What Factors Drive the Evolution of Mutualism?

Anya E. Vostinar
BEACON Center for the Study of Evolution in Action
Michigan State University
vostinar@msu.edu

Luis Zaman
BEACON Center for the Study of Evolution in Action
University of Washington
luis.zaman@gmail.com

Charles Ofria
BEACON Center for the Study of Evolution in Action
Michigan State University
ofria@msu.edu

CCS Concepts

•**Computing methodologies** → **Artificial life;**

Keywords

Artificial life; mutualism

1. INTRODUCTION AND METHODS

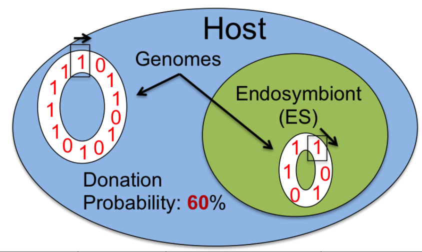
Mutualisms occur when interactions between two species lead to increased fitness in both partners and are widespread [2]. Mutualisms are at risk of cheaters, which can quickly destroy the mutually beneficial arrangement [1], leading to the question of how mutualisms can evolve and be maintained. While examining existing mutualisms can give some insight into how various factors affect the stability of the mutualism, it is difficult to experimentally test the influence of these factors on the evolutionary origins and long-term maintenance of a mutualism.

1.1 Symbulation - An Artificial Life Simulation for Endosymbionts

Symbulation models coevolution between hosts and endosymbionts. Genomes are circular bit-strings (subject to mutations at a rate of 1% per bit) for host (length 100) and endosymbiont (50). Hosts compete for space in the world. Each update, each host is allowed to read the next bit in its genome. Only if the bit is a '1', does the host's replication progress increase by 1%. A host is copied once its replication progress has reached 100%. When a host is copied, its offspring is put into a randomly-chosen adjacent cell, killing whatever organism was there previously. When a host reproduces, its own replication progress is reset to 0% and it must again count up to 100%.

1.2 Endosymbionts

In Symbulation, endosymbionts live exclusively in a host, as shown in Figure 1. Whenever a host is able to read one of its bits (a *CPU cycle*), the host's *donation probability*



Time step	Read Bit	Host Replication	ES Replication
1	Host: 1	1%	0%
2	ES: 1	2%	2%
3	ES: 0	2%	4%
4	Host: 0	2%	4%
5	ES: 0	2%	8% (Two 0's in a row)

Figure 1: The host and endosymbiont both have a genome of bits and the host has a donation probability (evolvable elements in red). Execution of the genomes could proceed with the host donating three updates to the endosymbiont. The endosymbiont has a block of the same bit and gains more replication progress. Blue arrows highlight when one partner's replication progress increases.

determines if the endosymbiont will be able to read a bit instead of the host. This donation probability starts at 60% and is mutated separately from the bit string via a normal distribution with a standard deviation of 0.1.

Endosymbionts can increase replication progress with blocks of the same bit up to the current gene. If the current bit is a zero, the endosymbiont's replication progress is increased by twice the number of uninterrupted zeroes and the host gains nothing. If the current bit is a one, the endosymbiont gains 2% progress and the host's progress is increased by the number of uninterrupted ones.

If an endosymbiont achieves at least 100% replication progress, it attempts *horizontal transmission*. It can fail because there is not a neighboring host, the offspring fails the user-configured horizontal transmission probability test, or the offspring fails to oust a pre-existing endosymbiont (50% probability). When a host reproduces, there is a user-configured probability that the host's endosymbiont will also reproduce and an offspring endosymbiont will infect the host's offspring, called *vertical transmission* rate (VTR).

The simulation and all statistical files are available at https://github.com/anyaevostinar/mutualism_model

