



The impact of interspecific competition on lineage evolution and a rapid peak shift by interdemetic genetic mixing in experimental bacterial populations

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ABSTRACT

Epistatic interactions between genes in the genome constrain the accessible evolutionary paths of lineages. Two factors involving epistasis that can affect the evolutionary path and fate of lineages were investigated. The first factor concerns the impact of competition with another species lineage that has different epistatic constraints. Five enteric bacterial populations were evolved by point mutation in medium containing a single limiting resource. Single-species and two-species cultures were used to determine whether different asexual lineages have different capacities for producing variants due to epistatic constraints, and whether their survival is determined by local inter-lineage competition with different species. Local inter-lineage competition quickly resulted in one successful lineage, with another lineage becoming extinct before finding a higher peak. The second factor concerns a peak-shifting process, and whether the sexual recombination between different demes can cause peak shifts was investigated. An *Escherichia coli* population consisting of a male (Hfr) and female strain (F^-) was evolved in a single limiting resource and compared to evolving populations containing the male or female strain alone. The *E. coli* sexual lineage was successful due to its ability to escape lower peaks and reach a higher peak, not because of a rapid approach to the nearest local peak the male or female asexual lineage could reach. The data in this study demonstrate that lineage survivability can be determined by the ability to produce beneficial mutations and checked by local competition between lineages of different species. Interspecific competition may prevent a population from evolving through crossing fitness valleys or adaptive ridges if it requires many generations to achieve peak shifts. The data also show that genomic recombination between different conspecific lineages can rapidly carry the combined lineage to a higher peak.

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1. Introduction

Adaptation evolves by natural selection on heritable phenotypic variation. Thus, given a particular selective regime, the capacity to generate variation, called evolvability, plays a pivotal role in the evolution of populations. Evolvability involves a genetic system, a genotype–phenotype mapping function involving robustness, which reduces the potential lethality of mutations, modularity, which reduces the number of mutations for producing phenotypically novel traits, and epistasis, the phenotypic consequences of interactions between different genes in the genome (Wagner and Altenberg, 1996; Kirschner and Gerhart, 1998). Evolvability is a higher-level adaptation distinct from the phenotypic adaptation of organisms. However, whether evolvability is a result of selection at a higher level, such as group (lineage) or species, or a by-product of

evolutionary processes at a lower level is controversial (Pigliucci, 2008).

Due to epistasis, the selective effect of a mutation may depend on the genetic background in which it appears (Cordell, 2002), and in this way, epistasis can constrain the accessible evolutionary paths. In a particular form of epistasis, called sign epistasis, the sign of the fitness effect of such a mutation is conditional on the genetic background, and interactions between loci can result in mutations that are individually deleterious but jointly beneficial (Weinreich et al., 2005). Many lines of evidence support the existence of sign epistasis in nature (Schrag et al., 1997; Maisnier-Patin et al., 2002; Weinreich et al., 2005; O'Hara et al., 1984; Giachetti and Holland, 1988; Burch and Chao, 2000).

Sign epistasis can give rise to multiple peaks on the fitness landscape and constrain the ability of natural selection to carry an evolving population to a genotype of highest fitness (Burch and Chao, 1999, 2000; Weinreich et al., 2005). The mechanisms of evolutionary escape from such local peaks have been a central and controversial issue in evolutionary biology for many years (e.g., Kirkpatrick, 1982; West-Eberhard, 1989; Whitlock, 1995; Coyne

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et al., 1997, 2000; Fear and Price, 1998; Wade and Goodnight, 1998; Pal and Miklos, 1999). Controversy also exists concerning the existence of the multi-peaked fitness landscape itself; it is a theoretical possibility that multi-peaks may disappear if the dimensionality of the fitness landscape is increased, indicating that apparently lower and higher peaks are connected through extra-dimensions without crossing fitness valleys (Gavrilets, 2003, 2004).

Wright (1932) proposed a mechanism by which species can break through the limitations of epistatic constraints in his shifting balance theory (SBT). Because phenotype determines fitness, a “genotype–phenotype” mapping function can be extended to a “genotype–fitness” mapping function, which is conceptualized as a fitness landscape in which populations (represented as a cloud of points) move on the surface of genotype–fitness space. The SBT postulates a complex process involving subdivided populations, drift, and inter-population selection; subdivided populations drift into an adjacent domain of attraction of a fitness peak with some crossing fitness valleys (phase 1), they climb uphill toward their fitness peaks (phase 2), the population at the highest peak spreads more migrants to other local populations, and the highest peak spreads into the entire species (phase 3). Although the SBT has enjoyed wide popularity among evolutionary biologists, it is still controversial with regards to its importance in the evolution of adaptation (e.g., Coyne et al., 1997, 2000; Wade and Goodnight, 1998; Goodnight and Wade, 2000). Specifically, the issue focuses on the validity of the process of shifting balance as a universal mechanism for adaptation, as it concerns the relative importance of the roles of drift (phase 1) and interdemic selection (phase 3), a special form of group selection, in the evolution of adaptation. The controversies surrounding this issue and the reality of the multi-peaked fitness landscape indicate that our understanding of the role of epistatic interactions, meta-population structure, and selection at the population level in the evolution of adaptation is incomplete.

