Evolution of complex adaptations

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Abstract

A central challenge in evolutionary biology concerns the mechanisms by which complex adaptations arise. Such adaptations depend on the fixation of multiple, highly specific mutations, where intermediate stages of evolution seemingly provide little or no benefit. It is generally assumed that establishment of complex adaptations is very slow in nature, as they demand special population genetic circumstances. However, blueprints of complex adaptations in molecular systems are pervasive and generally have multiple independent origins, indicating that they can readily evolve. Here we discuss the potential mechanisms whereby such complex adaptations evolve with the aim to derive testable predictions. We first summarize the limits of non-adaptive scenarios, and argue that complex molecular traits can readily evolve through series of adaptive steps in dynamically changing environments.

Introduction

Darwin himself was highly aware of the problem of complex adaptation problem. He stated "If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down". Complex adaptations in molecular systems are prevalent (Lynch, 2010), and the examples include 1) new protein functions involving multiresidue interactions (e.g. disfulfide bonds), 2) emergence of multimeric enzymes, 3) assembly of molecular machines (flagellum, centrioles, the nuclear pore complexes), establishment of interactions between transcription factors and their binding sites, and 4) multi-step metabolic pathways.

Population genetic models have a long tradition to study the problem of complex adaptations (Wright, 1988). Theoretical studies indicate that the time to establishment of complex adaptations depends on population size, mutation rate, recombination, magnitude of the selective disadvantage of intermediate-state alleles, and the complexity of the adaptation. The relative contribution of these factors is currently a matter of intense debates. However, the extent to which these abstract considerations apply to specific cellular subsystems have remained unknown largely, partly due to the shortage of laboratory studies. Recent advances in experimental evolution and systems biology allowed studying the problem of complex adaptation in specific cellular subsystems in a rigorous manner.

Non-adaptive scenarios

One theory suggests that complex adaptations have non-adaptive origins, where neutral or slightly deleterious mutations prepare the ground for later beneficial mutations that lead to new, beneficial traits (Lynch, 2007 ; Amitai et al., 2007 ; Wagner, 2011 ; Barve and Wagner, 2013). Direct empirical support comes from laboratory RNA and protein evolution studies (Bershtein et al., 2008 ; Romero & Arnold, 2009 ; Hayden et al., 2011). They indicate that the potential for evolving new functions can sometimes be enhanced by allowing a period for the accumulation of neutral mutations. Along with detailed cases, it indicates that evolution of new protein functions frequently demand prior fixation of other, so called permissive mutations (Bridgham et al., 2009 ; Harms and Thornton, 2014). These mutations do not alter the molecular function of the protein, but are necessary to tolerate large-effect mutations that cause shift in specificity and are generally destabilizing protein structure. However, protein evolution studies also indicate that neutral drift followed by positive selection have met with mixed success in evolving improved function. This suggests that when high-fitness genotypes are sparse and well isolated on the adaptive landscape, neutral drift alone cannot be the main driver of new function (Petrie and Joyce, 2014).

Dynamic environment scenario

In its most general form, the dynamic environment scenario claims that evolution of complex adaptation is accelerated by complex or temporally fluctuating conditions. Population genetic models, computer simulations of genetic circuits and RNA molecules (Kashtan et al., 2007), and verbal arguments on early expansion of molecular pathways (Horowitz, 1945) indicate the feasibility of this scenario. Because fluctuating natural selection appear to be common at all temporal scales, the dynamic environment scenario could be a widespread mechanism of evolving complex adaptations. However, until recently, empirical support of these theoretical claims remained anecdotal. Recent advances in experimental evolution and systems biology allowed studying the problem of complex adaptation on a specific cellular subsystem in a rigorous manner. The major barrier to the dynamic environment model of complex adaptation may be the absence of relevant series of environmental conditions. However,

Carole Knibbe et al, eds., Proceedings of the ECAL 2017, Lyon, France, 4-8 September 2017,
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when cross-environment tradeoffs are present and varying environments facilitates adaptation by displacing populations trapped in local fitness peaks then the specific sequence of environments might be of little importance.

Finally, these considerations have implications on evolutionary computation. In computer science, standard genetic algorithms have a tendency to quickly converge to a local solution, and hence frequently fail to identify more promising regions of the search space. Application of dynamically changing 'environments' offers a natural strategy to maintain the diversity required to explore the adaptive surface (O'Neill et al., 2010). Similar considerations apply to protein engineering: we anticipate that evolutionary engineering to obtain desired function could be facilitated by temporally varying selection regime.

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