GECCO '16 July 20-24, 2016, Denver, CO, USA

ACM ISBN 978-1-4503-4323-7/16/07.
DOI: http://dx.doi.org/10.1145/2908961.2908967

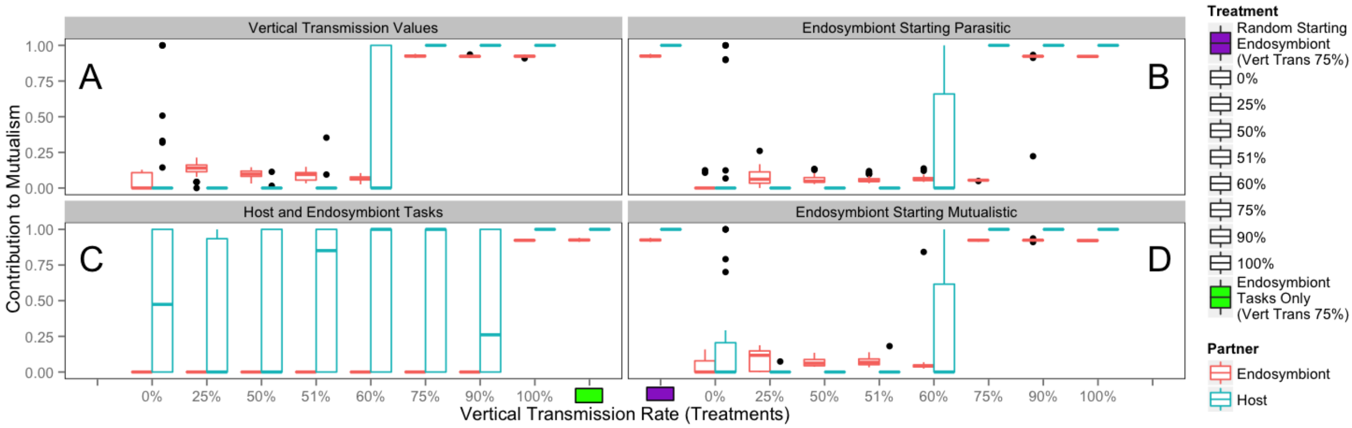


Figure 2: Mutualism after 200k updates. A) When the vertical transmission rate (VTR) is set above 60%, both partners are mutualistic. B) When the endosymbiont starts more parasitic than random, at 75% VTR the host cooperates with the endosymbiont (blue) and the endosymbiont is parasitic (red). C) Without division of labor between partners, mutualism only evolves at 100% VTR. D) When the endosymbiont starts more mutualistic than random, VTR above 60% is necessary for consistent evolution of mutualism.

2. RESULTS

2.1 Vertical Transmission Rates

As shown in Figure 2A, when the VTR is 75% or above, the endosymbiont and the host both evolve to invest fully in the mutualism. The host gives up control over its own replication and relies on its endosymbiont to drive the replication of the pair. When the VTR is 60% or lower, however, the endosymbiont evolves to contribute nothing to the host, and on average the host correspondingly evolves to prevent the endosymbiont from stealing any of its resources. This result means that a 100% VTR is not necessary for mutualism to evolve and VTRs of 75% and higher are sufficient for mutualism.

2.2 Endosymbiont-Only Tasks

We found that when the host can perform the same tasks as the endosymbiont, the host quickly evolves to exclude the endosymbiont by not providing any CPU cycles to it, as shown in Figure 2C. The exception to this result is when vertical transmission is at 100%, and the host continues to donate all CPU cycles to the endosymbiont and fully rely on the endosymbiont for replication. This result is due to the endosymbiont being basically a second chromosome in the host given that vertical transmission is guaranteed, and so there is no conflict between host and endosymbiont. When compared to the results of the previous experiment, it is clear that endosymbiont-only tasks make a mutualism possible when vertical transmission is 75%.

These results indicate that unless vertical transmission is guaranteed, the endosymbiont needs to be able to contribute to the host's replication in a way that the host cannot easily evolve to accomplish on its own.

2.3 Ancestral Symbiotic Relationships

As shown in Figure 2D, when the endosymbiont starts more parasitic in behavior than random, only VTRs of 90 and 100% select for the endosymbiont to contribute to the host replication. At a VTR of 75% it is interesting that the host contributes to the mutualism completely, but the endosymbiont does not contribute to the host at all, making it a true parasitism.

Conversely, when an endosymbiont starts with more mutualistic behavior, the host and endosymbiont evolve to completely contribute to the mutualism with VTR 75% and above.

These results highlight the difficulty for the endosymbiont to change from being a parasite to a mutualist and vice versa. To evolve away from one extreme, an endosymbiont must initially decrease replication progress either for the pair or for itself. However, over evolutionary time, large pressures can lead to endosymbionts changing their relationship with their host.

3. ACKNOWLEDGMENTS

The members of the Devolab was vital to this project. This material is based in part upon work supported by the National Science Foundation under Cooperative Agreement No. DBI-0939454. 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 National Science Foundation.

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