

Evolved digital ecosystems: Dynamic steady state, not optimal fixed point

Randal S. Olson^{1,2}, Masoud Mirmomeni^{1,2}, Tim Brom^{1,2}, Eric Bruger^{1,3},
Arend Hintze^{1,3}, David B. Knoester^{1,3}, and Christoph Adami^{1,3}

¹BEACON Center for the Study of Evolution in Action

²Department of Computer Science & Engineering

³Department of Microbiology & Molecular Genetics

Michigan State University, East Lansing, MI 48824

olsonran@msu.edu

Abstract

Traditional models of ecosystems often assume that the species composing an unperturbed ecosystem become fixed so that only the relative abundances of the species change over time. Such ecosystems are said to have reached an optimal fixed point. However, recent work has suggested that neutral evolutionary processes can significantly alter the species composition of an ecosystem, allowing the ecosystem to exist in a dynamic steady state. Here, we investigate the stability of ecosystems and the nature of the equilibrium that forms using the digital evolution platform Avida, tracking evolving ecosystems over thousands of generations. We find that the communities that form are remarkably stable, and do not experience a significant loss of diversity in the long run even in experimental treatments where the communities suffer catastrophic population bottlenecks. When diversity rebounds, ecological communities are reconstituted in a different form than the one that was destroyed, but this difference is comparable to the difference the system would have accumulated if it had been left untouched. Thus, digital ecological communities exist in a dynamic steady state, which ultimately eliminates the effect of historical disturbances.

Introduction

While the complexity of cellular and organismal biology is unquestionably stunning, it is often argued that the complexity of ecological communities is even more staggering, as they consist of co-adapted groups of organisms (Loehler, 2004). However, it is not immediately clear that ecological communities are necessarily any more complex. It is conceivable that general laws might guide the assembly, evolution, and even decay of ecosystems, simply because the interactions between species, as well as species with their environments, are simpler than the interactions between cellular components, or between cells within tissues that compose an organism. Indeed, simple ecosystems are usually modeled by systems of coupled differential equations that keep track of species and resource abundances (Tilman, 1982). In such models, ecosystems frequently exhibit an *ecological* steady state (Brock, 1967; Deakin, 1975; Aoki, 1988; Michaelian, 2005). In this state, resources flow through the system by being consumed and

replaced. Individuals come and go, but the species composition of the community is largely intact over large time scales. If this is so, then from the point of view of the species composition, the system has actually reached an *optimal fixed point*. In other words, the identity and frequency of a species is selected for, and does not change in the long run. Such ecological fixed points have been found experimentally in small systems (with a handful of species) (Rainey and Travisano, 1998) with evolution limited to only several weeks. Other experiments have found that communities will display different patterns of succession upon disruption by bottlenecks (e.g., in gut microbiota after administration of antibiotics), but the community ultimately arrives at a new stable state (Peterfreund et al., 2012).

It is difficult to ascertain whether any of these observations carry over to real ecological assemblies because tracking ecosystems over geological times is not possible, and modeling of such communities with standard methods such as systems of differential equations cannot shed light on this issue. While the stability of ecological communities can be studied (May, 1972, 1974; Montoya et al., 2006; Mougi and Kondoh, 2012), the existence of a dynamic steady state—where the community is constantly changing over evolutionary time scales and the only (approximate) constant is the number of species—cannot be studied because in the standard mathematical descriptions the number of possible participants is necessarily fixed from the outset. In contrast, in a dynamic steady-state, new species constantly emerge and established ones go extinct, while the ecological cohesion of the community remains intact.

If ecological assemblies are governed predominantly by neutral evolutionary processes (see, e.g., Chu and Adami 1999; Hubbell 2001; Volkov et al. 2003) rather than niche-specific adaptation, then dynamically changing fixed points should be expected. Here, we use digital evolution (Adami, 1998; Ofria and Wilke, 2004; Adami, 2006) as a tool to study the question of ecosystem evolution and stability from an “experimental” rather than mathematical point of view (see also Fortuna et al. 2013). We put the word experimental in quotes because not everyone is satisfied that what we learn

