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Beyond DNA: integrating inclusive inheritance into an extended theory of evolution

Étienne Danchin^{*‡}, Anne Charmantier[§], Frances A. Champagne^{||}, Alex Mesoudi[¶], Benoit Pujol^{**} and Simon Blanchet^{**#}

Abstract | Many biologists are calling for an ‘extended evolutionary synthesis’ that would ‘modernize the modern synthesis’ of evolution. Biological information is typically considered as being transmitted across generations by the DNA sequence alone, but accumulating evidence indicates that both genetic and non-genetic inheritance, and the interactions between them, have important effects on evolutionary outcomes. We review the evidence for such effects of epigenetic, ecological and cultural inheritance and parental effects, and outline methods that quantify the relative contributions of genetic and non-genetic heritability to the transmission of phenotypic variation across generations. These issues have implications for diverse areas, from the question of missing heritability in human complex-trait genetics to the basis of major evolutionary transitions.

Modern synthesis

The merging of Darwinism with genetics that occurred from the 1930s to the 1950s.

When Charles Darwin was born in 1809, the idea that species change over time — that is, evolve — had already emerged¹. However, it was only half a century later, when Darwin published *On the Origin of Species*², that the theory of evolution profoundly transformed our understanding of life. Darwin understood that natural selection can only affect traits in which there is variation that is transmitted from parents to offspring; namely, traits that are heritable. Since then, the merging of Darwinism with genetics into the modern synthesis has led to a semantic shift, resulting in the tendency to assume that only the DNA sequence is inherited across generations^{3–8}. However, evolution acts on any phenotypic differences that are stable across generations^{5,9}. According to this view, phenotypic variation should be partitioned into its transmitted versus non-transmitted components rather than into its classical genetic and environmental components⁹.

Today, the view that biological information is transmitted from one generation to the next by the DNA sequence alone appears untenable^{3,5–8}. This became strikingly obvious when genome-wide association studies (GWA studies) showed that most of the high heritabilities for phenotypic traits, such as height or common human diseases, could not be explained by common genetic variants¹⁰ (BOX 1). This lack of a link between variation in DNA sequence and heritability might have several

causes, one of which is that heritability estimates are incorrect¹⁰, or at least misinterpreted, mainly because non-genetic heritability is often confounded with purely genetic effects. There is increasing awareness that non-genetic information can also be inherited across generations (reviewed in REFS 8,11–13). The concepts of ‘general heritability’ (REF. 5) or ‘inclusive heritability’ (REF. 9) were recently proposed to unify genetic and non-genetic heritability; the two terms are synonymous and aim at encompassing all dimensions of inheritance.

Non-genetic inherited information can arise through several interacting mechanisms, including epigenetics, parental effects and ecological and cultural inheritance^{3,7–9,12,15}. All forms of genetic and non-genetic inheritance contribute to phenotypic resemblance between individuals⁷. Distinguishing among these various components is crucial because their distinct properties affect evolutionary dynamics in different ways. In particular, as described in BOX 1, accounting for the distinct properties of non-genetic inheritance may resolve some major evolutionary enigmas.

Here, we first briefly review the recent evidence for non-genetic inheritance. Understanding the different properties of the various modes of inheritance is necessary to fully grasp the impact of non-genetic inheritance on evolution. Second, we consider the

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Genome-wide association studies

(GWA studies). These are studies in which associations between genetic variation and a phenotype or trait of interest are identified by genotyping cases (for example, diseased individuals) and controls (for example, healthy individuals) for a set of genetic variants that capture variation across the entire genome. Tests of statistical association with a phenotype are performed locally along the genome.

Heritability

The percentage of variation in a trait that is genetically transmitted to offspring.

Inclusive heritability

The percentage of variation in a trait that is transmitted between generations, whatever the mechanism of transmission. Inclusive heritability should be greater than or equal to heritability.

Prions

Prion-forming proteins exist in different stable conformational states. In addition to a 'native' non-prion conformation, they occasionally fold into a prion conformation that replicates itself by templating the conformational conversion of other molecules of the same protein.

network of interactions occurring between these different forms of inheritance. Third, we introduce the rationale of formally decomposing phenotypic variation between transmitted versus non-transmitted components, while highlighting the variety and importance of non-genetic components of inclusive heritability. Fourth, we review methods that can be used to estimate the relative weight of each non-genetic component of inclusive heritability and their interactions with genetic inheritance. Finally, we call for an extended modern synthesis that would not reduce inheritance to genes and that would incorporate all forms of inheritance^{9,12,13} to constitute a comprehensive evolutionary theory.

Epigenetic inheritance

Today, species evolution through neutral divergence or as a response to natural selection is thought to act primarily on phenotypic variation resulting from variation in the DNA sequence¹⁶. However, phenotypic variation may also result from changes in DNA expression^{17–19}, which is determined by various epigenetic mechanisms. For example, post-translational modifications of histone proteins and methylation of cytosines in DNA can activate, reduce or completely silence gene expression without altering the DNA sequence^{18,19}. Epigenetics encompasses the study of these modifications and other gene-regulatory mechanisms involving small RNAs, which can regulate gene expression²⁰.

In metacellular organisms, epigenetic modifications of gene expression levels can be inherited during both mitosis (that is, during development) and through transgenerational epigenetic inheritance (across generations¹⁸). Mitotic epigenetic inheritance results from the transmission of epigenetic marks (for example, involving the methylation pattern of some genes) from parent to descendant cells. It allows cell differentiation without changes in the DNA sequence¹⁸. By contrast, transgenerational epigenetic inheritance leads to the inheritance of epigenetic marks across generations¹⁸. Although a small proportion of epigenetic marks seems to be transmitted to offspring in multicellular organisms, the transmission of epigenetic alterations of gene expression across generations has been demonstrated in numerous eukaryotes^{18,21}. Only transgenerational epigenetic inheritance can affect inclusive heritability.

