Digital Sex: Causes and Consequences

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Abstract

Many theories have sought to explain the evolution of sex, but the question remains unanswered owing to the scarcity of compelling empirical tests. Here we summarize the results of two of our published studies investigating the evolution of sex using digital organisms. We used these evolving programs to test the hypothesis that sexual reproduction is advantageous in changing environments. We found that sex evolved to be the dominant mode of reproduction only when the environment was changing rapidly and substantially. Additionally, we measured the effects of sexual reproduction on genetic architecture, specifically modularity and epistasis. We found that sex profoundly influences genome organization, increasing modularity and decreasing the effects of interactions between mutations. Our studies have contributed to understanding both the causes and consequences of sexual reproduction, while also demonstrating the efficacy and power of *in silico* approaches to these issues.

Introduction

Why sex? The paradox of sexual reproduction – a process that is costly and complicated, yet widespread in nature – has fascinated biologists for well over a century, and has in turn generated a wide range of hypothesis and experimental tests [1-3]. One of the simplest and perhaps most intuitive explanations is that sex accelerates the rate of adaptation to novel or changing environments by increasing genotypic and phenotypic variation [4]. Here we summarize a previously published study testing this theory *in silico* [5] as well as another study examining the effects of recombination on genetic architecture [6].

Methods

All experiments were conducted using Avida software (freely available at http://avida.devosoft.org/), previously used in many studies of evolutionary trajectories and outcomes [7-8]. Digital organisms in Avida are short self-replicating computer programs that mutate, evolve, and reproduce either asexually or sexually, depending on which divide instruction they execute. Genomes were built from the default instruction set with 27 instructions including 2 divide instructions, divide-sex and divide-asex, only one of which can be expressed by any individual. In these studies, point, insertion, and deletion mutations occurred at rates of 0.002, 0.0005, and 0.0005 per instruction copied, respectively, with the same mutation rates applied to the divide instructions as all others. When a population was at its carrying capacity (here 3600 organisms), each new offspring replaced a randomly chosen organism. All experiments ran for 100,000 updates (the Avida time unit), and a generation typically required 5–10 updates, with the precise number depending on the organisms' genomic and phenotypic complexity.

Digital metabolism. An organism's genome may contain instructions that encode the ability to metabolize one or more substrates present in the environment. Metabolism of a substrate either accelerates or decelerates an organism's replication rate by a factor of 2^m, where m is the substrate's metabolic value and is positive or negative, signifying a nutrient or a poison, respectively. Fitness is calculated as the organism's total energy (energy obtained via metabolism in addition to basal energy provided equally to all organisms) divided by the time used to produce an offspring.

Environmental conditions. For the study of the effects of sexual versus asexual reproduction on genetic architecture, we evolved populations in a constant environment with 9 substrates that were always available in unlimited amounts. When testing the possible benefit of sex in changing environments, we used the same constant environment for the first 1000 updates of each experimental run, after which additional and changing substrates were introduced.

Recombination mechanism. Recombination is initiated by pairing up the genomes of two progeny that were produced sexually (i.e., divide-sex was expressed) and consecutively. The pair then exchanges a single continuous genomic region. The recombining region is chosen at random, but is matched between the organisms based on its relative position in the genomes. After recombination, both offspring are placed at random locations in the population, in the same manner as asexually produced organisms. The Avida mechanism of recombination (see [9] for a more detailed explanation) differs from others presented elsewhere in the Artificial Life literature. For example, in Tierra, sex involved recombination between living and deceased organisms [10], while in another system recombination somewhat resembled plasmid transfer [11]. Moreover, those studies were not driven by hypothesis

testing, but rather were descriptive and phenomenological in scope, making any comparisons difficult.

Results

Effects of changing environment on reproductive mode. The trajectories of the relative abundance of sexual and asexual organisms were highly variable during our experiments. Overall, asexual reproduction prevailed, except at the highest rates of environmental change, when sexual reproduction tended to be more common. This result was obtained both when comparing the final mode of reproduction and when measuring the time that populations spent as predominantly sexual or asexual over the course of their evolution.

Origin versus maintenance of sex. Given the costs of sexual reproduction, it may be easier to maintain sex than to evolve it *de novo* [12]. We found that over the entire duration of the experiment, the populations started with sexual ancestors were predominantly sexual 38% more often than those with asexual ancestors. However, when considering only the latter half of the experiment, this difference was reduced to 25%, indicating the time necessary to make the switch between the modes of reproduction also played an important role. Overall, sex overcame the barriers that hindered its establishment in previously asexual populations only about half the time even under the most favorable treatments.

Mode of reproduction and modularity. We conducted extensive mutational analysis of organisms randomly sampled from populations that evolved in a constant environment with either obligatory sexual or obligatory asexual reproduction. We found that sexual organisms evolved to have both higher physical modularity (shorter distance between the genomic sites encoding a computational trait) and higher functional modularity (less overlap between the sites that encode two or more traits) than asexual organisms.

Mutational sensitivity and epistasis. Sexual populations also evolved to be significantly more robust to individual mutations than the asexual populations. Under both modes of reproduction, the predominant mode of epistasis was alleviating (positive), with multiple mutations reducing fitness less than expected from their individual effects. This epistasis was weaker, however, in sexual than in asexual organisms.

Discussion and Conclusions

Our experiments show that rapidly changing environments can promote the evolution of sex, but at the same time, they call attention to some limitations of this theory. In particular, the parameter space that favored sex was quite limited, and the origin of sexual reproduction was more difficult than its maintenance. We also failed to observe a preponderance of aggravating (negative) epistasis, which is a key component of the mutational deterministic hypothesis [13], another well-known theory for the evolution of sex, thus adding to evidence against this hypothesis obtained in other systems [14-16]. Instead, our results suggest that an indirect benefit for sexual reproduction might arise from increased genomic modularity, perhaps leading to greater evolvability that sustains long-term increases in fitness [17-19].

More generally, the studies summarized here highlight the utility of digital organisms for testing complex evolutionary theories because they allow one to manipulate any relevant features of the environment, control for the confounding effects of ancestry, compare the origin and maintenance of organismal traits under the same conditions, and obtain data across many replicate populations and for many thousands of generations. Finally, the insights gained from our experiments with digital organisms may also lead to future research on biological systems to examine the generality of these results.

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