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Book of Abstracts
Evolution and the Origin of Life

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Evolution and the Origin of Life

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14:00 - 16:00   Evolution and the Origin of Life

LEARNING GENERAL MODELS FROM PAST ENVIRONMENTS: HOW STOCHASTICITY AND THE COST OF ONTOGENETIC INTERACTIONS CAN FACILITATE EVOLVABILITY

Konstantinos Kouvaris, University of Southampton, UK (kk6g11@soton.ac.uk)

One of the most intriguing questions in evolution is how organisms exhibit novelty to adapt in a plethora of selective environments. Recent work has shown that developmental biases are structured such that random (undirected) genetic variation is channelled into potentially beneficial (directed) phenotypic variation, thus facilitating evolvability. In particular, when selective environments vary in a systematic manner (i.e., encompass structural information), development can constrain the phenotype space in regions that are evolutionarily more advantageous. Nonetheless, the underlying mechanism that enables the spontaneous emergence of such adaptive developmental constraints is poorly understood. We hypothesise that when organisms evolve to remember past environments and generate appropriate novel responses to unseen environments, this is functionally equivalent to the task a neural network faces when learning over a training set and then generalising to previously-unseen data (i.e., test set). We specifically argue that the failure of natural selection to enhance evolvability is directly analogous to the problem of over-fitting and failure to generalise in the area of machine learning. Here we show that conditions that are known to alleviate over-fitting in machine learning can provide insight into the conditions that enhance the evolution of evolvability under natural selection. More precisely, we describe how well-known techniques, such as Jittering (i.e., learning with noise) and L1 (or L2) regularisation (i.e., penalising model complexity), that improve the generalisation ability of neural networks can help us understand how noisy selective environments and the reproduction cost of the ontogenetic interactions can enhance evolvability in gene networks. This provides the first formal theory to characterise the conditions that enhance evolvability in natural systems.

THE EVOLUTION OF SHORT-TERM AND LONG-TERM EVOLVABILITY IN GENE-REGULATION NETWORKS

Loizos Kounios, University of Southampton, UK (lk9g12@soton.ac.uk)

How do evolving populations exhibit variation that enables adaptation in such a wide variety of challenging environments? One possibility is dumb luck – random variation. Another possibility is that via the slow adaptation of developmental biases and constraints, accumulated over a broad distribution of selective environments experienced in the past, evolution can tune the distribution of phenotypes explored to amplify promising variations and avoid less-useful avenues [1-3]. The problem for such evolution of evolvability [4-6], however, is that natural selection is myopic, and short-term benefits, e.g., from increased robustness, seem more likely to oppose than facilitate long-term evolvability [7]. As a result, no theory has been successful in characterising the general conditions for the evolution of evolvability. Here we simulate the evolution of a gene-regulation network and investigate how ontogenetic interactions affect evolvability. Specifically, we describe conditions under which the selective pressures on ontogenetic interactions systematically increase the speed of adaptation in the short term and the probability of finding high-fitness phenotypes in the long term. We show that there is a trade-off between mutational robustness and speed of adaptation when natural selection optimises ontogenetic interactions in varying selective environments characterised by smooth fitness landscapes. More importantly, we find that natural selection optimises ontogenetic interactions for long-term adaptation on rugged fitness landscapes, thus enabling evolution to find fitter phenotypes with higher probability.

[1] Pavlicev, M., Cheverud, J. M., and Wagner, G. P. (2011). "Evolution of Adaptive Phenotypic Variation Patterns by Direct Selection for Evolvability". Proc. R. Soc. B, Biol. Sci. 278.1713, pp. 1903–1912. [2] Clune, J., Mouret, J.-B., and Lipson, H. (2013). "The Evolutionary Origins of Modularity". Proc. R. Soc. B, Biol. Sci. 280.1755, 20122863.

doi:10.1098/rspb.2012.2863. [3] Watson, R. A., Wagner, G. P., et al. (2014). "The Evolution of Phenotypic Correlations and "Developmental Memory"". Evolution. In press. doi:10.1111/evo.12337. [4] Wagner, G. P. and Altenberg, L. (1996). "Perspective: Complex Adaptations and the Evolution of Evolvability". Evolution 50.3, pp. 967–976. [5] Pigliucci, M. (2008). "Is Evolvability Evolvable?" Nat. Rev. Genet. 9.1, pp. 75–82. [6] Brown, R. L. (2013). "What Evolvability Really Is". Br. J. Philos. Sci. doi:10.1093/bjps/axt014. [7] Clune, J., Misevic, D., et al. (2008). "Natural Selection Fails to Optimize Mutation Rates for Long-Term Adaptation on Rugged Fitness Landscapes". PLoS Comput. Biol. 4.9, e1000187. doi:10.1371/journal.pcbi.1000187."

THE RELATIONSHIP BETWEEN THE ADAPTATION OF INDIVIDUAL SPECIES AND WHOLE ECOSYSTEM BEHAVIOUR

Daniel Power, University of Southampton, UK (dap1e12@soton.ac.uk)

It is a priority to understand how ecosystems respond to, and recover from, environmental stresses, yet the inherent complexity of these natural systems makes analysing their underlying organisational principles a challenge. We are interested in how the behaviour of ecosystems are affected by the numerous coevolved interactions of their component species, and how the form of these interactions shapes the dynamical properties of ecosystems as a whole.