from digital experiments can carry over to biological assemblies of species. However, a significant amount of work with digital models has shown that they reproduce the basic phenomena associated with long-term evolution (Lenski et al., 2003; Wagenaar and Adami, 2004; Adami, 2006). Digital evolution experiments have even pointed to undiscovered effects in evolutionary theory (Wilke et al., 2001), which have subsequently been verified in “biochemicals.” The adaptive radiation of species in Avida has been studied previously (Cooper and Ofria, 2002; Chow et al., 2004; Walker and Ofria, 2013), but only a handful of studies have investigated the role of chance events on the outcome of evolution in digital systems. Previous studies on fluctuating environments, such as periods of resource scarcity (Yedid et al., 2008) and sudden changes in environment resource compositions (Wagenaar and Adami, 2004), and their effects on the evolution of specific tasks (i.e., specializing on a specific resource) have hinted that chance events do indeed affect the final outcome of evolution. Additionally, press (gradual) and pulse (instant) extinctions have been shown to alter the evolutionary path of a population enough to result in an entirely dissimilar final population (Yedid et al., 2009). Finally, an analysis of different forms of perturbations on digital ecosystems (such as mass extinctions) has shown that they affect the phylogenetic structure of the population, but leave little trace elsewhere (Yedid et al., 2012). These promising results highlight the need for more experiments studying the impact of historical contingency in the realm of digital evolution.

Here, we investigate the impact of population bottlenecks on the species composition of populations observed over the course of digital evolution. First, we show that population bottlenecks—even bottlenecks as small as a single organism—do not change the mean number of species in an ecosystem in the long run. Next, we provide evidence that populations evolve to use the same resources regardless of whether they experience a bottleneck. Finally, we demonstrate that while these populations use the same resources, the species that compose these populations do not remain at a single optimal fixed point. Rather, we suggest that evolving digital populations are in a dynamic steady state.

Methods

We use the digital evolution platform Avida (Adami, 1998; Ofria and Wilke, 2004; Adami, 2006) to investigate the impact of population bottlenecks on populations of evolving digital organisms over long periods of evolutionary time. Avida has previously been used to investigate many fundamental aspects of evolution, including the evolutionary origins of complexity (Lenski et al., 2003), genetic organization (Misevic et al., 2006), adaptive radiation (Chow et al., 2004), and the division of labor (Goldsby et al., 2012). In this study, we subject the evolving populations to bottlenecks of varying size, then compare (1) the num-

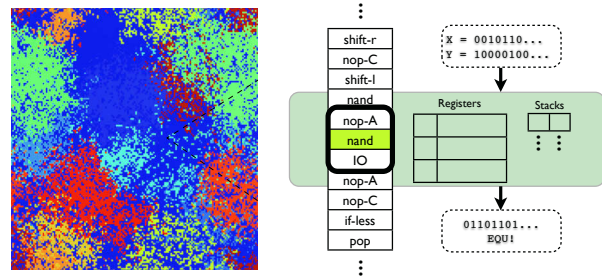


Figure 1: An Avida population containing multiple genomes (left) and the internal structure of an individual organism, called an Avidian (right).

ber of species, (2) the resource usage of the entire population, and (3) the resource usage of individual species between each experimental treatment. With these three measurements, we experimentally determine whether chance events such as population bottlenecks can significantly alter the evolutionary result of an evolving population. In the remainder of this section, we describe the main features of Avida and the experimental design of the study presented in this paper. All experiments were conducted with Avida version 2.12.3, which can be freely downloaded from <http://avida.devosoft.org/>.

Avida

Figure 1 shows a typical Avida population and the internal structure of a digital organism, called an Avidian. These Avidians metabolize resources and reproduce in a common environment that is split up into individual cells, where a single Avidian inhabits each cell. During their lifetime, the Avidians execute their genome—a circular list of assembly-like instructions—using their virtual CPU. Executing these instructions allows the Avidians to perform various tasks in the environment (e.g., metabolize resources, described in more detail below), which can be thought of as the Avidian’s phenotype. In this study, each Avidian’s virtual CPU contains a circular list of three general-purpose registers, two general-purpose stacks, and four special-purpose heads, which are pointers into the Avidian’s genome, similar to a traditional program counter and stack pointer.

Further, each Avidian in this study is self-replicating, which means that it must contain instructions in its genome to copy itself and produce an offspring. During the self-replication process, the genome copy experiences mutations that change a single instruction to a different random instruction. Once the Avidian finishes copying itself, the copy is placed into a random cell elsewhere in the environment, i.e., the population is well-mixed. If the chosen cell is already inhabited by another Avidian, the existing Avidian is replaced by the new Avidian. By repeatedly following this metabolization-replication-mutation process, the Avid-

ian population is able to evolve and adapt to the environment over long time periods.

