



## SFI WORKSHOP: INTEGRATING DEVELOPMENT AND INHERITANCE

13-15 February 2018. Noyce Conference Room, SFI

### Titles and Abstracts

*Tuesday 13th*

**Tobias Uller**

**Integrating development and inheritance - introductory remarks**

**Abstract:** An introduction to the workshop and its main aims. (1) To discuss the historical origins of the separation of development and inheritance and their description in genetic terms, and how this shaped the development of research programs within evolutionary biology; (2) To explore the possible implications of alternative conceptualizations of inheritance, and the development-heredity relationship, that are emerging through recent advances in the biological sciences. (3) To discuss how empirical work and mathematical modelling best can proceed with constructive views of development and inheritance, and what the implications might be for evolutionary processes.

**Erik Peterson**

**Waddington died disappointed; or: Weren't we integrating inheritance and development in the 1930s?**

**Abstract:** From the perspective of biologists working in the interwar period, we were on the threshold of a comprehensive theory combining inheritance and development. American scion of *Drosophila* genetics, Thomas Hunt Morgan, authored a 1933 book laying out just such a conjunction between his work and embryology. Promising discoveries in biochemistry, biophysics, and cytology occurred regularly and pointed to this kind of conjunction. By the early 1940s, there was even a name for the subfield that would outline the integration of development and inheritance: "epigenetics." But, decades later, the English biologist who coined that term, C. H. Waddington, despaired that no such conjunction had happened. If anything, the field of biology collectively seemed less interested in integrating development and inheritance in the 1970s than it had fifty years earlier. In this essay, I trace the reasons for optimism about such an integration in the first half of the twentieth century and why such an integration failed to come to fruition during the second half.

**Jessica Riskin**

**How the mouse lost its tail, or, Lamarck's dangerous idea**

**Abstract:** The clockwork cosmos of early modern science was for the most part a passive and static thing, its shape imposed by an external designer, its movements originating outside itself. The classical mechanists of the seventeenth century mostly evacuated force and agency from the cosmos, often even including from its living inhabitants, to the province of a supernatural Clockmaker. They thereby built a kind of supernaturalism into the very structure of modern science. But not everyone concurred in this banishment. From the late seventeenth century onward, a tradition of dissenters embraced the opposite principle, that agency -- a capacity to act, to be self-making and self-transforming -- was essential to nature, especially living nature. A crucial member of this dissenting, active-mechanist tradition was the French naturalist Jean-Baptiste Lamarck, professor of natural history at the *Muséum national d'histoire naturelle* in Paris, and author of the term "biology" as well as of the first theory of what we now call "evolution". This paper examines his rigorously naturalist approach -- which naturalized rather than outsourced agency -- and its exile from the halls of mainstream science.

**Benoit Pujol**

**An ecologist guide to disentangling genetic and non-genetic heritabilities in wild populations**

**Abstract:** Genetic variation for fitness related traits is not the only heritable source of adaptive potential. It is crucial to disentangle non-genetic sources (e.g., social interactions, epigenetic, ecological niche transmission) of heritable variation to refine our estimates of population evolutionary potential. We provide a practical guide for researchers interested in distinguishing between genetic and non-genetic heritabilities for phenotypic and/or fitness variation. One the transgenerational mechanism is identified, our tutorial shows how to estimate simultaneously both genetic and non-genetic sources of phenotypic similarity within the framework of the quantitative genetic "animal model". Quantitative genetic models can be used to quantify the genetic variance, and therefore the heritability, of complex traits. These models can account for general environmental categorical factors but our aim is to go further. I will outline how a matrix of similarity can be used alongside the genetic matrix of relatedness in the animal model of quantitative genetics to capture the impact of the environmental similarity on evolutionary parameters. This is particularly useful in wild populations where quantifying the environmental components of traits can be challenging because the environment is composed of many factors. We will trial this statistical technique in a wild population of snapdragons, *Antirrhinum majus*, in the South of France. All individual plants have been tagged, phenotyped, and genotyped since 2010. The environment of each individual has been recorded, and these environmental parameters were combined to form a matrix of environmental similarity, which was included in the animal model alongside the matrix of relatedness. We will also test this original approach on the basis of long term survey data in the Kimbe Island wild clownfish population and on

southern France wild roe deer population. We welcome any collaboration on similar datasets in order to test whether habitat transmission and other transgenerational non-genetic mechanisms generate population potential to respond to directional selection.

