
- Fisher, R.A. (1918). The correlation between relatives on the supposition of Mendelian inheritance. *Transactions of the Royal Society of Edinburgh*, 52, 399-433.
- Galton, F. (1869). *Hereditary genius*. New York: Meridian Books.
- Galton, F. (1889). *Natural inheritance*. London: MacMillan.
- Galton, F. (1897). The average contribution of each several ancestor to the total heritage of the offspring. *Proceedings of the Royal Society*, 61, 401-413.
- Gerbault, P., et al. (2011). Evolution of lactase persistence: an example of human niche construction. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 366(1566), 863-877.
- Hartl, D.L., & Clark, A.G. (2007). *Principles of population genetics*, Fourth ed. Sunderland, Mass.: Sinauer Associates.
- Keller, E.F. (2002). *Making sense of life: explaining biological development with models, metaphors, and machines*. Cambridge-London: Harvard University Press.

- Kendal, J.R., Tehrani, J.J., & Odling-Smee, J. (Eds.) (2011). Theme issue 'Human niche construction'. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 366(1566).
- Lewontin, R.C. (1980). Theoretical population genetics in the evolutionary synthesis. In E. Mayr, W.B. Provine (Eds.), *The Evolutionary Synthesis* (pp. 58-68). Cambridge & London: Harvard University Press.
- Mayr, E. (1980). Prologue: some thoughts on the history of the evolutionary synthesis. In E. Mayr, W.B. Provine (Eds.), *The Evolutionary Synthesis* (pp. 1-48). Cambridge & London: Harvard University Press.
- Mesoudi, A. (2007). A Darwinian theory of cultural evolution can promote an evolutionary synthesis for the social sciences. *Biological Theory*, 2(3), 263-275.
- Mesoudi, A. (2011). *Cultural evolution: how darwinian theory can explain human culture and synthesize the social sciences*. Chicago: University Of Chicago Press.
- Mesoudi, A., Whiten, A., & Laland, K.N. (2004). Is human cultural evolution Darwinian? Evidence reviewed from the perspective of the Origin of Species. *Evolution*, 58(1): 1-11.
- Mesoudi, A., Whiten, A., & Laland, K.N. (2006). Towards a unified science of cultural evolution. *Behavioral and Brain Sciences*, 29(4), 329-347; discussion 347-383.
- Odling-Smee, F.J., Laland, K.N., & Feldman, M.W. (2003). *Niche Construction: the neglected process in evolution*. Monographs in Population Biology 37. Princeton, NJ: Princeton University Press.
- Pearson, K. (1904). On a generalized theory of alternative inheritance, with special reference to Mendel's laws. *Philosophical Transactions of the Royal Society, A*, 203, 53-86.
- Provine, W.B. (1971). *The origins of theoretical population genetics*. Chicago & London: University of Chicago Press.
- Richerson, P.J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.
- Sarkar, S. (2004). Evolutionary theory in the 1920s: the nature of the "synthesis." *Philosophy of Science*, 71(5), 1215-1226.
- Weldon, W.F.R. (1893). On certain correlated variations in *Carcinus moenas*. *Proceedings of the Royal Society*, 54, 318-329.
- Weldon, W.F.R. (1895). Attempt to measure the death-rate due to the selective destruction of *Carcinus moenas* with respect to a particular dimension. *Proceedings of the Royal Society*, 58, 360-379.
- Wilson, E.O. (1975). *Sociobiology*, Cambridge, MA: Belknap/Harvard University Press.
- Yule, G.U. (1903). Professor Johannsen's experiments in heredity. *New Phytologist*, 2, 235-242.

## Concluding Remarks

# Removing Barriers in Scientific Research: Concepts, Synthesis and Catalysis

*Emanuele Serrelli*

So what? At the end of a book on 'cultural traits' which includes 20 contributions from the most diverse disciplines, from cultural anthropology to archaeology, from psychology to history of science, from economics to musicology, from philosophy to linguistics and evolutionary genetics... what have we learned about cultural traits? Well, much. But perhaps many readers will feel unsatisfied by an incomplete vast interdisciplinary venture without some sort of synthetic conceptual framework, some new understanding of cultural traits, or at least some good taxonomy of what is meant by a cultural trait, or minimally a list of conceptual problems. I will devote a few lines here to an analysis of 'cultural traits' as a putative scientific category emerging from our collection. But I need to make clear in advance that a precise conceptual synthesis is not here. We have been as thoughtful as we could, and we have tried to follow all the connections, but there is no such thing as a 'magic paragraph' able to capture such interconnectedness. Indeed, this concluding note is actually a critical comment against what I and Panebianco see as a *hurry to close* the discourse in a given logical scheme.