The Avida environment can be thought of as a “digital chemostat,” where simulated resources are constantly flowing in and out of the environment at predefined rates. Avidian genomes change over evolutionary time, and adapt to perform various logic tasks (e.g., AND, OR, and XOR), because the performance of such tasks is rewarded by “SIP” (single instruction processing) units. Each SIP unit gives an Avidian the ability to execute exactly one instruction, and can be thought of as the digital equivalent of ATPs, which power biochemical cells. Without SIPs, Avidian genomes cannot be executed. In order to perform a logic task, the Avidian program must have the correct sequence of instructions to input random binary numbers from the environment, perform a computation on them using a single logic instruction available to them (NAND), then write the resulting value back into the environment. At the same time, a resource associated with that logic task must be present in the environment. Because complex logic operations (such as EQU and XOR) can and must be built from simpler ones, Avidians must evolve the equivalent of metabolic pathways, only on a computational level. As an Avidian metabolizes more and more resources over its lifetime, it is able to execute more instructions faster than Avidians that have not metabolized any resources. Consequently, Avidians are indirectly selected to adapt to their environment and consume the available resources in the digital chemostat.

In this study, we use the “resource-9” environment, in which 9 logic tasks (NOT, NAND, AND, ORN, OR, ANDN, NOR, XOR, and EQU) are rewarded equally for completing them. The resource associated with each task flows into the digital chemostat at a fixed rate of 10 units/update. In general this rate can be varied, but we chose here the level at which the highest speciation rate was observed in Chow et al. (2004). Each Avidian can only consume each particular resource up to 5 times per update. Because resources are limited, the average amount of resource an Avidian consumes is proportional to the mean abundance of that resource across the population. In this limited resource environment, generalists that consume all 9 resources are selected against because they would consume each and every resource to the point that the net benefit of generalization is smaller than if each species specializes on one resource. As a consequence, mutants that evolve to tap into an unused resource have an advantage at first, and over time communities assemble that divide up the resource space roughly equally (as each resource is valued the same).

Any settings differing from the Avida defaults are described in Table 1. These settings are drawn from Chow et al. (2004) to replicate their Avida adaptive radiation experiments.

Setting	Value
Copy mutation rate	0.005
Insertion/deletion mutation rate	0.0
Min/max genome length	100
Max population	3000

Table 1: Custom Avida settings for this study.

Control and bottleneck experiments

As a control, we first perform a set of Avida experiments for 10^6 updates with no population bottlenecks. These experiments provide a base expectation for what the evolved communities should look like if bottlenecks have no impact on the evolutionary outcome of a population. Next, we carry out another set of Avida experiments for 10^6 updates, but with the populations experiencing a single bottleneck of varying sizes (1, 5, 10, 20, 100, 200, 300, 400, and 500) at update 5×10^5 . We execute the bottleneck procedure by removing random Avidians from the population until the population is reduced to the desired bottleneck size. After the bottleneck is applied, we allow the population to evolve without intervention for the remaining 5×10^5 updates.

We initialize each Avida experiment with the same default ancestor, an Avidian with a genome length of 100 that is only capable of self-replicating. We repeat each experiment in replicate 100 times with random number seeds of 1-100. Before every bottleneck and at the end of every Avida run, we record the entire current population and the population history for use in a species clustering algorithm (in order to count species), described below. In addition, we collect the standard Avida statistics (averages, counts, resource, tasks, etc.) every 100 updates to perform population resource usage comparisons.

Species clustering algorithm

To determine the species present in a population, we employ the species clustering algorithm from Chow et al. (2004), which clusters species based on phylogenetic distance. We calculated the phylogenetic distance between two Avidians by counting the number of ancestors between them along the lines of descent leading to their last most recent common ancestor. First, the algorithm requires the user to calibrate a threshold phylogeny depth value (T) by calculating the T value necessary for the clustering algorithm to predict $\leq 25\%$ of runs having 2 species, $\leq 2.26\%$ of having 3 species, and $\leq 0.1\%$ showing 4 species, when the algorithm is run on a set of 100 or more Avida runs with unlimited resources. It is known that when resources are unlimited, generalists will evolve, and the community will have exactly one species (Cooper and Ofria, 2002; Chow et al., 2004). With this calibrated T (here, $T = 200,142$), the clustering algorithm then forms clusters of species in the reconstructed phylogeny by grouping genotypes less than T away from the

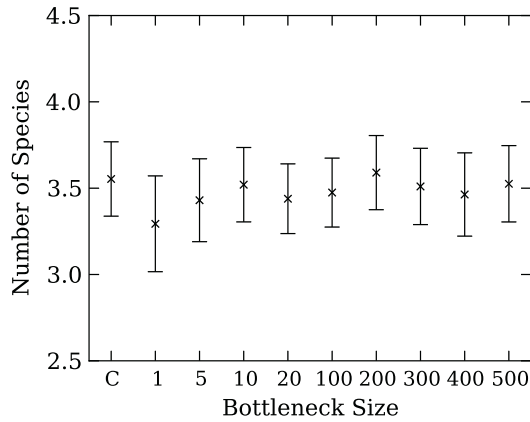


Figure 2: Average number of species for differing experiments based on the phylogenetic depth clustering algorithm. Each experimental treatment is listed along the bottom. The control experiment is labeled “C” and the bottleneck experiments are labeled with the size of the bottleneck. Error bars are two standard errors over 100 replicates.

