

Template and Guidelines for Using L^AT_EX in

The American Naturalist

Owen E. Cook^{1,*}

Generic H. Collaborator^{2,†}

Additional Q. Expert³

1. University of Chicago, Chicago, Illinois 60637;
2. University of Toronto, Toronto, Ontario M5S 1A5, Canada;
3. Middle Eastern Technical University, Çankaya, Ankara 06800, Turkey.

* Corresponding author; e-mail: amnat@uchicago.edu.

† Deceased.

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Abstract

1

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Introduction

A major evolutionary transition, in principal, is the transition from independent replicators to associations, and this process dictates the diverse complex life on Earth. Two kinds of major transitions are recognized: "fraternal" transitions and "egalitarian" transitions. "Fraternal" transitions involve related independent entities and are often promoted by collaboration among kins (ref). In contrast, the "egalitarian" transitions involves unrelated independent entities, and it remains a challenge to understand how they come together and form tight associations (ref). Intuitively, conflict may prevail such a relationship as these entities can replicate independently. Even when some form of dependence evolve, it may be difficult to maintain if it does not bring sufficient benefit to either party or both of them.

Tight associations of once independent entities such as eukaryotes show a complete renouncement of independent replication and a full cooperation from both parties. However, on the evolutionary transition process, it is natural that dependency may not evolve synchronously from both parties, and uncooperative behaviour such as exploitation and harmful effect exerted from one party might be common. Studying the major evolutionary transitions thus should involve studying two evolutionary continuum at the same time. The first continuum involves independent reproduction ranging from complete renouncement of independent reproduction (i.e. becoming tight association) to retaining full level of independent reproduction (i.e. full independent entity). The second continuum is the well-known mutualism-parasitism continuum. a key question arises: does obligate symbiosis evolve easier from free-living organism under mutualistic or parasitic relationships?

Because of the conventional thinking that the end of the major evolutionary transition is an association between two independent identities with high interdependency and low conflict, a majority of theoretical research focus on the evolution of how cooperation can be maintained in associations (ref). These studies ignore how the independent entities lose their ability to reproduce while it is very possible that they cooperate and still maintain their independence. In

fact, without considering the evolution of independent reproduction, these studies can be related to several work of mutualism-parasitism continuum (ref). In particular, if cooperation cannot be maintain, cheaters who do not contribute to the benefit of the association will prosper. These cheaters are parasites if harmness to the partners is considered whereas they are commensalism if no harm is induced or if harmness is not considered in the study.

Few studies actually consider the evolution of renouncement of independent reproduction. Nguyen and van Ballen (ref) showed that it is in fact difficult for a symbiont to lose its independent reproduction, suggesting that evolution toward tight associations such as eukaryotes is not as common as traditionally thought. This work, however, ignore the effect of symbionts on their hosts and assume that host dynamics is a fixed parameter. Athraya et al (ref) study how independent entities lose their reproduction ability, including the dynamics of both host and symbiont, and considering their roles as two equal partners. Their work, however, does not consider the nature of the two partners' relationship.

This work aims to study the evolutionary transition of free-living organism to obligate symbiont considering the effect that the symbiont has on its host. The effect can be negative, suggesting parasitism, or positive, suggesting mutualism. We focus on the evolution of the symbiont, assuming that it evolves faster than the host as symbionts are often organisms of smaller size and shorter lifespan such as microbial organisms. We found that ...

Methods

Ecological dynamics

The ecological dynamics of our system involve free-living organism (F), host (H), and association (A), which is formed by the meeting between free-living organisms and hosts. Free-living organisms reproduce independent of the host at a rate ρ , which we will call independent reproduction. They encounter hosts at a rate β and form association. Hosts reproduce independently at a rate r . When an association is formed, reproduction of new free-living organisms and hosts

57 decouple. Particularly, at a rate τ , new free-living organisms are born, and we call this rate
 58 bound reproduction. With probability p , symbionts reproduces together with their host at rate r ,
 59 making rp the vertical transmission rate. Symbionts only have effect on hosts' mortality at a rate
 60 ν , where ν can be positive, suggesting parasitic relationship, or negative, suggesting mutualistic
 61 relationship. Hosts have their own dynamics; they reproduce at rate r . At rate $(1-p)r$, new
 62 hosts are produced from associations. Both hosts and associations have natural mortality rate at
 63 d , and compete with all hosts and associations at rate γ . Description of the system dynamics are
 64 in fig 1, and parameter explanation are in table 1.