Transgenerational epigenetic inheritance can take two contrasting forms (FIG. 1). First, in germline epigenetic inheritance, the epigenetic state of the DNA is present in germline cells and is thus transmitted to the offspring over many generations by transgenerational epigenetic inheritance (FIG. 1a). For example, prenatal exposure to the pesticide vinclozolin induces changes in DNA methylation in the first filial generation (F₁) male offspring that are observed to persist to the F₄ generation and beyond in male gametes²². Conversely, in experience-dependent epigenetic inheritance, an epigenetic state affects parental behaviour in a way that generates the same epigenetic state in offspring. For example, in laboratory rats there is transgenerational continuity in individual differences in postnatal maternal pup licking (FIG. 1b). This inheritance depends on maternal licking-induced epigenetic changes in offspring neural circuits, which alter adult maternal behaviour of offspring²³. This effect may persist over many generations²³. In this example, parental effects and epigenetics interact in producing inheritance. However, if maternal behaviour is altered by changes in the quality of the environment (for example, stress or social isolation), there may be an interruption of the transgenerational continuity^{24,25}. This possibility to lose epigenetic marks and revert to the ancestral phenotype when environmental conditions change constitutes a major difference between genetic and epigenetic inheritance that has major implications for adaptation.

One process by which epigenetic marks are transmitted between generations is genomic imprinting, whereby certain genes are expressed in a parent-of-origin-specific manner^{18,21}. Imprinted genes are thus only expressed from the alleles that are inherited from one parent, which nullifies the benefits of diploidy of those genes²¹. Forms of genomic imprinting have been demonstrated in insects, mammals and flowering plants^{21,26}. Another process of transgenerational epigenetic inheritance involves an intimate interaction between transposable elements and DNA methylation, in which the activity of a transposable element affecting the expression of a coding gene is mediated by its methylation status²⁷. For example, the expression of the agouti gene in the agouti viable yellow (A^{vy}) mouse varies depending on the extent of DNA methylation in the intracisternal A particle (IAP) retrotransposon inserted upstream of the agouti gene. Accordingly, the coat colour of A^{vy} mice ranges from pure yellow (hypomethylation of the A^{vy} IAP) to pseudoagouti brown (hypermethylation of the A^{vy} IAP), and this epigenetic variation is inherited by offspring²⁸. Variation in DNA methylation within imprinted genes and transposable elements can be mediated by both abiotic^{22,29} and biotic³⁰ environmental components. Thus, transgenerational epigenetic inheritance has a “deliciously Lamarckian flavour” (REF. 11) that contrasts strikingly with the usual vision of inheritance^{8,26}. Prions (pathogens that induce protein misfolding) produce another robust epigenetic mechanism that leads to the acquisition and transgenerational inheritance of new traits^{20,31}, the evolutionary functions of which are still to be discovered.

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Partible paternity

Situations in which children are believed to have more than one biological father and each of those men provides resources for the child, enhancing its chances of survival.

Transgenerational epigenetic inheritance appears to be highly conserved in therian mammals, in which a complex imprinting mechanism has probably been highly conserved for almost 150 million years³². Transgenerational epigenetic inheritance contributes to parent–offspring resemblance and is, as such, a component of inclusive heritability. Despite the fact that the actual mechanisms of epigenetic inheritance are not clearly understood yet, the implications for evolution may be profound. Epigenetic inheritance can lead phenotypes to rapidly match natural-selection

requirements, making it an important mechanism for rapid adaptive evolution^{3,8,19,21}. However, inherited epigenetic marks can easily be confounded with mutations^{3,8,17}, as in some classic, so-called ‘genetic’ variants in flower symmetry, wherein subsequent studies suggest that they result from inherited epigenetic marks¹⁷.

Parental effects

Parental effects are defined as the effects that parents have on the phenotype of their offspring that are unrelated to the offspring’s own genotype³³. For example, parental effects are at the origin of surprising processes of inheritance in plants in which offspring life-history traits can be influenced by the maternal light environment³⁴. This transgenerational effect strongly affects the fitness of the offspring. Offspring grown in their maternal light environment (which is the natural situation, as seeds typically disperse at a short distance) had 3.4 times greater fitness than siblings moved to another light environment³⁴. Such parental effects provide a flexible mechanism by which sedentary organisms cope with heterogeneous environments³⁴, and they may result in lineages of plants that are specifically tuned to a particular light environment in ways that closely mimic patterns resulting from genetic variation. In the early development of quantitative genetics, parental effects were often viewed as “a frequent, and often troublesome, source of environmental resemblance” (REF. 35). However, the evolutionary implications of parental effects are now widely accepted and are considered to be an important source of heritability that contributes to parent–offspring resemblance^{9,33,36,37}.

Parental genetic effects occur when the expression of parental genes in one of the parents becomes an environmental component affecting the development of the offspring³⁸. Parental genetic effects can be accounted for by using quantitative genetic models, including indirect genetic effects (IGEs), which refer to the effects of genes that are expressed in one individual that influence the expression of traits in others over and above any directly inherited gene effects^{39,40}. There are many evolutionary implications of IGEs, ranging from genetic adaptation to optimal strategies for social organization^{40–42}.

Parental non-genetic effects (PNGEs) can also be a source of transgenerational inheritance of phenotypic variation. PNGEs often result in resemblance patterns similar to those produced by genomic imprinting⁴³. However, it is crucial to distinguish between these two processes as they generate entirely different patterns of gene expression and evolutionary dynamics⁴³. Classic examples of PNGEs include conditionally or socially mediated PNGEs that affect sexually selected traits as well as the preference for these traits⁴⁴. Such traits are most commonly thought to be genetically transmitted⁴⁵, but studies on birds and mammals have provided evidence that PNGEs have a large influence on secondary sexual characters^{46,47} and morphology³⁷. PNGEs can appear very early in life (sometimes even before fertilization) and are, as such, extremely difficult

Box 1 | Implications of non-genetic inheritance**The case of the missing heritability**

One puzzle of recent molecular genetics research is that of the missing heritability in humans¹⁰. A large number of genome-wide association studies for complex traits and common diseases have, in general, explained only a small proportion of the heritability of these phenotypes¹⁰. Genetic mechanisms may explain this discrepancy, including epistasis or the non-detection of genes with very small additive effects. However, another potential explanation is that heritability estimates may incorporate non-genetic components, which would, therefore, need to be accounted for in future studies.

The spread of novel alleles and maladaptive behaviour

Non-vertical transmission of information across generations (FIG. 2) vastly broadens the range of possible evolutionary processes^{3,8,13,126,127}. For example, cultural inheritance allows the selection of alleles that would otherwise not have spread, such as human lactose-absorption alleles, in response to the culturally transmitted practice of dairy farming¹²⁸. Cultural inheritance may also have caused a shift to more polygamous human mating systems in response to culturally transmitted beliefs in partible paternity¹²⁹. Models have also shown that features of cultural transmission can lead to the expansion of genetically maladaptive behaviours, such as the spread of excessive and painful tattooing by prestige bias⁶⁶ or the spread of prion-related neurodegenerative diseases by culturally transmitted cannibalistic practices⁶⁵.