computed genotype “species basins.” After the clustering algorithm identifies all of the species clusters, it outputs (1) the number of species and (2) the representative genotype of each species basin. This output allows us to compare species counts and species resource utilization between experimental treatments with and without population bottlenecks to determine whether the bottleneck had a significant effect on the evolutionary outcome of the population. The number of species predicted by this algorithm compares well with the “ecological” number of species, which is obtained by turning off mutation rate and counting the number of genotypes that remain in equilibrium after a long time (Cooper and Ofria, 2002; Chow et al., 2004).

Difference in resource usage

After identifying the species for a given time point, we use Avida’s Analyze mode to determine each of the species’ resource utilization vector $\vec{\phi} = (\phi_1, \phi_2, \dots, \phi_9)$, where ϕ_r is the average number of times the species has obtained resource r (associated with task r) during its lifetime. We then normalize this vector so that the ϕ_r of the resource that is used most by that species is set to 1.0.

In order to calculate the difference in resource usage between two species i and j , consider two resource utilization vectors $\vec{\phi}_i$ and $\vec{\phi}_j$. We define the difference in utilization between those species as the Euclidean distance $d_{ij} = |\vec{\phi}_i - \vec{\phi}_j|$. What is the difference between two communities? If community C_a is defined by the assembly $C_a = (\vec{\phi}_1, \dots, \vec{\phi}_m)$ and community b by $C_b = (\vec{\phi}_1, \dots, \vec{\phi}_m)$, we first pad the assembly vector C of the community with the smaller number of species with null vectors, and define

the assembly difference matrix as

$$D_{ij}^{(ab)} = |\vec{\phi}_i^{(a)} - \vec{\phi}_j^{(b)}|, \quad (i, j = 1, \dots, n). \quad (1)$$

Because this distance depends on the ordering of species in the community vector, we define the community distance D as the minimum of the trace of the distance matrix, minimized over all permutations of the species order. Thus, let P be a permutation matrix (of the set of $n!$). Then

$$D = \min_P \text{Tr}(PD^{(ab)}). \quad (2)$$

In other words, to find the difference between two communities, we compute all pairwise distances between the species of both populations. If both communities are identical, the sum of the diagonal of this pairwise distance matrix must be 0.0, but only if we have correctly matched all species. If the populations have a different number of species, we supplement the population with fewer species using no resources. To perform the match, we test all permutations of the distance matrix (i.e., with different species orders) to minimize the trace (the sum of the diagonal elements) of the matrix. This measure provides the minimum distance between two communities in species resource usage space.

Results

Species counts

Figure 2 shows the species counts based on phylogenetic depth for the control experiment in comparison to the varying bottleneck experiments. On average, the control resulted in 3.55 ± 0.22 species (mean \pm two standard errors) and none of the experiments resulted in a significantly different species count. It is interesting to note that even experiments with a bottleneck size of only one organism did not have their ultimate species counts significantly impacted.

Comparison of task distributions

Next, we compare the average population resource usage

$$\vec{R} = \frac{1}{N_{\text{tot}}} (N_1, \dots, N_9), \quad (3)$$

where N_r is the number of times resource r has been consumed by the population *per update*, and $N_{\text{tot}} = \sum_{i=1}^9 N_i$, for the final populations of each experiment. Differences in \vec{R} allow us to examine if there is a significant difference in overall resource usage before and after bottlenecks of different sizes.

Figure 3 shows the \vec{R} of the final control and bottleneck populations. Qualitatively, there appears to be little difference in the resource usage between the different experiments, indicating that the populations recovered from the bottleneck and eventually reconstituted an ecosystem that consumes resources at a rate comparable to an untouched