**Russell Bonduriansky**

**The parent as a developmental template**

**Abstract:** Shifting views of reproduction and development over the past 150 years have driven profound changes in the concept of heredity. Parents were once thought to build their offspring from their own soma, providing a direct conduit for the inheritance of acquired traits. This concept of reproduction was eventually supplanted by the idea that offspring development is guided by an autonomous blueprint containing hereditary information that cannot be altered by parental environment or experience. Today, a hybrid concept of development and heredity is emerging, with many researchers recognizing that offspring traits are shaped not only by the expression of a unique genome but also by the extended phenotypes of the parents. According to this view, many parental traits provide a developmental scaffold that shapes offspring phenotype. In this talk, I will focus on a particular type of scaffolding that has intriguing implications but has received little attention. Intriguing evidence from single-celled eukaryotes shows that some components of the cell can play a template-like role in shaping offspring traits, and thereby impart structural variations to descendants. I will discuss the potential for similar processes to occur in multi-celled organisms, and to contribute to the transmission of traits across generations.

**Troy Day**

**The role of adaptive variation in evolution**

**Abstract:** The Modern Synthesis (MS) posits that genetic material forms the main substrate for evolutionary adaptation but there is now a growing realization that nongenetic forms of information transmission between generations might also play an important role. This has engendered considerable debate among evolutionary biologists and one of the main points of contention is the nature of “mutation” in genetic vs nongenetic systems of inheritance. According to the MS, genetic variation is generated in an entirely random fashion whereas some researchers have suggested that nongenetic variation might be generated in an adaptive way. This claim has been particularly unpalatable to critics of nongenetic inheritance because it challenges Darwin’s most important insight that natural selection is the sole mechanism of adaptive evolution. In this talk I will attempt to formalize this debate in a more precise way with the goal of trying to achieve consensus on this increasingly controversial issue.

**Eva Jablonka**

**The evolutionary implications of extragenetic inheritance**

**Abstract:** There are many extra-genetic inheritance transmission pathways and extra-genetic variations, from epigenetic variations that can be described in molecular terms, to transmissible variation in socially transmitted non-symbolical and symbolical behavior and variations in the reconstruction of ecological legacies. What they all have in common is that they are based on variations in DNA base sequence. I discuss some of the evolutionary implications of these.

*Wednesday 14th*

**Alan Love**

**Developmental biology and the Modern Synthesis: perspectives and prospects for integrating development and evolution**

**Abstract:** The history of how development and inheritance parted ways in the early 20<sup>th</sup> century is crucial to understanding both how the Modern Synthesis emerged in evolutionary biology and why development was not constitutive of it. Although the genetic formulation of inheritance helps in accounting for the former, it is less relevant to understanding the latter. To understand why development was not centrally involved in the Modern Synthesis, we need to understand the trajectory of research programs that characterize developmental biology. These trajectories cluster around research questions unrelated to evolutionary change and can be recovered in part through an examination of the topics and themes found in forty years of the Annual Symposia for the Society for Developmental Biology. Developmental biologists concentrated on understanding recurring similarities in model organisms that were domesticated—both in terms of their genetic constitution and environmental homogeneity—to minimize variation. This analysis shows that a major barrier between evolutionary biology and developmental biology through the 20<sup>th</sup> century was divergent investigative practices arising from a lack of shared problems, which coalesced during their distinctive periods of disciplinary professionalization. Additionally, much of evolutionary developmental biology has been shaped by the practices and problems of developmental biology, reframed comparatively, and ignores aspects of development and heredity germane to evolutionary change. To achieve a more integrated theoretical perspective, the problems and practices of professionalized evolutionary and developmental biology must be bridged by an intentional articulation of linkages between their disparate research questions and methods. I suggest one fruitful strategy for doing so lies in coordinating empirical inquiry around temporal stages of a life history where questions about the developmental origin of variation and its evolutionary relevance converge.

**Karen Kovaka**

### **Interacting inheritance channels**

**Abstract:** This offers an account of what it is for an inheritance process to be evolutionarily powerful. At the heart of the account is the claim that we should take an *interactive approach* to assessing the evolutionary power of different inheritance processes. Other philosophers (Sterelny 2001; see discussion in Griesemer et al. 2005, Godfrey-Smith 2011, Sterelny 2011) have proposed three criteria—internal policing, stable transmission, and generation of variation—that an evolutionarily powerful inheritance process must meet. I modify this proposal by showing that an inheritance process may meet these criteria either independently, or in interaction with other inheritance processes. This is an important difference: the interactive approach opens up space for us to view extra-genetic inheritance as evolutionarily powerful while also clarifying how and why there appear to be such differences in power between genetic and extra-genetic inheritance.