In Chapter 1, we summarized in our words the contents of all Chapters, with particular focus on what the authors mean by cultural trait, and on some conceptual problems that, however, are much better explained in the Chapters themselves. We provided three ways of navigating the book: spontaneous interdisciplinary links, guided Connections that help the reader 'jump' between different points to deepen concepts and issues, and the criteria we embedded in the Chapters sequence. Let us review these latter criteria. A first 'block' of Chapters presents two takes in cultural anthropology on cultural traits: the first inviting generalizing attempts, the second showing the reasons for locality. Then two essays show how societies and nations educate their people, explicitly and implicitly, *to* their own typical cultural traits and *by means of* cultural traits (typical institutions and objects). Two contributions address the psychology of the trait, emphasizing its nature of 'evocator' of something deeper or larger. Two Chapters show the importance of geographical meeting points and melting pots, and a third Chapter problematizes the ideas of trait, of culture, of geographical map, and of maps and diagrams in general, exposing our obstinate hunt for 'origins'. Two authors demonstrate the importance of mathematical models, the plurality of modeling strategies, and the influence of modeling strategies on ways of thinking, and two more essays show how these ways of thinking can be applied to understand concrete situations of cultural contact, between countries and between generations. Three contributions, revolving around archaeology and material culture, show how lineages of artifacts can be

traced, and what mechanisms govern their change. Another essay introduces the important repository and historical record of cultural traits: language. Three more Chapters formulate theories of 'why' traits such as visual art, aesthetic preferences, and the passion for literature exist in the first place, being, in the second place, domains of circulation of cultural traits such as styles, preferences, genres.

'Synthesis', 'integration', 'unification' and similar phenomena have long gained important place in philosophy of science. Philosophers actively seek examples of interdisciplinary and inter-field 'coordination', and ask: how do different areas of science combine or integrate their divergent methods and conceptual resources? What are the limits and facilitating conditions? There was a time when philosophers reasoned in terms of "theory reduction", using conceptual analysis to identify *the* most fundamental theory other theories would get *reduced to*. Now philosophers talk about theories pluralism and mechanisms heterogeneity (Mitchell 2003, Craver 2009). Yet, they typically continue to see conceptual analysis as the main tool and clarification as the ultimate goal. Their urge for conceptual grip can, I claim, divert their attention away from their own goal, and perhaps from the meaning of the experiences they are studying.

In 2010, philosophers Brigandt and Love (2010) urged philosophers to study "integration in action" in order to understand the nature and dynamics of interdisciplinarity. To set a good example, they organized a meeting of 20 experts in different fields of biology to work on the non-trivial concept of 'evolutionary novelty', with the perspective of a time-extended research on the same topic. In biology, 'evolutionary novelty' is an elusive concept just like 'cultural trait': it is a 'false friend', full of conceptual pitfalls. It means different things to different specialists (geneticists, morphologists, phylogeneticists etc.), and nothing to many others. How do you delimit a novelty? Is a new gene a novelty, even though it makes its carrier organism only slightly different? Sometimes an unchanged gene in a new context can be much more innovative than a new gene in a familiar context. Are birds' wings innovative even though they are just modified limbs? Probably they are, but exactly at what degree of modification do they become a novelty? 'Evolutionary novelty' can be a framework for interesting questions, or a source of confusions and dead ends. During the 2010 meeting, definitions were elicited, and participants were stumbling and striving for "single, unambiguous" definitions, under the assumption that conceptual clarification would have brought about some kind of "coordination" among them and their fields. Brigandt and Love's brief account illustrates their firm focus on concepts: philosophers hunt for conceptual clarification as a priority, as a primary and ultimate goal, loaded with bright scientific expectations. The 'evolutionary novelty' concept was considered interesting *just in it being* the focal point of opposite conceptual tensions, that were expected to be solved in some way. The concept was thus both the assembling criterion of a 20-people research group *and* the transactional object in the group. To the philosopher's eye, concepts are the domain-delimiting factor, and, within the domain, they are the positive or negative measure of coordination. But this unconditional confidence in concepts is insensitive to evidence that concepts are often *followers* in scientific community processes. For example, they are subject to fashion and to economic pressures: Brigandt and Love themselves cite workshop participants reporting that they used to mention 'evolutionary innovation' just as "a rhetorical device in the process of grant writing", despite their

conviction of its biological unimportance. Scientists use concepts they don't find useful in order to set up a research project and get some funds, and later they are forced to maintain that same troublesome word, incoherent with their research assumptions – a “semantic curse”. Concepts are also cruxes of identity fights, so that putting conceptual convergence as a goal may be exactly the move that shuts up the dialogue (see the Mesoudi et al. vs. Ingold case in Chapter 1). In sum, my impression is that concepts are often a way to close rather than a way to open a discourse. The philosophers' insistence on concepts can eventually do harm or be just tangential to the directions of science.