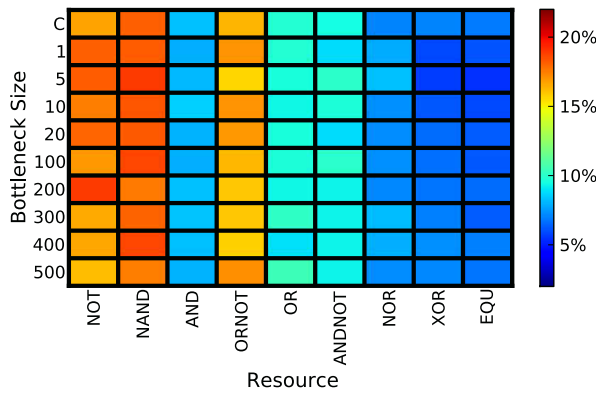


Figure 3: Average fraction of tasks performed per update R_r (defined in Equation 3) by the Avidians in the final population of different experiments over 100 replicates. The experiments are listed along the left side. The control population at update 10^6 is labeled “C” and the experimental populations are labeled with the size of the bottleneck. Each task along the bottom is a logical function in Avida which can be considered a resource that a digital organism can adapt to metabolize.

ecosystem. To confirm our qualitative analysis, we compute the Pearson correlation coefficient between the \vec{R} of the bottleneck populations and the control populations. The smallest correlation is between the control populations and the 5-organism bottleneck experimental populations ($\rho = 0.98$), which still indicates a strong correlation in the resource usage vectors. Thus, even the most severely bottlenecked populations reconstituted the same resource usage after a long period of evolutionary time, even though the species composition could be very different. Similar overall resource usage by different communities could be an indication of *functional redundancy* (Tilman et al., 1997; Wohl et al., 2004).

Comparison of individual species resource usage

The populations evolve to use the same resources over all experimental conditions, but the species within a population (the community assembly) may look very different from one experiment to another. To establish a baseline, we look at the differences in species resource usage among the experimental populations after 5×10^5 updates. Shown in Figure 4, we compute the mean difference in species resource usage between communities evolved in 100 independent populations (excluding a direct comparison of a population with itself) and find $D = 2.26 \pm 0.025$. With this measure, we characterize the differences that arise in communities simply because each population takes its own historical path.

Next, we compare the communities between the reference populations at 5×10^5 updates to two sets of populations at update 10^6 : One set of control populations that never experienced a population bottleneck, and another set of experimen-

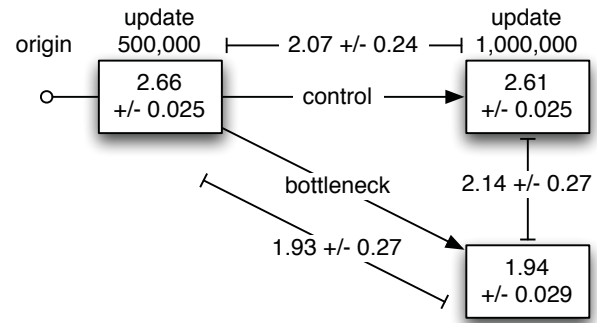


Figure 4: Overview of the population’s species resource usage differences. The values shown are the mean difference D (\pm two standard errors) between and within populations. All populations from update 0 (labeled “origin”) to update 5×10^5 had the same evolutionary history. At update 5×10^5 , the experimental populations (labeled “bottleneck”) experienced a single bottleneck reducing the population to one organism, whereas the control populations (labeled “control”) were untouched. After the treatment at update 5×10^5 , the populations were then allowed to evolve for another 5×10^5 updates. The resulting populations are labeled “update 1,000,000.”

tal populations that experienced a severe population bottleneck (a single organism) at update 5×10^5 . We found that there was no significant difference in inter-population differences between the reference populations at update 5×10^5 (mean \pm two standard errors, $D = 2.66 \pm 0.025$) and the control population at update 10^6 ($D = 2.61 \pm 0.025$). In contrast, the inter-population differences within the experimental populations were significantly reduced ($D = 1.94 \pm 0.029$).

While populations evolve to use the same resources regardless of treatment (Figure 3), it is not clear whether or not the populations are at a dynamic steady state or an optimal fixed point. If the populations do not change over evolutionary time (i.e., the populations are at an optimal fixed point), we would expect the difference in species resource usage between the baseline populations at update 5×10^5 and the control populations at update 10^6 to be minimal, if not 0.0. Instead, when comparing each control population at update 10^6 with its corresponding reference population at update 5×10^5 , we observe that the populations are composed of significantly different species (Figure 4, $D = 2.07 \pm 0.24$). Additionally, we find a significant difference when performing the same comparisons between the reference populations and experimental populations that experienced a population bottleneck ($D = 1.93 \pm 0.27$). This is the same difference that we find when we again perform the same comparison between the control populations and experimental populations at update 10^6 ($D = 2.14 \pm 0.27D$). Thus, although

