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Editorial: Digital evolution: Insights for biologists

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Editorial on the Research Topic Digital evolution: Insights for biologists

Over the past 30 years, digital evolution research has established itself as a valuable technique in biology, bridging experimental research with computational modeling (Ray, 1991; Adami, 2006). The articles in this Research Topic cover various aspects of digital evolution, ranging from the role of phenotypic plasticity on the adaptation process to that of ecological interactions in promoting diversification. In this editorial, we provide the context for the those papers, as well as summarize the main contributions of digital evolution to the development of ecology and evolutionary biology. We have organized those contributions by main topics, starting from the evolution of complexity.

1. Complexity

When evolution is free to proceed in a fashion most closely analogous to the way it operates in creating organic life on Earth, complexity arises at different levels (Ray, 1997). The complexity of a genetic architecture can be quantified by studying the exponent of the scale-free degree distribution of the network resulting from a functional genomic array. *In silico*, the exponent of the distribution depends on the mutation rate: low mutation rates give rise to distributions with high exponents and hence complex genetic architectures (Gerlee and Lundh, 2008). Complexity is highly linked to epistasis. The genes of complex digital organisms have a higher degree of interdependence than their simple counterparts (Lenski et al., 1999). Indeed, the evolution of complex traits is possible as long as the building blocks of the complex function are favored by selection (Lenski et al., 1999). This is so because novel traits appear by reusing existing information (Ofria et al., 2008) leading to a “complexity ratchet” that can be stronger than selection (Liard et al., 2020). The amount of information that a genome encodes about the world in which it evolves always increases when the fitness of the organism depends only on their own sequence information (Adami et al., 2000).

2. Robustness and evolvability

The ability of organisms to persist in the face of changing conditions requires a balance between robustness and evolvability, that is, between resisting and allowing phenotypic change (Lenski et al., 2006). This robustness is the most likely cause for the connected genotype networks and asymmetric phenotypic transitions found in digital organisms (Fortuna et al., 2017). Robustness increases with mutation rate and decreases with population size (Elena et al., 2007). Nevertheless, robustness is achieved at expenses of losing epistatic interactions (Edlund and Adami, 2004). This ability to produce adaptive evolutionary change is related to robustness. *In silico*, robustness promotes evolvability only at the last stages of the adaptive process (Elena and Sanjuán, 2008). Moreover, mutations are more frequent in changing environments (Crombach and Hogeweg, 2008) and encode more novel phenotypes in digital organisms with complex phenotypes (Fortuna et al., 2017).

3. Phenotypic plasticity

Using digital evolution to understand the mechanisms responsible for phenotypic plasticity (Fortuna, 2022) has shed light on the selective pressures that could favor one type of plasticity (genetic-based) over another (non-genetic-based). The simplest strategy for selection is to evolve plasticity with no genetic basis, which is analogous to the effect of the temperature on the phenotype (e.g., nearly all enzyme activity is temperature-dependent). This kind of plasticity comes at no fitness cost to the organisms. In contrast, changing gene expression in response to the environment requires much more complex selective pressures for plasticity to prevail (Clune et al., 2007). In changing environments, phenotypic plasticity provides a mechanism for organisms to regulate trait expression, which can stabilize populations. In this Research Topic, Lalejini et al. used *in silico* experiments to show that plasticity slows down evolutionary change in fluctuating environments because the genome of plastic organisms experiences less mutations compared to that of non-plastic organisms evolving under identical environments (Lalejini et al.).

4. The role of historical contingency in evolution

The role of chance variation and history on the adaptation process has been explored using populations of digital organisms. For example, long-term evolutionary change is highly contingent (Yedid and Bell, 2001, 2002) and depends on the mutation rate: at low mutation rates, dominant

genotypes descend from previous dominant genotypes, but at high mutation rates new dominant genotypes descend from one of the many rare genotypes (Yedid and Bell, 2001). In addition, evolutionary history influences the adaptation to a new environment, which suggests that past adaptation may hinder or promote some evolutionary outcomes over others (Wagenaar and Adami, 2004). Phylogenetic reconstruction methods and hypothesis on the diversification process that takes place after mass extinctions can also be tested *in silico*. On the one hand, phylogenetic reconstruction methods often fail when selection between branch points is absent (Hagstrom et al., 2004). On the other hand, diversification takes place faster after random mass extinctions than after selective extinctions (Yedid et al., 2009). Moreover, phenotypic traits that arise earlier in a lineage's history also tend to be expressed earlier in the development of individuals (Clune et al., 2012), which supports the hypothesis that ontology recapitulates phylogeny.