**Lynn Chiu**

### **Holobionts as units of evolutionary processes**

**Abstract:** A holobiont is a specific collection of living entities: a single macroorganism (usually a multicellular eukaryotic host) and the stably-persistent microorganisms that reside in or on it (including viruses, protists, bacteria, fungi, and sometimes, helminthes). Macroorganisms have clearly evolved in the context of microorganisms, yet it is highly controversial whether holobionts have a specific evolutionary status and thus a theoretical role in evolutionary theory. Proponents of Hologenome Theory argue that holobionts are *bona fide* units of selection. Yet many argue that holobionts do not satisfy the stringent criteria of classical units of selection. In this paper, I argue that holobionts are important units of evolution even if they are not units of selection. The unit of selection debate asks whether holobionts are evolutionary transitions, that is, products of evolution object to selective forces. I propose a revised notion of evolutionary units that reframes holobionts not as objects of evolution but a nexus of interacting evolutionary causes and processes of *organismal* origin. In recent decades, the scope of evolutionary causes has expanded to include the evolving organisms and other organisms, which influence evolution through ecological development and niche construction. The dynamic holobiont is such processes writ large. I will examine accounts of evolutionary units that already integrate developmental processes, in particular, James Griesemer's processual account of reproducers and developmentally scaffolded "hybrids" and analyze how adding niche construction implies an evolutionary unit of processes. Then I will argue that holobionts are exemplars of such units. Such an account spells out the evolutionary significance of holobionts, thus satisfying the theoretical goals of Hologenome supporters, without committing to the more restrictive view that holobionts are units of selection.

**Rose Thorogood**

**Can culture have evolutionary effects across species boundaries?**

**Abstract:** The behaviour of others comprises an important part of an animal's ecology - observing how individuals interact with their own abiotic and biotic environments provides information and facilitates behavioural plasticity. If social information is used in decision-making, it should then have potential to influence selection across species boundaries. However, beyond human culture, there has been little consideration of how socially-transmitted behaviours within species may lead to different evolutionary outcomes in co-evolving species. Here I'll present two examples from my group's work where we are exploring the emergent properties of social transmission for evolutionary arms races between predators and prey (using Parid tits), and parasites and hosts (using brood parasitic cuckoos as our study system).

**Hal Whitehead**

**The reach of gene-culture coevolution in animals**

**Abstract:** Culture, shared behaviour acquired by social learning, is present in diverse animal species. It is well established that culture affects human genetic evolution. Here we review the increasing evidence that this also occurs in non-humans through several linked processes. Culture may have driven early phases of speciation in both birds and killer whales. There is increasing evidence that culture can lead to low diversity of neutral genes through cultural hitchhiking or culturally mediated migration (in matrilineal whales and humans). Culture can drive the adaptive evolution of functional genes (in killer whales and birds). Additionally, in cultural species selection should favour traits with a genetic basis that support or enhance social learning, including longer lives, lengthened juvenile periods, menopause, and enhanced cognitive abilities. Conceptions of adaptive evolution should include how organisms' cultures facilitate adjustment to environmental challenges or new opportunities, dragging genetic change in their wake.

**Karthik Panchanathan**

**The evolution of sensitive periods in a model of incremental development**

**Abstract:** Sensitive periods, in which experience shapes phenotypic development to a larger extent than other periods, are widespread in nature. Despite a recent focus on neural-physiological explanation, few formal models have examined the evolutionary selection pressures that result in developmental mechanisms that produce sensitive periods. I'll present an evolutionary model of development I've been working on with colleagues. We model development as a specialization process during which individuals incrementally adapt to local environmental conditions, while receiving a constant stream of cost-free, imperfect cues to the environmental state. We compute optimal developmental programmes across a range of ecological conditions and use these programs to simulate developmental trajectories and



obtain distributions of mature phenotypes. I'll discuss both the modelling framework and some of the results of the model.

*Thursday 15<sup>th</sup>*

**Sean Rice**

**Evolutionary consequences of interactions between development, inheritance, and selection**

**Abstract:** Inheritance is the key factor making biological evolution possible. Despite this central role, transmission is often bundled into the simplifying assumptions of evolutionary models, making it difficult to see how changes in the patterns of transmission influence evolutionary dynamics. I will discuss a new mathematical method that allows us to derive patterns of inheritance from developmental processes, and to incorporate the results into models of evolution. I will illustrate the approach with an example in which an environmental factor influences both inheritance (through its impact on development) and fitness. I show that the resulting correlation between inheritance and selection can have a pronounced impact on evolutionary dynamics.

**Michael Lachmann**

**The thrifty watchmaker**

**Abstract:** In my talk I will explore the types of variation that evolution gets to tinker with. I will re-examine points made about plasticity before, by Wolff, West-Eberhard and others. I will, however, claim that genes and environment should not be seen as acting on an even footing. Instead I will argue that the genotype should be seen as an interpreter of the environment, and that most of the information, and even most of the functional information in the phenotype comes from the environment. Neuronal learning guiding behavior should not be seen as an outlier but instead as the norm of developmental processes.

**Marc Feldman**

**On the evolution of cultural transmission and fitness optimization**

**Abstract:** We study competition between vertical and oblique cultural transmission of a dichotomous phenotype under constant, periodically cycling, and randomly fluctuating selection. Conditions are derived for the existence of a stable polymorphism in a periodically cycling selection regime. Under such a selection regime, the fate of a genetic modifier of the rate of vertical transmission depends on the length of the cycle and the strength of selection. The evolutionarily stable rate of vertical transmission differs markedly from the rate that maximizes the geometric mean fitness of the population.