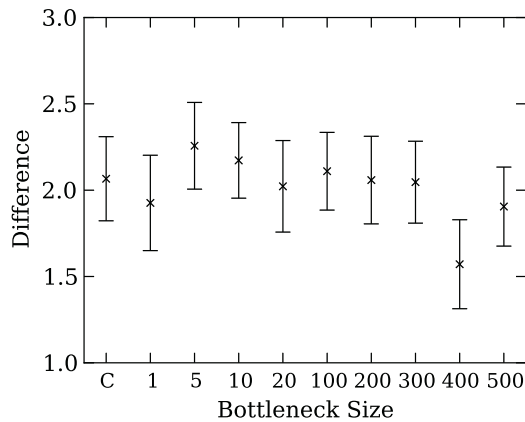


Figure 5: Mean difference D in species resource usage between the populations at update 5×10^5 and the populations at update 10^6 . Each experimental treatment is listed along the bottom. The control populations are labeled “C,” whereas the bottleneck populations are labeled with the size of the bottleneck. Error bars are two standard errors over 100 replicates.

the experimental populations are significantly different from the reference populations, they are just as different as they would have become if they never experienced a population bottleneck. Together, these data highlight our two major findings:

- (1) population bottlenecks do not have a significant effect on the species composition of a population over long evolutionary periods, and
- (2) over sufficiently long evolutionary periods, populations are in a dynamic steady state rather than at an optimal fixed point.

In a catastrophic population bottleneck, only one organism survives the bottleneck, which effectively destroys the ecosystem and reduces the number of species to 1. By subjecting the populations to such a severe population bottleneck, the population is forced to re-evolve every other species, which may explain the results above. What if the populations experience a less severe population bottleneck? A less severe population bottleneck would preserve most, if not all, of the ecosystem and its species. In Figure 5, we further demonstrate that regardless of the population bottleneck size, populations do not maintain an optimal fixed point. Additionally, we show in Figure 6 that regardless of the population bottleneck size, all experimental populations at update 10^6 have the same difference from the control population at update 10^6 . Thus population bottleneck size does not affect the species composition of populations over sufficiently long evolutionary periods.

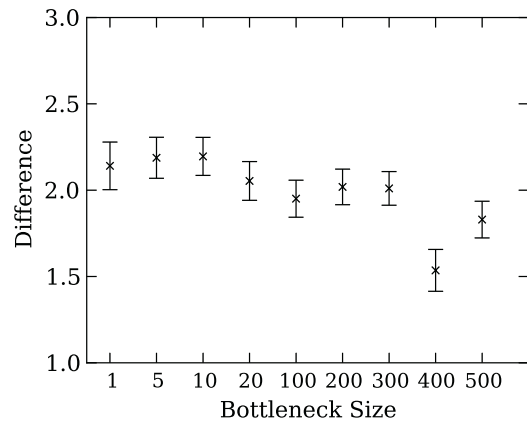


Figure 6: Mean difference D in species resource usage between the control populations at update 10^6 and the bottleneck populations at update 10^6 . Each experimental treatment is listed along the bottom. The bottleneck populations are labeled with the size of the bottleneck. Error bars are two standard errors over 100 replicates.

Discussion

Competition over resources shapes ecological communities, and creates assemblies that are highly adapted to their environment. Species (or ecotypes in microbial communities) can only be maintained if they are adapted to different niches, which means that they must each “make a living” differently. In our model system, this means that each species must specialize to predominantly use a different resource. Here we have asked: Once an ecosystem is established, will it maintain its species composition over long periods of time (i.e., an optimal fixed point), or do species continue to change over evolutionary time (i.e., a dynamic steady-state)?

We find that populations evolve the same number of species regardless of the bottleneck size, and that the number of species in a population is much smaller than the number of available resources (on average around 4, compared to the theoretical maximum of 9). Each population has approximately the same distribution of consumed resources, again regardless of experimental conditions. Analyzing populations in detail, we find that species partition the resources (i.e., niches) in many different ways, and continue to do so during evolution. While technically speaking, no new species form after the establishment of a community (as opposed to what is observed in perfectly neutral models of species diversity, e.g. de Aguiar et al. (2009), where the rate of speciation is constant over time), we notice that the species themselves continue to change, and the community with them. Applying bottlenecks of different sizes, including catastrophic events where only a single organism survives, has no effect on this phenomenon. Ecosystems re-

form after the catastrophic event (either in a form similar to the community before the event, or differently), but continue to change thereafter. Thus, evolving ecosystems resemble a dynamic steady-state rather than an optimal fixed point.

