



OPEN ACCESS

EDITED AND REVIEWED BY
George L. W. Perry,
The University of Auckland,
New Zealand

*CORRESPONDENCE
Miguel A. Fortuna
fortuna@ebd.csic.es

SPECIALTY SECTION
This article was submitted to
Models in Ecology and Evolution,
a section of the journal
Frontiers in Ecology and Evolution

RECEIVED 05 September 2022
ACCEPTED 27 September 2022
PUBLISHED 13 October 2022

CITATION
Fortuna MA, Beslon G and Ofria C
(2022) Editorial: Digital evolution:
Insights for biologists.
Front. Ecol. Evol. 10:1037040.
doi: 10.3389/fevo.2022.1037040

COPYRIGHT
© 2022 Fortuna, Beslon and Ofria. This
is an open-access article distributed
under the terms of the [Creative
Commons Attribution License \(CC BY\)](#).
The use, distribution or reproduction
in other forums is permitted, provided
the original author(s) and the copyright
owner(s) are credited and that the
original publication in this journal is
cited, in accordance with accepted
academic practice. No use, distribution
or reproduction is permitted which
does not comply with these terms.

Editorial: Digital evolution: Insights for biologists

Miguel A. Fortuna^{1*}, Guillaume Beslon² and Charles Ofria^{3,4,5}

¹Computational Biology Lab, Estación Biológica de Doñana, Spanish National Research Council, Seville, Spain, ²Université de Lyon, INSA-Lyon, LIRIS UMR CNRS 5205, INRIA Beagle Team, Lyon, France, ³BEACON Center for the Study of Evolution in Action, Michigan State University, East Lansing, MI, United States, ⁴Ecology, Evolution, and Behavior Program, Michigan State University, East Lansing, MI, United States, ⁵Department of Computer Science and Engineering, Michigan State University, East Lansing, MI, United States

KEYWORDS

artificial life, evolvability, complexity, ecological networks, robustness

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.

Funding

This work was supported by the Spanish Ministry of Science and Innovation through the Ramón y Cajal Programme (RyC2018-024115-1) and Knowledge Generation Grant Programme (PID2019-104345GA-I00), as well as by Plan Andaluz de Investigación, Desarrollo

e Innovación (PAIDI 2020) of Junta de Andalucía (PY20_00765).

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.