5. Ecological interactions among species

Many contributions to this Research Topic deal with eco-evolutionary dynamics. Digital evolution has been used to address ecological questions (Dolson and Ofria), involving pairwise competitive interactions (Cooper and Ofria, 2003); mutualism (Johnson and Wilke, 2004; Rocabert et al., 2017; Vostinar et al.), predator-prey (Shao and Ray, 2010), host-parasite (Zaman et al., 2011, 2014; Acosta and Zaman) and even entire ecological networks (Fortuna et al., 2013). The transition from generalist to specialist shows that antagonistic pleiotropy reduces niche breadth (Ostrowski et al., 2007). Coevolution among mutually dependent organisms reduces the amplitude of the oscillations of species abundances compared to purely ecological scenarios (Johnson and Wilke, 2004). Positive frequency-dependent selection promotes coexistence in digital predator-prey populations (Shao and Ray, 2010). Hosts coevolving with parasites are significantly more diverse than hosts evolving alone (Zaman et al., 2011) and their traits are more complex relative to that otherwise achieved (Zaman et al., 2014; Acosta and Zaman). Indeed, host resistance traits arising spontaneously as exaptations increase the complexity of host-parasite networks (Fortuna et al., 2017).

6. Genome architecture

One of the main results from digital evolution experiments on genome architecture is that mutation rate limits genome size, supporting the Drake's empirical rule observed *in vivo* (Drake, 1991). When mutation rate per site is high, evolution

promotes small-size genomes at expenses of reducing fitness since evolving more complex functions involves more genes (Knibbe et al., 2007). This is so because smaller genomes undergo less mutations per replication and hence move a population away from an error threshold (Wilke et al., 2001). In contrast, under low mutation rates, insertions are more beneficial than deletions (Gupta et al., 2016) and the gain of robustness allows for the accumulation of non-coding sequences (Knibbe et al., 2007), driving genome expansion and the exploration of the mutational neighborhood. Selection plays also an important role in shaping genome size. Indeed, the genome reduction observed in some bacteria can be reproduced *in silico* by lowering the selection pressure (Batut et al., 2013).

7. Gene regulatory networks

Small genomes with few genes have only a very basic regulation activity while large ones develop complex regulatory networks with the number of transcription factors scaling quadratically with the number of metabolic genes (Molina and van Nimwegen, 2009). The same trend evolves *in silico* as response to the mutational pressure (Beslon et al., 2010). Moreover, breaking up interactions among genes (i.e., reducing the epistatic effects of mutations) diminishes the deleterious effect of mutations in environments with high mutation rates (Edlund and Adami, 2004). Yet, deleterious mutations facilitate the evolution of complex, beneficial functions (Covert et al., 2013). Indeed, interactions among genes are required to evolve complex traits (Lenski et al., 2003). These epistatic interactions among genes to increase fitness take place as well between plasmids and the chromosome (Misevic et al., 2013).

8. The evolution of sex

Digital evolution can also be used to test the hypothesis that sexual reproduction is advantageous in changing environments (Misevic et al., 2010). When the environment changes rapidly and substantially, it is easier to maintain sexual reproduction than for asexual organisms to invade a formerly asexual population. It can also be used to test hypothesis on the evolution of sexual displays and mating preferences (Chandler et al., 2012). Mate preferences spread easily once they appear and are only limited when they are very costly, which suggests that sexual displays and viability might be regulated by common genetic mechanisms (i.e., pleiotropy). Indeed, sexual reproduction shapes the genetic architecture (e.g., the genomes of sexual organisms being more modular than those of asexual ones). By evolving genomes of digital organisms, Misevic et al. (2006) find that genes encoding different functional traits have less overlap and genes encoding a

particular trait are more tightly clustered on the genome of sexual organisms than on the genome of the asexual ones. Moreover, epistasis is weaker in sexual than in asexual organisms (Misevic et al., 2006).

9. The evolution of cooperation

Genetic architecture may promote the evolution of cooperation in populations of digital organisms (Frénoy et al., 2013). The properties of the public good also influence the evolution of cooperation (Misevic et al., 2012). Group selection (Knoester et al., 2007) and kin selection (Goings et al., 2004; Clune et al., 2011) are also explored *in silico*. For example, kin-altruism persists despite the presence of kin-cheaters (Goings et al., 2004), and altruistic genes are favored by natural selection only if they target altruism to only their copies (Clune et al., 2011).

10. Major evolutionary transitions

Dividing tasks among specialized group members is an important aspect of the major transitions in evolution. For example, when task-switching costs increase, groups of digital organisms increasingly evolve division of labor strategies (Goldsby et al., 2012). In addition, digital evolution provides experimental evidence supporting the hypothesis that the cells that contribute to the body's functionality but cannot produce an offspring themselves arise as an adaptation to confine metabolic work that damages a cell's DNA, which allows germ cells to keep their DNA pristine for future multicellular offspring (Goldsby et al., 2014). This transition to multicellularity is observed even allowing each organism to manage its own spatial distribution and reproductive process, which lead to the emergence of several distinct life histories as Moreno and Ofria show in this Research Topic.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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