In this paper, two factors that can affect the evolutionary path and fate of lineages and have been focused on less by previous authors are highlighted. Here, “lineage” is used interchangeably with “evolving population of organisms”. The first factor concerns the impact of local interspecific competition on the evolutionary path and fate of a given lineage. Species as global sets (“meta-populations”) of local populations do not evolve in isolation, but interact with other species in shared localities (van Valen, 1973). Among biotic interactions between species, interspecific (inter-lineage) competition can strongly affect the fate of species because it is a reciprocal negative interaction by which one can exclude the other. Because niche differentiation is a result of evolution, competition potentially works between different species in a common niche. Although major ecological rules are known to predict the outcomes of competition (Nakajima, 1998), interspecific competition on an evolutionary timescale cannot be predicted by these rules because ecological parameters for populations may change through mutation/recombination and selection. In other words, the outcome depends on the population’s evolvability. Different species are likely located in different domains of attraction of the fitness optima in a given niche. Therefore, interspecific competition could produce a large difference in the mean fitness between winning and losing lineages, where the winner completely excludes others or keeps their mean fitness very low, which magnifies differential emigration. Furthermore, if this is the case, the pressure of interspecific competition could prevent populations from evolving slowly through fitness valleys or nearly equal fitness ridges. However, such an impact of interspecific competition has not been effectively explored in the context of the above issues.

The second factor concerns peak shifts, a creative process of new lineages in the domain of attraction of a higher fitness optimum. If the above speculation is true, rapid peak shifts are important for lineage survival because populations at a lower peak may be

at a higher risk of extinction by competition with another species evolving in a shared niche. As a candidate mechanism for rapid peak shifts, sexual recombination between different demes is highlighted in this paper. Recombination has been suggested as being able to produce progeny that are not adjacent to either parental genotype in sequence space, permit evolutionary jumps through sequence space, and generate selectively accessible paths on landscapes where none are available to an evolving asexual population (Weinreich et al., 2005). Furthermore, the mixing of different demes increases genetic or phenotypic variance, which may facilitate peak shifts (Kirkpatrick, 1982; Whitlock, 1995). Therefore, rapid peak shifts can occur by genetic mixing between local populations of different genetic compositions, which may cause the mixed population to jump into a new domain of attraction of higher fitness peaks. Several direct experiments have tested the advantages of sex using microbial populations and support the hypothesis that sex speeds adaptive evolution by reducing clonal interference between beneficial mutations in the Fisher–Muller model (Colegrave, 2002; Cooper, 2007), removes deleterious mutations (Zeyl and Bell, 1997), and increases the rate of adaptation to a new harsh environment (Goddard et al., 2005). However, whether sex is able to carry the population from a low fitness peak to a higher one by reducing epistatic constraints remains unclear.

A series of experiments tested the above hypotheses. First, the evolutionary dynamics of asexual bacterial populations in vitro, with or without interspecific competition for a single limiting resource, were analyzed to determine the impact of interspecific competition. Second, interdemic mixing was evaluated using a sexual population of *Escherichia coli*. A mixture of F[−] and Hfr (“high frequency of recombination”) populations in the presence of a single limiting resource was evolved to adapt to the niche and compared to the evolution of asexual parental lineages in the same conditions. The Hfr strains arise from the integration of a conjugative plasmid, F factor, into the bacterial chromosome, which transfers a part or the whole of the chromosome to recipient F[−] (female) cells by conjugation (Lederberg and Tatum, 1946; Tatum and Lederberg, 1947; Hayes, 1953; Firth et al., 1996; Low, 1996). We examined whether the sexual lineage can reach a higher adaptive peak than the parental asexual lineages, and whether the sexual lineage excludes asexual parental lineages by local competition.

2. Materials and methods

2.1. Evolution of asexual populations with or without interspecific competition

Long-term cultures of single species and two-species interspecific competitions were carried out, in which the bacterial populations evolved by mutation in the presence of a single carbon/energy resource in a constant physical environment. The five enteric bacterial species, one including three different strains, used in the single-species culture are shown in Table 1. Strains with code ‘JCM’ were obtained from the Japan Collection of Microorganisms of RIKEN (The Institute of Physical and Chemical Research, Saitama, Japan). Strains with code ‘IFO’ were obtained from the Institute for Fermentation in Osaka. All these strains were purified by streaking five times on agar, and each was used as an original ancestral population stored at −80 °C with 15% glycerol until use. Several species pairs were chosen from among the five species for competition between post-evolved and pre-evolved populations. The evolutionary dynamics of competition were observed and compared with the evolution of single populations.

2.1.1. Long-term serial transfer cultures of single species/strain

Each single species or strain was grown at 30 °C for 24 h in a test tube containing 10 ml TN medium (1.2 g/l K₂HPO₄, 0.4 g/l KH₂PO₄, 0.5 g/l (NH₄)₂SO₄, 0.1 g/l MgSO₄·7H₂O, 0.01 g/l NaCl, 0.02 g/l CaCl₂·2H₂O) with 0.05 g/l glucose (sterilized using a 0.2 μm filter) as the single limiting resource. After vortexing, 0.1 ml of the suspension was transferred to the next new culture (i.e. 100-fold dilution). This procedure of incubation and transfer was repeated 70 times (465 generations). Temporal changes in specific growth rate were examined. Samples were periodically taken from the culture and stored at 4 °C until the growth characteristics were measured (within 10 days). The samples were also stored at −80 °C for additional tests when needed. Long-term serial transfer cultures were conducted in triplicate for all species/strains except for *Escherichia vulneris*, for which it was performed with one line.

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