References

- Adami, C. (2006). Digital genetics: unravelling the genetic basis of evolution. *Nat. Rev. Genet.* 7, 109–118. doi: 10.1038/nrg1771
- Adami, C., Ofria, C., and Collier, T. C. (2000). Evolution of biological complexity. *Proc. Natl. Acad. Sci. U.S.A.* 97, 4463–4468. doi: 10.1073/pnas.97.9.4463
- Batut, B., Parsons, D. P., Fischer, S., Beslon, G., and Knibbe, C. (2013). *In silico* experimental evolution: a tool to test evolutionary scenarios. *BMC Bioinformatics* 14, S11. doi: 10.1186/1471-2105-14-S15-S11
- Beslon, G., Parsons, D. P., Sanchez-Dehesa, Y., Pena, J. M., and Knibbe, C. (2010). Scaling laws in bacterial genomes: a side-effect of selection of mutational robustness? *Biosystems* 102, 32–40. doi: 10.1016/j.biosystems.2010.07.009
- Chandler, C. H., Ofria, C., and Dworkin, I. (2012). Runaway sexual selection leads to good genes. *Evolution* 67, 110–119. doi: 10.1111/j.1558-5646.2012.01750.x
- Clune, J., Ofria, C., and Pennock, R. T. (2007). “Investigating the emergence of phenotypic plasticity in evolving digital organisms,” in *Proceedings of the European Conference on Artificial Life* (Lisbon), 74–83. doi: 10.1007/978-3-540-74913-4_8
- Clune, J., Goldsby, H. J., Ofria, C., and Pennock, R. T. (2011). Selective pressures for accurate altruism targeting: evidence from digital evolution for difficult-to-test aspects of inclusive fitness theory. *Proc. R. Soc. B.* 278, 666–674. doi: 10.1098/rspb.2010.1557
- Clune, J., Pennock, R. T., Ofria, C., and Lenski, R. E. (2012). Ontogeny tends to recapitulate phylogeny in digital organisms. *Am. Nat.* 180, E54?E63. doi: 10.1086/666984
- Cooper, T., and Ofria, C. (2003). “Evolution of stable ecosystems in populations of digital organisms,” in *Proceedings of the International Conference on Artificial Life* (Dortmund), 227–232.
- Covert, A. W., Lenski, R. E., Wilke, C. O., and Ofria, C. (2013). Experiments on the role of deleterious mutations as stepping stones in adaptive evolution. *Proc. Natl. Acad. Sci. U.S.A.* 110, E3171?E3178. doi: 10.1073/pnas.1313424110
- Crombach, A., and Hogeweg, P. (2008). Evolution of evolvability in gene regulatory networks. *PLoS Comput. Biol.* 4, e1000112. doi: 10.1371/journal.pcbi.1000112
- Drake, J. W. (1991). A constant rate of spontaneous mutation in DNA-based microbes. *Proc. Natl. Acad. Sci. U.S.A.* 88, 7160–7164. doi: 10.1073/pnas.88.16.7160
- Edlund, J. A., and Adami, C. (2004). Evolution of robustness in digital organisms. *Artif. Life* 10, 167–179. doi: 10.1162/106454604773563595
- Elena, S. F., and Sanjuán, R. (2008). The effect of genetic robustness on evolvability in digital organisms. *BMC Evol. Biol.* 8, 284. doi: 10.1186/1471-2148-8-284
- Elena, S. F., Wilke, C. O., Ofria, C., and Lenski, R. E. (2007). Effects of population size and mutation rate on the evolution of mutational robustness. *Evolution* 61, 666–674. doi: 10.1111/j.1558-5646.2007.00064.x
- Fortuna, M. A. (2022). The phenotypic plasticity of an evolving digital organism. *R. Soc. Open Sci.* 9, 220852. doi: 10.1098/rsos.220852
- Fortuna, M. A., Zaman, L., Wagner, A., and Bascompte, J. (2017). Non-adaptive origins of evolutionary innovations increase network complexity in interacting digital organisms. *Philos. Trans. R. Soc. B.* 372, 20160431. doi: 10.1098/rstb.2016.0431
- Fortuna, M. A., Zaman, L., Wagner, A., and Ofria, C. (2013). Evolving digital ecological networks. *PLoS Comput. Biol.* 9, e1002928. doi: 10.1371/journal.pcbi.1002928
- Frénoy, A., Taddei, F., and Misevic, D. (2013). Robustness and evolvability of cooperation. *Artif. Life* 13, 53–58. doi: 10.1162/978-0-262-31050-5-ch008
- Gerlee, P., and Lundh, T. (2008). The emergence of overlapping scale-free genetic architecture in digital organisms. *Artif. Life* 14, 265–275. doi: 10.1162/artl.2008.14.3.14303
- Goings, S., Clune, J., Ofria, C., and Pennock, R. T. (2004). “Kin-selection: the rise and fall of kin-cheaters,” in *Proceedings of the International Conference on Artificial Life* (Boston), 303–308.
- Goldsby, H. J., Dornhaus, A., Kerr, B., and Ofria, C. (2012). Task-switching costs promote the evolution of division of labor and shifts in individuality. *Proc. Natl. Acad. Sci. U.S.A.* 109, 13686–13691. doi: 10.1073/pnas.1202233109
- Goldsby, H. J., Knoester, D. B., Ofria, C., and Kerr, B. (2014). The evolutionary origin of somatic cells under the dirty work hypothesis. *PLoS Biol.* 12, e1001858. doi: 10.1371/journal.pbio.1001858
- Gupta, A., LaBar, T., Miyagi, M., and Adami, C. (2016). Evolution of genome size in asexual digital organisms. *Sci. Rep.* 6, 25786. doi: 10.1038/srep25786
- Hagstrom, G. L., Hang, D. H., Ofria, C., and Torng, E. (2004). Using Avida to test the effects of natural selection on phylogenetic reconstruction methods. *Artif. Life* 10, 157–166. doi: 10.1162/106454604773563586
- Johnson, T. J., and Wilke, C. O. (2004). Evolution of resource competition between mutually dependent digital organisms. *Artif. Life* 10, 145–156. doi: 10.1162/106454604773563577
- Knibbe, C., Coulon, A., Mazet, O., Fayard, J. M., and Beslon, G. (2007). A long-term evolutionary pressure on the amount of noncoding DNA. *Mol. Biol. Evol.* 24, 2344–2353. doi: 10.1093/molbev/msm165
- Knoester, D. B., McKinley, P. K., and Ofria, C. (2007). “Using group selection to evolve leadership in populations of self-replicating digital organisms,” in *Proceedings of the Annual Conference on Genetic and Evolutionary Computation* (Lisbon), 293–300. doi: 10.1145/1276958.1277016
- Lenski, R. E., Barrick, J. E., and Ofria, C. (2006). Balancing robustness and evolvability. *PLoS Biol.* 12, E428. doi: 10.1371/journal.pbio.0040428
- Lenski, R. E., Ofria, C., Collier, T. C., and Adami, C. (1999). Genome complexity, robustness and genetic interactions in digital organisms. *Nature* 400, 661–664. doi: 10.1038/23245
- Lenski, R. E., Ofria, C., Pennock, R. T., and Adami, C. (2003). The evolutionary origin of complex features. *Nature* 423, 139–144. doi: 10.1038/nature01568
- Liard, V., Parsons, D. P., Rouzaud-Cornabas, J., and Beslon, G. (2020). The complexity ratchet: stronger than selection, stronger than evolvability, weaker than robustness. *Artif. Life* 26, 38–57. doi: 10.1162/artl_a_00312
- Misevic, D., Frénoy, A., Parsons, D. P., and Taddei, F. (2012). Effects of public good properties on the evolution of cooperation. *Artif. Life* 13, 218–225. doi: 10.7551/978-0-262-31050-5-ch030
- Misevic, D., Ofria, C., and Lenski, R. (2006). Sexual reproduction reshapes the genetic architecture of digital organisms. *Proc. R. Soc. B.* 273, 457–464. doi: 10.1098/rspb.2005.3338
- Misevic, D., Ofria, C., and Lenski, R. E. (2010). Experiments with digital organisms on the origin and maintenance of sex in changing environments. *J. Hered.* 101, S46–S54. doi: 10.1093/jhered/esq017
- Misevic, D., Frénoy, A., and Taddei, F. (2013). “*In silico* evolution of transferable genetic elements,” in *Proceedings of the European Conference on Artificial Life* (Taormina), 200–207. doi: 10.7551/978-0-262-31709-2-ch030