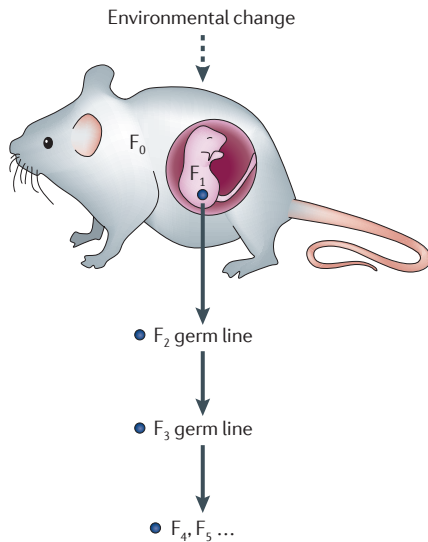
Non-genetic inheritance and major evolutionary transitions

The non-vertical components of genetic and non-genetic inheritance may help to explain the enigma of major evolutionary transitions¹³⁰ — that is, the emergence of new levels of organismal complexity.

A fascinating major evolutionary transition is that from uni- to multicellular organisms^{127,130–133}. Initially, autonomous cells are thought to have cooperated through molecular communication^{134–136}. When such communication eventually led to the reconstruction of the same trait value in a descendant multicellular organism, inheritance was thus generated (either genetic or non-genetic) within the lineages of the multicellular organism. The emergence of this new level of complexity probably integrated inheritance systems that were operating before the transition as functional processes within the new organisms. For instance, some communication molecules may have become hormones. Additionally, pre-transition epigenetic alterations (which might have constituted a form of cell plasticity or immunity against parasite strands of DNA) are thought to have been recruited for cell differentiation⁸, which allowed the division of labour among cell lineages, thereby stabilizing the new organism. According to such scenarios, mitotic epigenetic inheritance is thought to have played a major part in the emergence of mechanisms that prevent individual cells from behaving independently¹³⁰. However, recent biophysical models provide alternative explanations for the origin of multicellularity¹³³.

The emergence of a central nervous system eventually set the stage for cultural inheritance and participated in the major transition to sociality^{130–132}. The fact that the transmission of cultural inheritance is not necessarily vertical may strongly affect other evolutionary transitions⁶⁵. Non-vertical cultural transmission homogenizes the behaviour of individuals within a group, leading to higher variation in behaviour among groups than within groups. Models show that this may lead to the emergence of the social group as a new unit of selection^{63,65,66,87,88,104} and to the evolution of high levels of cooperation even within large groups of unrelated individuals — these have constituted a long-standing puzzle in studies of human evolution^{102–104,127,137}.

a Germline inheritance



b Experience-dependent inheritance

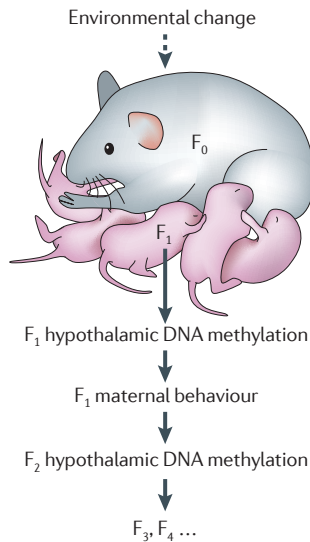


Figure 1 | Alternative forms of transgenerational epigenetic inheritance.

a | In germline epigenetic inheritance, an environmental effect occurring during development results in an epigenetic change within the first filial generation (F_1) offspring's germ line that is transmitted to F_2 offspring, F_3 offspring, and so on. Examples of this process have been observed in rodents after exposure to endocrine disruptors²², as shown, and in inherited epigenetic marks that affect flower symmetry (not shown), which have been transmitted for over 250 years in some plants¹⁷.

b | In experience-dependent epigenetic inheritance, the epigenetic marks in the caring parent modify their behaviour in a way that provokes the occurrence of the same epigenetic marks in their offspring. The behavioural change thus recreates the epigenetic marks *de novo* at each generation. An example is that of variation in maternal care in rodents²⁶, as shown (see text).

to control for, even in experiments⁴⁸. For example, female birds of some species place antibodies against specific pathogens in their eggs' yolk^{49,50}, thereby affecting their offspring's resistance to specific pathogens. The resulting parent-offspring correlation in resistance could be interpreted as revealing either heritability of resistance, genomic imprinting or both⁴³, although it might in fact result from transfers of antibodies independently from genetic variation, thus constituting a form of non-genetic heritability. Because such parental effects develop so early in life, they are often unwillingly captured within estimates of purely genetic effects. Parental effects can last over several generations — for example, in mice, changes in social environment can reduce anxiety-like behaviour for at least two generations⁵¹.

Moreover, non-genetic and genetic parental effects can interact in complex developmental pathways to produce inheritance. For instance, an experiment showed that mutant mouse mothers who are genetically impaired in various aspects of maternal care also socially transmit their impaired behaviour to wild-type daughters, with the effects being detected for at least two generations⁵². This situation corresponds to an indirect genetic maternal effect in the first generation, but constitutes a PNGE in the second generation. A great variety of epigenetic, morphological and physiological pathways exist through which parental effects and,

more specifically, PNGEs could arise. However, the mechanisms that are responsible for parental effects are still poorly understood²⁶, which hampers our capacity to detect them and study their evolutionary impact. Distinguishing epigenetic and early parental effects from direct, purely genetic effects is difficult, but it can be done either using molecular approaches¹⁷ or statistical analyses^{37,53,54}. However, it is currently unknown whether parental effects are mediated by separate mechanisms or by the other mechanisms we describe here, such as experience-dependent epigenetic inheritance. In the case of mediation by separate mechanisms, avoiding confounding parental effects in the genetic component of inclusive heritability is a crucial step towards our understanding of the multiple dimensions of evolutionary dynamics⁴³.

Ecological inheritance

As Darwin noted⁵⁵, individuals modify their environments in such a way that it can affect their fitness, thereby altering the selection pressures acting on them. Familiar examples include the webs, nests, dams and burrows that numerous animal species create, but also the changes in atmospheric gases and soil nutrients brought about by bacteria and plant species. Thus, members of many species inherit the cumulated environmental changes that previous generations have induced. These non-genetically inherited changes in environments have recently been termed ecological inheritance and stem from organisms' niche construction activities^{56,57}.