In search for insights about ‘synthesis’ in science, I recently visited the U.S. National Evolutionary Synthesis Center (NESCent) in Durham, North Carolina.<sup>15</sup> I will say something on the more general ideas, and then describe NESCent *catalysis meetings*. In fact, if our book cannot absolutely be compared to a working group or a synthesis project, it may bear some similarities to NESCent catalysis meetings.

At NESCent, synthesis is not at all considered a conceptual phenomenon in the first place. Synthesis is, first of all, the combination of *data* collected by many people working in different ways, fields, approaches, regions of the world, in order to answer new, bigger, and pressing research questions. Genomes can be an easy example. Whole genome sequences that are periodically announced in the news – the human genome, the platyus genome, the carrot genome – are assembled by dozens of labs in the world. Genome data can then be combined, for example, with medical data which are collected in a completely different – but systematic – way. Further on, these syntheses can be compared cross-species, and so on. As for cultural data, an example can be seen in the combination of linguistic, cultural, geographic world databases like those we cited in Chapter 1. Now, for synthesis to happen, researchers have to be willing to share and to combine their data, seeing the advantage of doing that, and they need to know how to gather, store, and share data for them to be useful to others. In other words, they need to have a certain ‘culture of data’ (notice the importance of databases and informatics). To do all this, researchers *may* need common concepts, but concepts are secondary and instrumental to answer their communal, new, pressing research questions.

In 2009, NESCent published a paper formalizing the ‘synthesis’ idea (Sidlauskas et al. 2009). Question-driven data synthesis is the fundamental idea, but there are actually four modes of synthesis, depending on the kind of elements getting combined. Multiple modes can coexist in any particular synthetic study. As the genomes example shows, synthesis does not coincide with interdisciplinarity:<sup>16</sup> intra-disciplinary syntheses, which are surprisingly rare and most needed, combine elements from multiple studies. There are also barriers to synthesis, and ways to overcome them.

The first mode of synthesis, *Data aggregation*, “reinterprets raw data underlying prior investigations to answer questions at new and typically larger scales” (Sidlauskas et al. 2009: 873). While this may look simple, in fact

---

<sup>15</sup> The National Evolutionary Synthesis Center (NESCent) is an American NSF-funded collaborative research center operated by Duke University, the University of North Carolina at Chapel Hill, and North Carolina State University (see Cunningham 2005, Sidlauskas et al. 2009, Rodrigo et al. 2013).

<sup>16</sup> Interdisciplinary syntheses exist, and they may eventually “erode disciplinary boundaries or create new fields of study”.

“the vast majority of data supporting previous studies are unavailable, often because the data are lost or preserved in inaccessible forms” (ivi: 876). The second mode, *Reuse of results*, focuses, indeed, on results of other studies used as data in a new context. But results, too, are scarcely available in standardized and compatible forms. These two first modes of synthesis both undergo publication problems, since “many mainstream journals emphasize primary data collection over synthesis” (ivi: 875), and publication of results over publication of datasets (in spite of the fact that datasets demand a remarkable number and degree of technical skills). For Sidlauskas et al., to promote data aggregation and reuse of results

solutions are reasonably straightforward. Journal editors should encourage the publication of synthetic datasets and analyses and should make an effort to invite objective reviews from scientists who are also engaged in synthesis.

The third mode of synthesis, *Methodological integration*, “links two or more methods to create a new analytical pathway” (Sidlauskas et al. 2009: 873). Finally, *Conceptual synthesis* does not resume elements from previous studies, rather “bridges the theories or paradigms of thoughts that underlie and motivate prior studies” (ivi: 873).

Obstacles to synthetic research lie, for Sidlauskas et al., in training, job search and tenure evaluation, grant review, publication policies, and language barriers. Not only should there be a more interdisciplinary early training, but it should “become easier for scientists to develop skills in aggregating and reusing information at every career stage” (ivi: 874). Synthesis training will address not only specific skills such as software programming, but also basic skills: “information literacy (the ability to locate relevant information and assemble a knowledge base), statistical literacy (understanding how statistical manipulation affects data and inference), and data literacy (the skills required to manipulate and present data)” (Sidlauskas et al. 2009: 874).