Here we present a study of species coevolving in an ecosystem whose dynamics are governed by Lotka-Volterra dynamics. By subjecting this model to specific patterns of environmental forcing that differentially affect the species within it, and simulating the effects of evolutionary pressures under these conditions, we find that the system develops attractors for these patterns. The development of these attractors creates an ecosystem that will consistently return to configurations of species densities corresponding to these previously experienced states, even in the absence of any simulated forcing. These 'memory-like' ecological dynamics are emergent from evolutionary changes at the species level. We recognise that the emergence of this adaptive system-level behaviour can be understood via a mechanical isomorphism with well-understood models from neural networks. Specifically, we illustrate how our system evolves in accordance with the principle of Hebbian learning: we find that species that co-occur 'wire together'.

Recognition of this isomorphism provides insight into how ecosystems may differentially respond to changes in environmental conditions: they may resist certain patterns of environmental forcing, but exhibit catastrophe in response to others, particularly if changes correlate with a historically experienced attractor. Similarly we observe how this conditioning affects the stability of species compositions, and recognise that the disturbance of particular sets of species is most likely to cause a regime shift between ecological attractors.

DIVISION OF LABOUR GAMES IN RELATION TO THE MAJOR TRANSITIONS IN EVOLUTION

Simon Tudge, University of Southampton, UK (sjt4g11@soton.ac.uk)

Throughout the history of life there are a number of examples of so called "major-transitions". These occur when previously independent entities coalesce to form higher level individuals. One such example is the emergence of multicellular organisms from single celled individuals. A salient feature of all such transitions is high levels of cooperation. The overwhelming majority of studies that formally study the evolution of cooperation use the prisoner's dilemma as their definition of cooperation. I argue that this game does not properly represent the biological reality of cooperation as it does not model gains from specialisation. I extend the notion of a cooperative dilemma (such as the prisoner's dilemma) to include the potential for the division of labour, and parameterise the conditions under which this may emerge.

CHANGING THE GAME

Adam Jackson, University of Southampton, UK (aj3e10@soton.ac.uk)

Why do social creatures play particular social games? The fitness consequences of social behaviours are initially set by the physical and ecological nature of the social interaction, such as competition for limited resources. But all social

behaviours occur against a social context. The same physical action, such as altruistic self-sacrifice, can have very different fitness outcomes depending on the context. Many different factors contribute to this social context, such as the population structure and relatedness of individuals. Individual-level adaptions can alter the social context, for example by changing the level of behavioural assortment - the likelihood that individuals interact with others with the same social strategies. Assortment on social behaviours is argued to be the ultimate cause for the successful spread of cooperative behaviours. A complete account of social evolution must consider how altruism and assortment-promoting traits evolve - that is, consider the coevolution of social behaviours and social context.

We can then ask, if a population can evolve to change the social game it is playing, how does it do so? Will the game become more of a selfish Prisoner's Dilemma scenario, because of the inherent benefits to selfish individuals of receiving the benefits of cooperation without paying the costs? Or it might change to a more harmonious game, because of the advantages to groups of increased cooperation? By considering metagames, 'games of games' in which the game played is also subject to evolutionary control, we investigate the coevolution of individual's social strategies with traits that affect the social conditions. In simple metagames we find that both these possibilities and others for the game change can happen, with the equilibria of the social game the strongest influence on the path the population takes through game-space.

PRE-TEMPLATE METABOLIC REPLICATORS: GENOTYPE-PHENOTYPE DECOUPLING AS A ROUTE TO EVOLVABILITY

William Hurndall, University of Southampton, UK (w.hurndall@soton.ac.uk)

The RNA World is generally heralded as the leading candidate for a template first vision of the origin of life, yet doubts as to the plausibility of the natural formation of RNA with catalytic function have led to revived interest in the metabolism first paradigm. Recent studies of the evolvability of reflexively autocatalytic sets of polymers have also revealed the nature of limited heredity in Farmer & Kaufmann's compartmentalised reaction networks. In the algorithmic sense, the lack of a meaningful distinction between data storage and functional expression results in a heritability-fitness dichotomy which gives an intrinsic selective advantage to those compartments with limited heredity. An idealised model is used explore a minimal set of dynamical requirements necessary to weaken the dichotomy. This is achieved by explicitly modelling an outer compartment 'phenotype', heritable only indirectly, in which competitive exponential growth may occur without compromising heredity of previously discounted non-competitive growth in an inner

sub-compartment, 'genotype'. Results show that heritable variation can be achieved under simulations of natural selection in populations of such metabolic replicators." The RNA World is generally heralded as the leading candidate for a template first vision of the origin of life, yet doubts as to the plausibility of the natural formation of RNA with catalytic function have led to revived interest in the metabolism first paradigm. Recent studies of the evolvability of reflexively autocatalytic sets of polymers have also revealed the nature of limited heredity in Farmer & Kaufmann's compartmentalised reaction networks. In the algorithmic sense, the lack of a meaningful distinction between data storage and functional expression results in a heritability-fitness dichotomy which gives an intrinsic selective advantage to those compartments with limited heredity. An idealised model is used explore a minimal set of dynamical requirements necessary to weaken the dichotomy. This is achieved by explicitly modelling an outer compartment 'phenotype', heritable only indirectly, in which competitive exponential growth may occur without compromising heredity of previously discounted non-competitive growth in an inner sub-compartment, 'genotype'. Results show that heritable variation can be achieved under simulations of natural selection in populations of such metabolic replicators.