In some cases, these environmental modifications persist for long enough to be inherited by subsequent generations, with these inherited environmental changes substantially affecting long-term evolutionary dynamics. For example, successive generations of earthworms have, through their burrowing activities, substantially and permanently altered the structure and nutrient content of soil by mixing decomposing organic material with inorganic material⁵⁵. This has not only increased plant growth, as a result of the nutrient enrichment, but has also affected earthworm physiology. The well-mixed soil that results from earthworms' burrowing activities makes it easier to absorb water and has allowed them to retain their ancestral freshwater kidneys, rather than evolve novel adaptations to a terrestrial environment^{56,58}. On a global scale, the evolution of photosynthesis in early bacteria led to an increase in atmospheric oxygen content, which, in turn, led to the evolution of organisms with the capacity for aerobic respiration. This is one of many macroevolutionary patterns that are thought to have been shaped by interactions between genetic and ecological inheritance^{59,60}.

Niche construction is therefore not an end product of evolution but rather a cause of evolutionary change, and thus contributes to biodiversity^{60,61}. Mathematical models have shown that niche construction can change the evolutionary trajectory that is followed by phenotypes. Niche-constructing traits and traits that are favoured within that niche are therefore associated in the long term. Niche-constructing traits then spread because of their indirect benefits for future generations^{56,57,62}.

Niche construction

This occurs when individuals modify their environments in such a way that it can affect their fitness, thus altering the selective pressures acting on them. Hence, members of many species inherit the cumulated environmental changes that previous generations have induced.

Macroevolutionary

Evolutionary processes that occur above the species level and over protracted periods of geological time (for example, speciation, morphological change and extinction).

Box 2 | Criteria for culturally transmitted traits

Although there are many different definitions of culture in the literature, here we define culture as the part of the phenotypic variation (V_{Tsoc} in BOX 4) that results from information transmitted across generations through social learning^{4,9,15,66,87,90,100,137,150}. It is the inclusively heritable information that is inherited by social learning and sexual imprinting, imitation, copying and teaching^{71,151}. From a practical point of view, the first step in the study of animal culture is to identify traits that are at least partly inherited culturally. The literature on this topic has highlighted four criteria that potentially reveal cultural transmission. The four criteria need to be met simultaneously to unambiguously demonstrate that a trait is at least partly inherited culturally⁹.

First, the expression of the trait must result from social learning, which is learning from others (reviewed in REFS 4, 152–154), rather than being transmitted by any of the other inheritance pathways (namely, genetic, epigenetic, parental or ecological) or resulting from individual or asocial learning.

Second, variation in information must be transmitted across generations, or more generally from older to younger individuals, enabling the resulting variation in behaviour to be inherited across generations^{71,72,155–157}. This criterion ascertains that cultural transmission has a vertical or oblique component. This criterion is crucial because horizontal transmission alone does not lead to inheritance across generations. Only vertical or oblique transmission can lead to some information being inherited across generations, thus opening the way to evolution⁹.

Third, social learning must modify the phenotype of the learning individual for sufficient time in order to allow other individuals to observe the behaviour and learn it^{85,158,159}. In other words, we only transmit habits to which we stick.

Fourth, the modification of the phenotype must be generalized to similar situations^{82,85,160,161}. This is because only general rules (such as choosing big over small, shiny over dull or deciduous forest over evergreen forest), not specific situations, can be transmitted across generations.

These criteria provide conceptual and practical tools to identify cultural traits in order to study the ecological and evolutionary consequences of cultural transmission in animals. Despite the fact that behaviours such as song dialects in birds probably fulfil these four criteria, they have never, to our knowledge, been tested simultaneously on a single system.

Niche construction is likely to be especially potent in humans, given our ability to modify environments⁶³, particularly as a result of culture (see the next section). Parent–offspring resemblance that is observed in human behavioural genetics may, as such, result from gene–environment correlations, in which genes shape environmental conditions via personality or behavioural traits⁶⁴. Note that, unlike genetic inheritance, ecological inheritance can occur both between generations and within generations, and it can even occur between different species. Because ecological inheritance leads to the inheritance of the extended phenotype, it contributes to inclusive heritability.

Cultural inheritance

The final form of inheritance that we discuss here is in the information that is transmitted through culture, which can be defined as the part of phenotypic variation that is inherited socially (that is, learnt from others, see BOX 2). Being inherited, culturally transmitted variation in behaviour can evolve^{65–68}. Recent conceptual developments that were generated by the hot debates around culture in non-human animals^{69,70} have set the stage for empirical and experimental studies in this field^{4,9,71–73}. For instance, adaptive social learning, which — as we discuss in BOX 2 — is the first criterion of culture, has been documented in many contexts, such as foraging⁷⁴ and habitat^{75–77}, mate⁷⁸ and host choice^{79,80}

in vertebrates and invertebrates^{81,82}. The widespread existence of social learning suggests that stable, intergenerational cultural inheritance may be present in many taxa, which would imply that cultural inheritance may not be limited to ‘higher’ animals⁸³. Ironically, social learning has been demonstrated to affect behaviours that biologists often consider as being under strong, if not exclusive, genetic control. For instance, the tendency of cockroaches to flee light and head towards darkness is usually considered to be genetically encoded because of its anti-predator selective advantages. However, a recent study showed that this presumed innate tendency may be at least partly acquired socially: cockroach-like robots that were programmed to head towards a light shelter were sufficient to lead groups of cockroaches to often choose the light shelter when given the choice between a light and a dark shelter⁸⁴.

However, within-generation, one-to-one social learning is a necessary, but not sufficient, criterion for the notion of intergenerational transmission of culture that we are interested in here. Although social learning is essential for cultural evolution, and despite the fact that several behavioural patterns are clearly evocative of culture^{69,72,85,86}, studies demonstrating that some behavioural patterns fulfil all four criteria of culture (BOX 2) are still lacking^{9,83}.