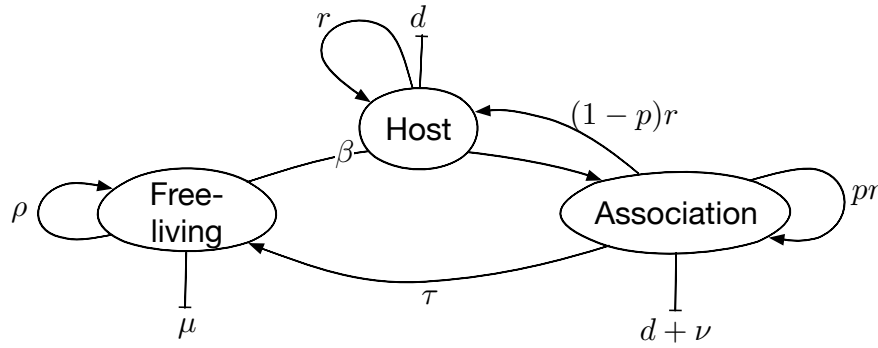


Figure 1: Model sketch

65 The dynamics of the system are described by the following differential equations

$$\frac{dF}{dt} = \rho F + \tau A - \alpha F^2 - \mu F - \beta HF \quad (1)$$

$$\frac{dA}{dt} = \beta HF + prA - \gamma(A+H)A - (\nu + d)A \quad (2)$$

$$\frac{dH}{dt} = r(1-p)A + rH - \beta HF - \gamma(A+H)H - dH \quad (3)$$

Mutant dynamics

66
 67 We consider the evolution of three traits: independent reproduction ρ , bound reproduction τ ,
 68 and effect of the symbiont on the host ν . A rare mutant, with trait values ρ_m , τ_m , and ν_m arises

| Parameter | Description |
|-----------|---|
| ρ | Independent reproduction |
| τ | Bound reproduction |
| α | Competition coefficient of free-living organisms |
| μ | Mortality rate of free-living organisms |
| β | Transmission rate |
| r | Reproduction rate of associations and hosts |
| p | Probability of vertical transmission |
| γ | Competition coefficient of hosts and associations |
| ν | Effect of symbiont on hosts |
| d | Natural mortality rate of hosts and associations |

Table 1: Parameter explanation

when the resident population reaches its equilibrium, has the following dynamics

$$\begin{pmatrix} \frac{dF_m}{dt} \\ \frac{dA_m}{dt} \end{pmatrix} = \begin{pmatrix} \rho_m - \alpha F^* - \mu - \beta H^* & \tau_m \\ \beta H^* & pr - \gamma(A^* + H^*) - (\nu_m + d) \end{pmatrix} \begin{pmatrix} F_m \\ A_m \end{pmatrix} \quad (4)$$

where F^* , A^* , and H^* are the resident population at equilibrium, which depends on the resident trait values ρ , τ , and ν .

Invasion condition

A mutant can invade if the determinant of the matrix that governs dynamics (4) is negative, which results in the following conditions

$$\tau_m > \frac{(\alpha F^* + \beta H^* + \mu - \rho_m)(\gamma(A^* + H^*) + d + \nu_m - pr)}{\beta H^*} \quad (5)$$

We show in the Supplementary Information that this condition is equivalent to having the reproduction ratio R_{0m} of the mutant greater than one.

77 *Three way trade-off*

78 We consider a three way trade-off between independent reproduction ρ , bound reproduction τ
 79 and the effect that symbionts exert on their hosts ν . In particular, each symbiont has a total budget
 80 θ that can be spent on independent reproduction ρ or bound reproduction τ . Additionally, if the
 81 symbiont exert harmness on the host, i.e. positive ν , it gain additional energy on the total budget,
 82 although this increase is limited to a value of ν_{max} . On the other hand, if the symbiont provides
 83 some kind of protection, i.e. negative ν , then it rips off some energy from the total budget.
 84 We assume that the protection value is always smaller than the natural death $\nu < d$ because if
 85 negative value $\nu > d$ then it becomes additional reproduction to the association.

$$\theta = \tau + v\rho^h - \eta \frac{v(v+d)^g}{v_{max}} \quad (6)$$

86 *Singular strategy in multidimensional trade-off*

87 Here, we consider a multidimensional trade-off instead of the conventional two dimensional
 88 trade-off in adaptive dynamics (ref). We particularly introduce a graphical analysis of the evolu-
 89 tionary stable strategies for our model. In particular, condition (5) suggests that any mutant with
 90 the bound reproduction greater than the right hand expression can invade the resident. If we re-
 91 fer to the right hand side of the invasion condition (5) as the invasion surface $\mathcal{I}(\rho, \nu)$, then on the
 92 3D trait space (ρ, τ, ν) , this condition suggest that all values of τ above the invasion surface satisfy
 93 the condition. However, τ is limited to the tradeoff surface $\mathcal{O}(\rho, \nu) = \theta - v\rho^h + \eta v(v+d)^d / v_{max}$
 94 that is derived from expression (6). Consequently, given a resident population that define an in-
 95 vasion surface $\mathcal{I}(\rho, \nu)$, mutants with bound reproduction values that lie on the trade-off surface
 96 $\mathcal{O}(\rho, \nu)$, that is above the invasion surface $\mathcal{I}(\rho, \nu)$ will be able to invade (fig 2).