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

- Molina, N., and van Nimwegen, E. (2009). Scaling laws in functional genome content across prokaryotic clades and lifestyles. *Trends Genet.* 25, 243–247. doi: 10.1016/j.tig.2009.04.004
- Ofria, C., Huang, W., and Torng, E. (2008). On the gradual evolution of complexity and the sudden emergence of complex features. *Artif. Life* 14, 255–263. doi: 10.1162/artl.2008.14.3.14302
- Ostrowski, E. A., Ofria, C., and Lenski, R. E. (2007). Ecological specialization and adaptive decay in digital organisms. *Am. Nat.* 169, E1–E20. doi: 10.1086/510211
- Ray, T. S. (1991). “An approach to the synthesis of life,” in *Artificial Life II, Santa Fe Institute Studies in the Sciences of Complexity*, eds C. Langton, C. Taylor, J. D. Farmer, and S. Rasmussen (Redwood City, CA: Addison-Wesley), 371–408.
- Ray, T. S. (1997). Evolving complexity. *Artif. Life Robot.* 1, 21–26. doi: 10.1007/BF02471107
- Rocabert, C., Knibbe, C., Consuegra, J., Schneider, D., and Beslon, G. (2017). Beware batch culture: seasonality and niche construction predicted to favor bacterial adaptive diversification. *PLoS Comput. Biol.* 13, e1005459. doi: 10.1371/journal.pcbi.1005459
- Shao, J., and Ray, T. S. (2010). “Maintenance of species diversity by predation in the Tierra system,” in *Proceedings of the International Conference on Artificial Life* (Odense), 533–540.
- Wagenaar, D. A., and Adami, C. (2004). Influence of change, history, and adaptation on digital evolution. *Artif. Life* 10, 181–190. doi: 10.1162/106454604773563603
- Wilke, C. O., Wang, J. L., Ofria, C., Lenski, R. E., and Adami, C. (2001). Evolution of digital organisms at high mutation rates leads to survival of the flattest. *Nature* 412, 331–333. doi: 10.1038/35085569
- Yedid, G., and Bell, G. (2001). Microevolution in an electronic microcosm. *Am. Nat.* 157, 465–487. doi: 10.1086/319928
- Yedid, G., and Bell, G. (2002). Macroevolution simulated with autonomously replicating computer programs. *Nature* 420, 810–812. doi: 10.1038/nature01151
- Yedid, G., Ofria, C., and Lenski, R. E. (2009). Selective press extinctions, but not random pulse extinctions, cause delayed ecological recovery in communities of digital organisms. *Am. Nat.* 173, E139–E154. doi: 10.1086/597228
- Zaman, L., Devangam, S., and Ofria, C. (2011). “Rapid host-parasite coevolution drives the production and maintenance of diversity in digital organisms,” in *Proceedings of the Annual Conference on Genetic and Evolutionary Computation*, 219–226. doi: 10.1145/2001576.2001607
- Zaman, L., Meyer, J. R., Devangam, S., Bryson, D. M., Lenski, R. E., and Ofria, C. (2014). Coevolution drives the emergence of complex traits and promotes evolvability. *PLoS Biol.* 12, e1002023. doi: 10.1371/journal.pbio.1002023