Starting in the late 1970s, the role of cultural inheritance has been theoretically formalized. Models suggest that culture can increase an organism’s fitness (that is, its chances of survival and reproduction) under a wide range of conditions by allowing individuals to acquire and transmit adaptive behaviour that they could not have acquired by costly ‘trial-and-error’ learning and by providing a faster means of adapting to rapid environmental change than genetic inheritance alone^{63,65,66,87,88}. More recently, cultural evolution has been theoretically demonstrated to provide an important source of biodiversity through speciation^{89–92}. For instance, the capacity of two sympatric sister species of cichlid fishes — *Pundamilia pundamilia* and *Pundamilia nyererei* — to avoid hybridization was first attributed to genes controlling female preferences⁹³. Subsequently, early-in-life cross-fostering experiments between these sister species resulted in the complete reversal of each species’ assortative mating preferences, suggesting that early social imprinting is sufficient to explain variations in mating preferences⁹⁴. This example highlights the danger of using only patterns of transmission to infer mechanisms of inheritance.

It is sometimes claimed that culture cannot substantially influence evolution because it is too prone to copying errors; high cultural-innovation rates (for example, because of immigration from other societies) can result in a ‘cultural shift’ or ‘cultural meltdown’ in less than one generation⁹⁵. However, several empirical and theoretical studies suggest that conformity (that is, behaving as the majority) is a powerful process of normalization^{7,86,96,97} and that rates of genetic and cultural evolution may be similar⁹⁸. Nonetheless, we still have too little empirical evidence to estimate the strength of conformity or the rate of cultural evolution in natural

Sympatric

Sympatric is the condition in which the distributions of two species or differentiated populations overlap and hybridization between taxa would be possible if they were not reproductively isolated by factors other than spatial separation.

Assortative mating

Nonrandom mating; it occurs when individuals select their mates on the basis of one or more physical or chemical characteristics. For instance, big males mate with big females and small males with small females.

Box 3 | **Gene–culture interactions in human and animal evolution**

The classic example of an interaction between genetic and cultural inheritance concerns the culturally transmitted practice of dairy farming that has favoured the spread of alleles for lactose tolerance in some human populations^{99,128,138,139}. More generally, researchers from diverse backgrounds now accept the view that human evolution has been shaped by gene–culture interaction⁹⁹. This view is supported by the observation that hundreds of human genes have been, and probably still are, under positive selection in response to human culturally transmitted activities⁹⁹. Furthermore, cultural processes such as conformity and pay-off-based imitation can lead to the evolution and maintenance of altruistic behaviour even within large groups of unrelated individuals^{102–106}. Such models also resolve the controversy on the role of religions in the emergence of high levels of cooperation within large groups of unrelated humans (see REF. 140). Furthermore, famous examples of the role of culture in speciation in animals have been highlighted⁹². Similarly, the most promising examples of animal cultural transmission concern song dialects in birds and whales^{141–146}. Cultural transmission has been suspected to be responsible for the lack of genetic diversity in matrilineal whales¹⁴⁷, suggesting that culture may be an important evolutionary force in this taxon. Similarly, no relationship between the degree of genetic and song divergence among populations was found in one bird species with song dialects¹⁴⁸, suggesting that the distribution of genetic and dialect variation can be unrelated because of the independent transmission of genes and culture. Finally, various studies suggest that song dialect may lead to reproductive isolation, paving the way to speciation¹⁴⁹.

populations. The conceptual and methodological tools that are discussed below provide a framework to begin addressing such issues.

Gene–culture co-evolution is thought to have played a major part in the evolution of both humans⁹⁹ and animals (BOX 3). All of these findings suggest that cultural selection constitutes another engine of evolution when it interacts with natural selection. Genetic information can produce the template, largely in the form of learning capacities, on which behaviour can develop and thus can vary according to the multiple forms of information obtained during development. After the capacity for social learning has evolved, the social component of inherited phenotypic variation that is defined as culture^{4,9,15,87,100} becomes part of inclusive heritability, a fact that has been largely overlooked or considered to be negligible. The four integrated criteria of culture (BOX 2) provide a basis for further empirical studies of animal culture and allow us to evaluate the role of culture in non-human species evolution.

Networks of interacting mechanisms

Evolutionary changes result from changes in the information transmitted across generations, be they genetic or otherwise. Consequently, to understand evolutionary processes inclusively, it is necessary to account for all forms of inheritance. However, non-genetic inheritance systems often produce patterns of transmission that may be confounded with genetic transmission^{9,26,41,43,53,54}. Furthermore, the fact that the various inheritance systems form an intricate network of interacting mechanisms makes them notoriously difficult to distinguish from each other^{26,37,41,43,53,54}. For instance, parental effects often take the form of a specific dietary or behavioural environment that can trigger inherited epigenetic change, thereby modifying an offspring's phenotype and making these two kinds

of inheritance non-dissociable^{16,39,101}. Similarly, ecological inheritance can be confounded with parental effects, and parallels exist between ecological and cultural inheritance. Ecologically inherited entities are habitat patches or constructed niches, whereas culturally inherited entities can take the form of knowledge about the environment. In both cases, individuals inherit the cumulative changes resulting from the activities and knowledge of their ancestors. In effect, the genetic code constitutes the template from which mechanisms of non-genetic inheritance can develop and with which they interact. Identifying the contribution of each of these mechanisms to phenotypic variation constitutes one of the main challenges of evolutionary biology⁷.

A stunning example of how inheritance mechanisms interact is that of the maternal care provided by female rodents to their young litters that leads to the inheritance of their own behaviour by their daughters²⁶. Recent studies have shown that this inheritance of behaviour results from a sequence of processes involving the interaction of genes, epigenetics and behaviour. The level of maternal care affects the level of DNA methylation of genes coding for oestrogen receptors that are normally expressed in the brain. This DNA methylation pattern is maintained throughout life and decreases the expression of the corresponding genes at the adult stage, which, in turn, decreases the sensitivity of the female offspring to oestrogens and thus lowers the level of maternal care they provide soon after giving birth²⁶. Such examples suggest possible links between inheritance mechanisms and constitute promising opportunities for explaining, for instance, how behavioural imprinting can emerge from, and translate into, genomic imprinting.

Accounting for non-genetic inheritance

The distinct properties of the non-genetic mechanisms that are described above — by which biological information is transmitted across generations — are likely to strongly and differentially affect the output of evolution. For instance, many theoretical approaches already provide evidence for a major impact of social transmission on evolutionary dynamics^{62,63,65,66,87,88,102–106}. This reinforces our view that cultural inheritance is an important part of the evolutionary framework and should be considered as having its place in an extended view of the theory of evolution. More generally, it is vital for our understanding of mechanisms of heredity and evolutionary processes to set up novel approaches and experimental designs to isolate these components and determine how they interact in producing inheritance.