The current lack of training reverberates upwards to the level of panels who evaluate grant proposals, where a few “synthetically minded scientists”, if any, are present. Notice how the “synthetic scientist” is presented as a specific profile, corroborated by published official guidelines<sup>17</sup> that still lack incorporation into the hiring criteria of research institutions. But many points made by Sidlauskas et al. concern another, very important issue: that synthesis can never ever be an exclusive concern of synthetic scientists. On the contrary, for synthesis to happen, *all* the scientific community must be involved in it. Journals and funding agencies have their part to do, by requiring “all data to be shared at the time of publication”. Data repositories and their hosting organizations should standardize formats, develop vocabularies, and establish minimal reusability requirements. Software developers should ensure the longevity of softwares (for example, by using software repositories) because, even when data endure, analyses cannot be repeated if tools are not stable. In fact, “technology can also hinder synthesis if a proliferation of methods, data standards, languages, and protocols hampers communication and interoperability”. While synthetic scientists, experts and managers work at all these levels, at the same time “a culture of data sharing” has to prevail, along with a different culture of “science as a collective, rather

---

<sup>17</sup> Also in consideration of these documents and official declarations, Sidlauskas et al. are however optimistic that a new cultural shift is leading synthetic science to receive more support than ever (Sidlauskas et al. 2009: 874).

than individual enterprise”. Only in this way the deposition of data can become “a normal part of the research flow”, and all other necessary changes can happen. For synthesis to happen, scientific communities must “embrace a culture in which sharing is normative, methods exist to be combined, and the potential longevity and utility of data exceeds the life span of the scientists that create it” (Sidlauskas et al. 2009: 877).

Synthesis – the purposeful and innovative combination of existing data – requires specific ‘working groups’ and meetings among scientists who concretely develop the common project. But, in the cultural context just described, the ground needs to be prepared for synthesis. In fact, sometimes synthesis cannot even begin because suitable data haven’t been collected at all, or haven’t been treated in systematic ways conducive to synthesis. This lack of preparation may affect particular *questions*:

...assembling existing data is not enough. For many questions, it is too early to attempt a grand synthesis, and in many cases the data has not been collected in the coordinated manner needed for a grand synthesis. A mechanism is needed for networks of scientists to form among scientists in very different disciplines to coordinate their primary research efforts (NESCent 2004: 5).

Pre-synthetic activities are those activities that potentially *shape* the involved people’s *data collection* activities and data sharing practices, by influencing their culture of data. Here come catalysis meetings, which, as I put forth above, can be seen as a model for our cultural traits book.

In chemistry, catalysis is the increase in the rate of a chemical reaction of one or more reactants due to the participation of an additional substance called a catalyst. Importantly, the presence of the catalyst lowers the energy that is required to reach the transition state of the reaction. A foundational document of NESCent explains that catalysis meetings “bring together diverse groups of scientists on a wide range of subjects, not only to inspire cross-disciplinary collaboration, but to inspire the large scale of scientific vision that can only come from cooperation and coordination” (NESCent 2004: 2). Several themes are recognizable in this statement. One theme is a *culture of data*, which is enclosed in the broader theme of the *large scale scientific vision*. Another theme is the *generation of scientific collaborations*. Catalysis meetings are expected to trigger “large cooperative ventures necessary to collect *primary data* in the coordinated fashion necessary to synthesis” (NESCent 2004: 1, emphasis added). Catalysis meetings are also specifically organized to attract and engage *fields* that, for example, are distant from informatics tools and related data-collection methods. As Joel Kingsolver, one of the original leaders of NESCent, told me:

we realized that there are several important fields, areas, questions where you are not quite at that stage yet. You know there is something interesting to synthesize, but you are not sure of what it is, or what different data or tools are available, what actual focused research questions can be addressed (Kingsolver 2014).

Catalysis meetings are also *generators of scientific collaborations*. I remark this role because I think it is fair to maintain scientific collaboration distinct from the construction of common data flows. The two phenomena don’t seem to be completely overlapping, although tightly related. Indeed, according to my reconstruction, catalysis meetings at NESCent were never thought as just functional to motivating people to become able to use informatic tools and to start using them. Many other kinds of scientific collaboration are possible.

Catalysis meetings are also seen as a factor to change the scope and vision of primary research. The NESCent foundational document (2004) remarks that members of a pilot project, “By dramatically increasing the scale of their scientific vision to encompass the historical ecology of an entire biota [...] quickly realized that this vision offered them a chance to make rapid progress on their own scientific agendas as well as advancing their scientific careers” (NESCent 2004: 2). Along this line, catalysis meetings were aimed at this dramatic increase of “ambition, scale and vision of *primary* research” (ivi: 6, emphasis added), even before or in absence of direct collaboration.