These results have significant implications for experimentalists who work with biological systems that require regular bottlenecks on the population to conduct the experiment, e.g., the *E. coli* long term evolution experiment (LTEE) (Lenski, 2011). This study demonstrates that these regular population bottlenecks do not affect the long-term evolution of populations, nor do they significantly affect the species composition of the population in the long-term. We note that at least one population of the LTEE seems to have developed a community of coexisting types (Blount et al., 2012).

Prior biological experiments suggested that population bottlenecks imposed on ecological communities leads to several waves of succession followed by the establishment of a new stable state with a similar degree of diversity compared to the initial stable state (Peterfreund et al., 2012). These experiments, however, were all conducted on a very short time scale. We evolved our populations for 25,000 generations between measurements (assessment of species composition), which allows for much more neutral evolution. We note that in these experiments, each of the 9 possible resources were worth the same to an Avidian, i.e., switching from one resource to another would not be beneficial (nor detrimental) as long as the concentration of that resource in the community is the same. It is possible that this setting creates more neutrality in the landscape compared to a setting where each resource has a distinct metabolic payoff, and it would be interesting to study a fitness landscape with different metabolic payoffs in detail in future work.

It might also seem surprising that we observe drift in the community even though the number of species in the community is quite low (between 2-6, on average). Most of the interesting biological communities consist of many more species: It has even been suggested that soil microbial communities could harbor up to 10^6 species (Gans et al., 2005). It would be interesting to test community drift and turnover when there are an order of magnitude more niches to be occupied, which can be done in Avida by placing digital organisms in the “logic-77” environment, giving 77 distinct niches. We have also not addressed the effect of trophic levels on ecosystem stability and turnover. Recent modeling efforts (Mougi and Kondoh, 2012) suggest that the variety of trophic interactions stabilize these communities, which could in principle lead to a reduction in community drift.

Conclusions

We found that populations of digital organisms exposed to an environment with limited resources rapidly radiate to take advantage of the available niches, but that the rate of speciation stops long before all niches are occupied. Severe bottle-

necks can destroy these communities, but stable communities rapidly re-evolve, albeit with a different species composition. We have shown that the species composition of these communities is not affected by bottlenecks of any size in the long run, simply because these communities are in a state of constant flux anyway: The communities form dynamic steady-states, where the species are constantly changing the resources they specialize on. While the evolved communities are resistant to invasion (Chow et al., 2004), they are not resistant to change. Because the available niches can be occupied by a multitude of functionally similar or even identical species (and perhaps because each resource in the logic-9 environment is worth the same), the communities themselves are subject to a considerable amount of drift, even when the community as a whole remains cohesive. The communities are resistant to invasion due to the particular trade-offs each species has incurred in its adaptive specialization. In this respect, Avidian communities behave much as predicted by Tilman’s “stochastic niche theory” (Tilman, 2004): They are dominated by both adaptive forces (generating the trade-offs) as well as neutral forces (stochastic assembly and drift). Thus, we suggest that further experimentation with Avidian ecosystems can generate significant progress in our understanding of ecological theory and experiments.

Acknowledgements

Part of this work (including all data) is the result of a BEACON class final project (CSE 845) at Michigan State University. We would like to thank the instructors Drs. Charles Ofria and Ian Dworkin for their advice on the interpretation of the results during the class period. This work was supported in part by the Paul G. Allen Family Foundation, the National Science Foundation (NSF) BEACON Center for the Study of Evolution in Action under Cooperative Agreement DBI-0939454, and NSF grant OCI-1122617. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the NSF. We wish to acknowledge the support of the Michigan State University High Performance Computing Center and the Institute for Cyber Enabled Research (iCER).

References

- Adami, C. (1998). *Introduction to Artificial Life*. TELOS Springer Verlag, New York, NY.
- Adami, C. (2006). Digital genetics: unravelling the genetic basis of evolution. *Nat Rev Genet*, 7(2):109–118.
- Aoki, I. (1988). Entropy laws in ecological networks at steady state. *Ecological Modelling*, 42:289–303.
- Blount, Z. D., Barrick, J. E., Davidson, C. J., and Lenski, R. E. (2012). Genomic analysis of a key innovation in an experimental *escherichia coli* population. *Nature*, 489:513–518.