Ongoing advances in quantitative genetic methodology for exploring the sources of phenotypic inheritance set the stage for the estimation of the non-genetic components of heritability. Drawing a parallel from classic quantitative genetics, the challenge we face in estimating components of non-genetic heritability lies in understanding the processes of transmission of information for the various components. For example, cultural transmission displays inherent complexity

Social imprinting

The process by which young individuals of many vertebrates become imprinted on an object, usually their parents, observed during a critical period, usually very early in life. At the adult stage, social imprinting allows individual animals to recognize members of their own species with which to interact or mate. However, young individuals can be artificially imprinted on humans or any other object presented at the right time.

Matrilineal

A social structure of species in which females spend their entire lives with close female relatives and form new groups primarily by group fissions.

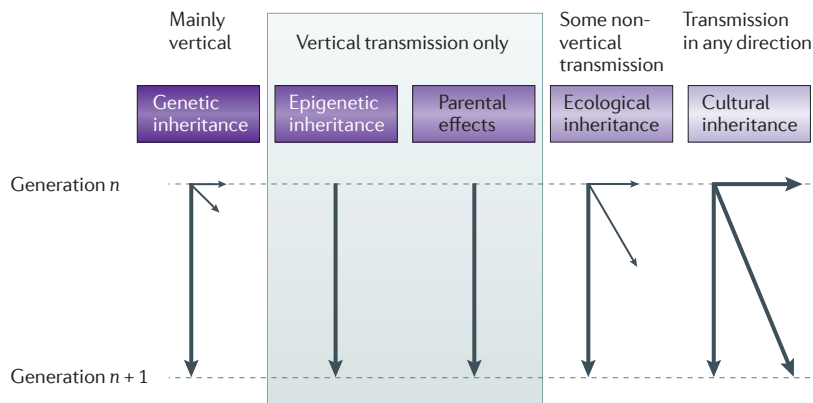


Figure 2 | Main vectors of transmission for the various forms of information inheritance. Vertical arrows represent lineages, and horizontal and oblique arrows indicate information that is transmitted across lineages. In the case of genetic inheritance, horizontal and oblique arrows indicate that genes are sometimes exchanged among microorganisms^{126,162} and between microorganisms and plants; such genetic exchanges, however, are uncommon in multicellular organisms (see REF. 7 for a complete overview). Despite the fact that horizontal gene transfer is fairly common in bacteria and archaea, many evolutionary studies of these species usually adopt approaches that do not account for such horizontal transfer. In the case of ecological inheritance, horizontal and oblique arrows indicate that ecological inheritance is also not exclusively vertical, with environmental modifications affecting kin and non-kin in current and subsequent generations. As indicated by the lengths of the arrows, it is with cultural inheritance that the horizontal and oblique components of inheritance are the most prominent.

because it can act not only through vertical information transfer but also through horizontal information transfer (among individuals of the same generation) and oblique information transfer (among non-kin individuals of different generations) (FIG. 2). Additionally, the effectiveness of this transmission can depend on many factors, such as distance between territories of interacting individuals or the amount of time they spend interacting. Furthermore, cultural dominance (that is, the fact that, when two populations with different cultural patterns are in contact, one behaviour will be transmitted over the other rather than intermediate phenotypes emerging) might occur through behavioural conformism^{96,97,107,108}; therefore, cultural dominance may affect phenotypic variation in ways that are similar to those of genetic dominance. However, as for genetic dominance, these effects on estimates of cultural heritability will depend on the form of behavioural dominance. There is no doubt that the accumulation of studies on this topic in animals (for instance, see REF. 109) will soon allow us to conduct theoretical studies that explore the statistical properties of cultural transmission within and between generations (as has been done in humans^{110,111}) and compare them to genetic effects.

Dissecting inclusive heritability

Dissecting the effects of genetic and non-genetic inheritance is challenging. Statistical measures of heritability suppose that the inheritance of identical genes leads to the expression of identical phenotypes. Estimates of heritability thus measure the relationship

between phenotypic resemblance (the phenotypic covariation among individuals) and genetic relatedness (the proportion of alleles shared among individuals). Heritability is thus often quantified on the sole estimation of the additive genetic variance component (V_A) of phenotypic variance (V_P). This leads to narrow sense heritability ($h^2 = V_A / V_P$), which is usually interpreted as a predictor for the potential of a population to produce an evolutionary response to selection¹¹². However, it is only recently that researchers have begun to regard the influence of third-party, non-genetic factors (such as the environment or the influence of another phenotype) as more than just a statistical nuisance.

A first step towards the incorporation of non-genetic heritability occurred with the identification of IGEs^{39,40}. IGEs mark the intersection between genetic and non-genetic inheritance and merge parts of non-genetic components of inclusive heritability into a single parameter. As we propose here, it is now necessary to separate each inheritance system to better study them and understand how they interact in producing inheritance. Furthermore, to our knowledge, several aspects of non-genetic inheritance are not included in IGEs. For instance, language inheritance is not only influenced by the genes of neighbours but also by the actual language spoken by these neighbours, which is independent of their genes.