In sum, being in a catalysis meeting can lead to synthesis, but also to other kinds of scientific collaborations, or even “only” to a widening of scientific vision in one’s own everyday research. Catalysis meetings allow heterogeneous disciplinarians to learn each other’s languages, to see if they are talking about the same things, to understand what their data are, and theoretical frameworks are, and to ask *whether* they can identify some clear questions and a research setting. If not, they will be anyhow more aware of each other, recognize the others in their expertise, and be curious about other ways of knowledge. It is clear that synthesis cannot be demanded a priori from a catalysis meeting, least of all can conceptual synthesis. As current Director Allen Rodrigo told me very effectively:

if you are bringing people from different disciplines, you can’t just Skype! You really need to engage, to have people there, over beer, over wine, talking about their differences, really struggling to understand what the other person is saying. Maybe getting frustrated, maybe going away and thinking “this is rubbish”, but then coming back the next day and saying “ok, now I think I understand what you are talking about”. You need that kind of passion and energy and enthusiasm... What we try to do in our catalysis meetings is to share those vocabularies and make those vocabularies explicit, so that what was previously incommensurable [...] between two disciplines becomes commensurable: people understand what they are talking about. That’s the first step towards at least understanding the differences in different disciplines. Now that doesn’t really solve the problem to synthesis because of course if we agree with what Kuhn was talking about there are still underlying beliefs about utility, about which way science should progress, how science should be done, and those things may still be different enough that you’re not going to reconcile disciplines. But at least what we try to do is make sure that people are talking about the same thing (Rodrigo 2014).

All of this is similar to what we have tried to do in our ‘Cultural Traits’ project. As a final remark, I want to get back to the possible negative effect of a philosopher’s obsession for concepts, conceptual clarity, conceptual summaries, conceptual change and the like. As Rodrigo continues:

I also feel that there is going to be some instances where – because of the differences in beliefs about utility and the like – we’re never going to achieve and overall synthesis. And I think as a Center what we haven’t done is give enough guidance to accept that that might be an outcome, that at least they get people talking about the same thing and knowing what they are talking about: that might be a good outcome in itself, rather than try to force a situation to a synthesis (Rodrigo 2014).

Even within biology, and even within evolutionary biology, scientists who aim for synthesis like Rodrigo agree that we shouldn’t always aim for synthesis, but recognize that “discordance and disagreement can be fruitful as well”, particularly if they lead to greater understanding down the road. The pressure to close down a catalysis meeting with some kind of conceptual outcome goes against the goal of curiosity for opening new explorations, to which concepts are often provisional and instrumental. In the project that led



to this book, and in the book itself, we wanted to maintain ‘cultural traits’ as *a key to open* interdisciplinarity, and so it worked. We see no hurry to shut up now. We showed that it is possible to publish interesting things on this topic. We removed some barriers. We gathered people in a virtual (and actual) room to try to “make the incommensurable commensurable”. The best continuation of this book would be someone starting scientific collaborations of various kinds. And you, readers, may be those who will.

## **Acknowledgements**

I thank all NESCent leaders and staff, in particular Allen Rodrigo and Joel Kingsolver, for their great generosity in letting me interview them. My research on NESCent, synthesis and catalysis was supported by the National Evolutionary Synthesis Center (NESCent), NSF #EF-0423641.

## **References**

- Brigandt, I. & Love, A.C. (2010). Evolutionary novelty and the evo-devo synthesis: field notes. *Evolutionary Biology*, 37(2-3), 93-99.
- Craver, C. (2009). *Explaining the brain: mechanisms and the mosaic unity of neuroscience*. Oxford: Oxford University Press.
- Cunningham, C. (2005). The right time for synthesis in evolutionary biology. *BioScience*, 55(2), 99.
- Kingsolver, J. (2014). Interview to Emanuele Serrelli. University of North Carolina, Chapel Hill, NC. July 7, 2014.
- Mitchell, S. (2003). *Biological complexity and integrative pluralism*. Cambridge University Press.
- NESCent (2004). A place for evolutionary synthesis in North Carolina’s Research Triangle. Original grant proposal to NSF [not online, courtesy of Jory Weintraub and Cliff Cunningham].
- Rodrigo, A. et al. (2013). Science incubators: synthesis centers and their role in the research ecosystem. *PLoS Biology*, 11(1), p.e1001468.
- Rodrigo, A. (2014). Interview to Emanuele Serrelli. NESCent, Durham, NC, July 3, 2014.
- Sidlauskas, B. et al. (2009). Linking big: the continuing promise of evolutionary synthesis. *Evolution*, 64(4), 871-880.