- Brock, T. D. (1967). The ecosystem and the steady state. *BioScience*, 17:166–169.
- Chow, S. S., Wilke, C. O., Ofria, C., Lenski, R. E., and Adami, C. (2004). Adaptive radiation from resource competition in digital organisms. *Science*, 305(5680):84–6.
- Chu, J. and Adami, C. (1999). A simple explanation for taxon abundance patterns. *Proc Natl Acad Sci U S A*, 96(26):15017–9.
- Cooper, T. and Ofria, C. (2002). Evolution of stable ecosystems in populations of digital organisms. In Standish, R. K., Bedau, M. A., and Abbass, H. A., editors, *Proceedings of the Eighth International Conference on Artificial Life*, pages 227–232.
- de Aguiar, M. A. M., Baranger, M., Baptestini, E. M., Kaufman, L., and Bar-Yam, Y. (2009). Global patterns of speciation and diversity. *Nature*, 460(7253):384–7.
- Deakin, M. A. B. (1975). The steady states of ecosystems. *Mathematical Biosciences*, 24:319–331.
- Fortuna, M. A., Zaman, L., Wagner, A. P., and Ofria, C. (2013). Evolving digital ecological networks. *PLoS Comput Biol*, 9(3):e1002928.
- Gans, J., Wolinsky, M., and Dunbar, J. (2005). Computational improvements reveal great bacterial diversity and high metal toxicity in soil. *Science*, 309(5739):1387–90.
- 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(34):13686–13691.
- Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Lenski, R. E. (2011). Evolution in action: a 50,000 generation salute to charles darwin. *Microbe*, 5:30–33.
- Lenski, R. E., Ofria, C., Pennock, R. T., and Adami, C. (2003). The evolutionary origin of complex features. *Nature*, 423(6936):139–144.
- Loehler, C. (2004). Challenges of ecological complexity. *Ecological Complexity*, 1:3–6.
- May, R. M. (1972). Will a large complex system be stable? *Nature*, 238:413–414.
- May, R. M. (1974). *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, N.J.
- Michaelian, K. (2005). Thermodynamic stability of ecosystems. *J. Theor. Biol.*, 237:323–335.
- Misevic, D., Ofria, C., and Lenski, R. E. (2006). Sexual reproduction reshapes the genetic architecture of digital organisms. *Proc Biol Sci*, 273(1585):457–64.
- Montoya, J. M., Pimm, S. L., and Solé, R. V. (2006). Ecological networks and their fragility. *Nature*, 442(7100):259–64.
- Mougi, A. and Kondoh, M. (2012). Diversity of interaction types and ecological community stability. *Science*, 337(6092):349–51.
- Ofria, C. and Wilke, C. O. (2004). Avida: a software platform for research in computational evolutionary biology. *Artificial Life*, 10(2):191–229.
- Peterfreund, G. L., Vandivier, L. E., Sinha, R., Marozsan, A. J., Olson, W. C., Zhu, J., and Bushman, F. D. (2012). Succession in the gut microbiome following antibiotic and antibody therapies for clostridium difficile. *PLoS One*, 7(10):e46966.
- Rainey, P. B. and Travisano, M. (1998). Adaptive radiation in a heterogeneous environment. *Nature*, 394:69–72.
- Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc Natl Acad Sci U S A*, 101(30):10854–61.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., and Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277:1300–1302.
- Tilman, G. D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, N.J.
- Volkov, I., Banavar, J. R., Hubbell, S. P., and Maritan, A. (2003). Neutral theory and relative species abundance in ecology. *Nature*, 424(6952):1035–7.
- Wagenaar, D. A. and Adami, C. (2004). Influence of Chance, History, and Adaptation on Digital Evolution. *Artificial Life*, 10(2):181–190.
- Walker, B. L. and Ofria, C. (2013). Evolutionary potential is maximized at intermediate diversity levels. In Adami, C., Bryson, D. M., Ofria, C., and Pennock, R. T., editors, *Proceedings 13th International Conference on the Simulation and Synthesis of Life*, pages 116–120.
- 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(6844):331–333.
- Wohl, D. L., Arora, S., and Gladstone, J. R. (2004). Functional redundancy supports biodiversity and ecosystem function in a closed and constant environment. *Ecology*, 85:1534–1540.
- Yedid, G., Ofria, C. A., and Lenski, R. E. (2008). Historical and Contingent Factors Affect Re-evolution of a Complex Feature Lost During Mass Extinction in Communities of Digital Organisms. *Journal of Evolutionary Biology*, 21(5):1335–1357.
- Yedid, G., Ofria, C. A., and Lenski, R. E. (2009). Selective press extinctions, but not random pulse extinctions, cause delayed ecological recovery in communities of digital organisms. *The American Naturalist*, 173(4):E139–E154.
- Yedid, G., Stredwick, J., Ofria, C. A., and Agapow, P.-M. (2012). A comparison of the effects of random and selective mass extinctions on erosion of evolutionary history in communities of digital organisms. *PLoS One*, 7(5):e37233.