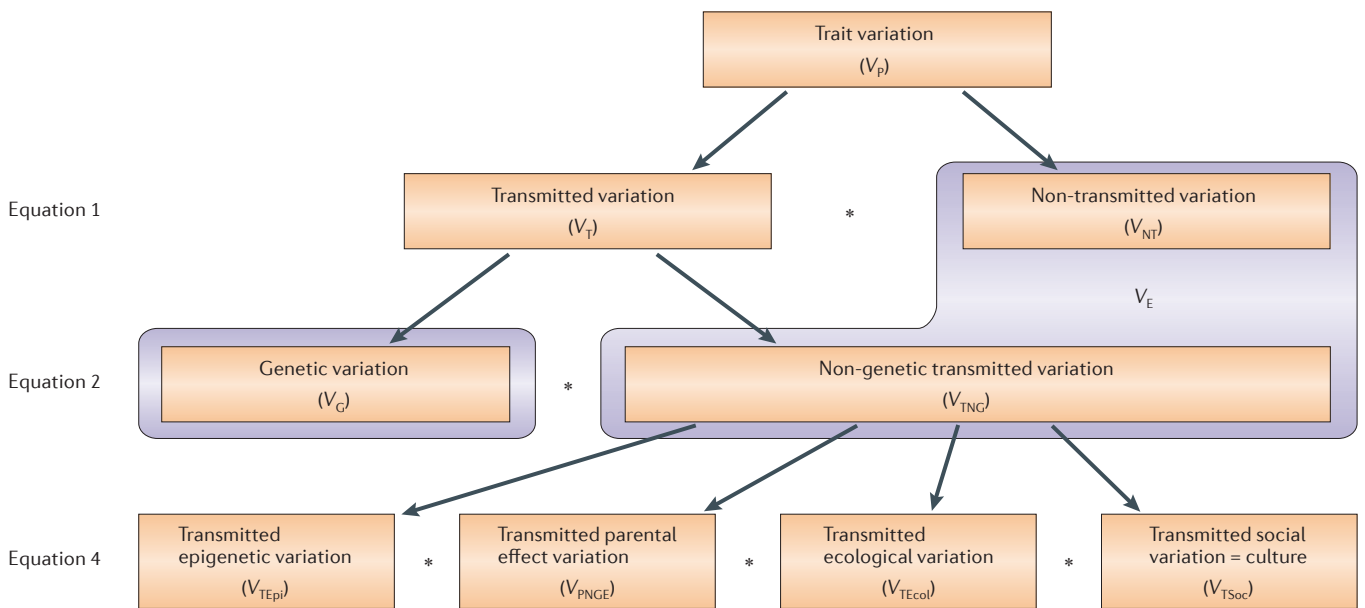
The next step in the study of non-genetic inheritance is therefore to isolate the various mechanisms of non-genetic inheritance to better evaluate their impact on evolution. Building on the conceptual framework of genetic heritability, we formally identify the non-genetic effects that influence trait heritability in BOX 4. In the rest of this section, we discuss various approaches used to estimate genetic heritability, propose extensions to existing methods and show how they can be adapted to the estimation of the various components of heritability. They involve longitudinal and experimental approaches.

Longitudinal individual approaches. Evaluating the parts played by mechanisms of non-genetic inheritance in evolutionary processes of phenotypic change requires using the quantitative genetic framework that is described above and formalized in BOX 4. When applied to observations made in the field, it classically uses correlations to associate resemblance among individuals with a pattern of genetic relatedness that is either known *a priori* or reconstructed *a posteriori*. In this context, the use of quantitative genetics mixed-effect models that are based on pedigrees and known as animal model approaches is of particular interest because it allows us to estimate several variance components simultaneously. This approach constitutes a statistical model based on individuals that combines all of the information from multigenerational pedigrees into a matrix of the relatedness among individuals. When analysing quantitative traits using animal models to estimate genetic parameters, the phenotypic variance–covariance matrix (P matrix) is decomposed into a matrix of additive genetic variance–covariance (G matrix) and a residual

Covariation

The association between two variables that characterizes the tendency for the two variables to covary around their mean in a systematic way.

Box 4 | The quantitative contribution of the components of inclusive heritability



As recognized by Darwin when he wrote that “Any variation which is not inherited is unimportant for us” (REF. 2), only traits for which variation is transmitted may evolve. This is true whatever the mechanism of inheritance^{5,8,9,12}. Any phenotypic differences that can be stably inherited across generations, whether of genetic or environmental origin, are subject to natural selection⁵. Phenotypic variation results from both the genetic and non-genetic information carried by organisms⁷³. As such, from the perspective of evaluating the evolutionary potential of a trait, phenotypic variance (V_P) should be partitioned into its transmitted (V_T) versus non-transmitted (V_{NT}) components:

$$V_P = V_T + V_{NT} + V_T * V_{NT} \tag{1}$$

The term V_T incorporates all inherited types of information (be it genetic or non-genetic) that leads to resemblance among individuals from different generations. V_T can be split into the following components: genetic effects (V_G) and non-genetic effects (V_{TNG}), as in equation 2 and illustrated in the figure.

$$V_T = V_G + V_{TNG} + V_G * V_{TNG} \tag{2}$$

Genetic variance V_G is classically decomposed into additive genetic effects (V_A), genetic dominance effects (V_D) and the effect of gene epistatic interactions (V_{GE}). However, in sexual organisms, only the variance attributable to additive genes is transmitted across generations and contributes to a microevolutionary response to directional selection. Hence, dominance and epistasis are neglected most of the time.

$$V_G = V_A + V_D + V_{GE} \tag{3}$$

We did not include indirect genetic effects V_{IGE} in V_G because, as we discuss in the main text, this term is likely to capture parts of the interaction between V_G and V_{TNG} . Indirect genetic effects, V_{IGE} , include expressions of genes in an individual that affect the phenotype of another individual. In the classic case of parental effects, parents can influence the phenotype of their offspring by environmental or genetic sources of variation that can be transmitted, but only the latter will be included in V_{IGE} . It is possible to determine the genetic component of maternal effects by decomposing grandparental effects¹¹⁹. The environmental part of parental effects — parental non-genetic effects (PNGEs) — is included in V_{TNG} (see the figure).

Therefore, V_{TNG} encompasses the effects of the various non-genetic mechanisms of inheritance. It can be written as

$$V_{TNG} = V_{TEpi} * V_{PNGE} * V_{TEcol} * V_{TSoc} \tag{4}$$

which includes all of the main effects plus all of the possible two-, three- and four-way interactions.

These conceptual terms quantify the effect of transgenerational epigenetic inheritance (V_{TEpi}), inheritance through parental non-genetic effects (V_{PNGE}), ecological inheritance (V_{TEcol}) and social inheritance (V_{TSoc}). In all of the terms in equation 4, the T starting the subscript stands for ‘transmitted’. The reality of these terms is reviewed in the first part of this paper. As we discuss in this Review, these various components may have independent effects and interact in an intricate way, and equation 4 incorporates all of the potential interaction terms. Note, however, that it is currently unknown whether parental effects are mediated by separate mechanisms or through the other mechanisms we describe here; in the latter case, the term V_{PNGE} should be removed from equation 4.

Grey boxes in the figure illustrate the classic decomposition opposing genetic V_G to environmental variance (V_E), which rejects V_{TNG} as irrelevant to evolutionary processes.

The ratio V_T / V_P has recently been called ‘inclusive heritability’ (REF. 9). It quantifies the whole evolutionary potential of a trait and can be seen as the result of both genetic and non-genetic heritability. Only a full experimental design in which individuals are cross-fostered across environments and other sources of inheritance can allow one to separate those various components. The goal of the concept of inclusive heritability is to explicitly incorporate the effect of every form of inheritance (and the interactions between these forms) in order to capture the resulting evolutionary potential of a trait.

Authors have argued that the standard quantitative genetic models are too complex to be useful as a tool for empirical studies of phenotypic variation^{8,12}. Recently, however, Helanterä and Uller⁷ used the Price equation to unify inheritance systems into a single mathematical framework. These authors’ analyses reinforce the necessity to disentangle the respective roles of these inheritance systems. It is, therefore, necessary to distinguish these effects in order to understand how they act and interact among themselves and with genetics in producing evolutionary change (see REF. 7 for a more complete analysis).

matrix (R matrix) so that $P = G + R$. The G matrix is defined by $G = A \times V_A$, where V_A is the additive genetic variance and A is the additive relationship matrix with individual elements $A_{ij} = 2\Theta_{ij}$ (where Θ_{ij} is the coefficient of coancestry between individuals i and j)^{53,113}. Solving an animal model thereby requires the construction of an additive genetic relationship matrix, A , based on pedigree information. In a similar way, we could envisage solving the proposed partition of non-genetic heritability by building matrices of shared information for each described process. For example, variance due to epigenetic inheritance (V_{TEpi}) could be estimated by including the number of times that epigenetic marks may be reset between generations¹⁴, variance due to ecological inheritance (V_{TEcol}) could be estimated by including a vector of shared habitat, and variance due to culture (V_{TSoc}) could be estimated by including a matrix of overlap between individual territories or number of interactions between individuals¹⁰⁹.

Experimental approaches. A way to improve the identification and evaluation of the relative weight of each of the non-genetic components of inclusive heritability is to manipulate the related sources of information. For this purpose, most tools and methods that were originally designed to study patterns of genetic evolution can be adapted. For example, to estimate the contributions of culture to inclusive heritability, most tools and methods of quantitative genetics can be adapted to explain patterns of cultural evolution in humans and animals¹⁴, including quantitative genetic models^{15,65,66,90,115}, phylogenetic methods¹¹⁶ and laboratory experiments^{72,117}. Methods to study social learning can also be used to demonstrate the existence of cultural variation. For instance, captive, hand-raised, naive New Caledonian crows (*Corvus moneduloides*) spontaneously manufacture and use tools without any contact with conspecifics¹¹⁸, suggesting the existence of a genetic component that contributes to the ability to use tools. Hand-raised crows also paid close attention to demonstrations of tool use by their human foster parents, suggesting that they might also learn tool use from them. Geographical variations in tool use among crows were observed in New Caledonia, which may result from an interaction between genetic and social inheritance. These results indicate the benefit of coupling genetic and cultural inheritance within a single theoretical framework, as we suggest here.

Partial cross-fostering experiments¹¹⁹ constitute the most powerful way to estimate the various components of inclusive heritability. Traditional approaches, combined with the use of statistical methods incorporating pedigrees^{41,53,54,120,121}, could be modified and adapted to account for all forms of inheritance. Cross-fostering experiments can, for instance, be used to estimate the role of ecological inheritance in heritability by modifying some of the habitat patches at the beginning of a multigenerational experiment and incorporating a matrix that describes the habitat type during development into an animal-model type of analysis. This would decouple the genetic genealogy

from the ecological genealogy. Similarly, a theoretical framework has been proposed to estimate the roles of genetic and epigenetic heritability¹⁴. The idea is to estimate the number of times that epigenetic marks may be reset between generations, in combination with assumptions about environmental induction, to provide novel expressions for covariances among relatives¹⁴. Concerning the cultural component of phenotypic variation, cross-fostering experiments can be used to decouple the genetic genealogy from the cultural genealogy of individuals of known kinship. Results can be analysed with animal model approaches incorporating two variance-covariance matrices — one for the genetic relationships and one for the cultural relationships — to estimate the V_{TSoc} component of inclusive heritability and to study its interaction with genetic heritability¹⁰⁹.

Towards an extended modern synthesis

As it stands, the modern synthesis reduces inheritance to genes and considers the development of forms as the consequences of variation in the DNA sequences of structural genes. The growing field of ‘evo-devo’ has been the main contributor to a new way of thinking about the link between genes and forms, with the development and diversification of forms arising from alterations in the expression of very few conserved regulatory genes, rather than from mutations of structural genes^{3,122–124} (but see REF. 125). Several authors^{3,13,122,123} have argued that the time is ripe for using the theory of development to modernize the modern synthesis. However, here we suggest that many of the arguments proposed by advocates of the extended synthesis have consequences that need to be formalized in terms of inheritance. Thus, the theory of inheritance that currently prevails also needs to be extended in order to incorporate all non-genetic inheritance as participating to the development and inheritance of the phenotype. Such an inclusive conception of inheritance can be paralleled with the input brought by the concept of inclusive fitness. By broadening the notion of fitness to include not just individual fitness but also the broader fitness of related individuals, we were able to make predictions regarding behaviour (such as kin selection, altruism and cooperation) that we could not otherwise explain. Likewise, broadening the notion of inheritance should allow us to resolve major evolutionary enigmas, as suggested in BOX 1.

In every aspect, the concept of inclusive inheritance calls on us to redefine evolution as “the process by which the frequencies of variants in a population change over time” (REF. 110), where the word ‘variants’ replaces the word ‘genes’ in order to include any inherited information, be it genetic or non-genetic and with continuous or discontinuous effects. Obviously, this term encompasses genes, but also all of the other inheritance processes that we have discussed here.

Several evolutionary biologists have argued for the development of an ‘extended evolutionary synthesis’ (REFS 3,5,8,12,13,122,123). Our goal is to go beyond DNA in order to build a broader conception of

evolution. We call for a multidimensional modern synthesis that would merge the current modern synthesis with an inclusive view of inheritance into a single framework. In particular, this new theory should include cultural inheritance, which has been largely dismissed as insignificant in animal phenotypic inheritance. However, as we have discussed, the existence of numerous culturally transmitted traits⁹ suggests that cultural (or social) inheritance is likely

to have a profound effect on evolution. Similarly, epigenetic and ecological inheritances, as well as parental effects, currently emerge as new sources of inheritance and heritability. Accounting for all types of inheritance and their intricate interactions will considerably expand the range of potential evolutionary mechanisms that can be incorporated into models and studies and should help to solve major evolutionary enigmas.

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Competing interests statement

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