97 As a consequence, the singular strategy $x^* = (\rho^*, \tau^*, \nu^*)$ is the tangent point between the
 98 invasion surface \mathcal{I} and the tradeoff surface \mathcal{O} (fig), which has to satisfy the following conditions

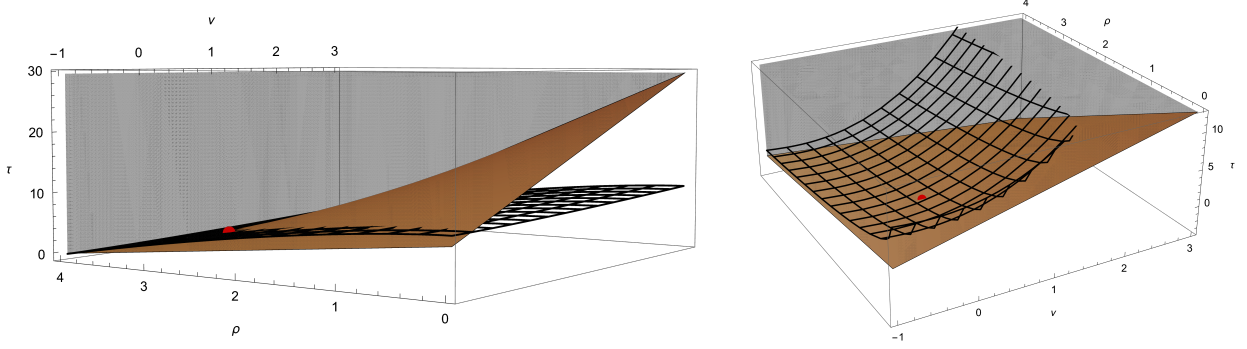


Figure 2: Example of graphical invasion analysis. Orange surface is the invasion surface \mathcal{I} , black meshed surface is the tradeoff surface \mathcal{O} . Gray shade indicates invadable area, suggesting that only mutants with smaller ρ , and smaller v can invade.

$$\begin{aligned}
 \mathcal{O}(v, \rho) &= \mathcal{I}(v, \rho, v_m, \rho_m) \Big|_{\substack{\rho=\rho_m=\rho^* \\ v=v_m=v^*}} \\
 \frac{\partial \mathcal{O}(v, \rho)}{\partial \rho} &= \frac{\partial \mathcal{I}(v, \rho, v_m, \rho_m)}{\partial \rho_m} \Big|_{\substack{\rho=\rho_m=\rho^* \\ v=v_m=v^*}} \\
 \frac{\partial \mathcal{O}(v, \rho)}{\partial v} &= \frac{\partial \mathcal{I}(v, \rho, v_m, \rho_m)}{\partial v_m} \Big|_{\substack{\rho=\rho_m=\rho^* \\ v=v_m=v^*}}
 \end{aligned} \tag{7}$$

However, since we are dealing with multidimensional tradeoff, there can be more than a singular strategy that satisfy condition (7). This happen when the invasion surface \mathcal{I} intersect with the tradeoff surface \mathcal{O} at a border line (supfig). In this case, there exist a set of singular strategy \mathbf{x}^* where individuals share at least one trait value while the other two can be different. This could also mean the potential of coexisting of multiple strategies. However, geometric analysis of branching cannot be done with multidimensional tradeoff. Note that it can be done for two dimensional tradeoff in (ref) and in some other case of 3D tradeoff (Vasconcelos 2020).

In addition, singular strategy at

Results

Discussion

Conclusion

Acknowledgments

OEC would like to thank Madlen Wilmes, Gyuri Barabás, Flo Débarre, Vlastimil Křivan, and Greg Dwyer for their comments and suggestions on this template.

Statement of Authorship

OEC conceived the experiments, collected the data, and wrote the original draft. GHC provided specimens and analyzed the model. AQE oversaw data analysis and developed the code. All authors reviewed and edited the writing at all stages of revision.

Data and Code Availability

On initial submission, you may use this section to provide a URL for editors and reviewers that is ‘private for peer review’. After acceptance, this section must be updated with correct, working DOIs for data and code deposits (such as in Zenodo, Dryad, or DataVerse). An example statement could resemble the following: All data and code for this work are available from the Dryad Digital Repository, Cook et al. 2015).

Appendix A: Additional Methods and Parameters

Further insights

Literature Cited

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Tables

Table 1: Founders of *The American Naturalist*

| Early editor | Years with the journal |
|----------------------------------|------------------------|
| Alpheus S. Packard Jr. | 1867–1886 |
| Frederick W. Putnam | 1867–1874 |
| Edward S. Morse | 1867–1871 |
| Alpheus Hyatt | 1867–1871 |
| Edward Drinker Cope ^a | 1878–1897 |
| J. S. Kingsley | 1887–1896 |

Note: Table titles should be short. Further details should go in a ‘notes’ area after the tabular environment, like this.

^a Published the first description of *Dimetrodon*.

Figure legends

Figure 1: Figure legends can be longer than the titles of tables. However, they should not be excessively long—in most cases, they should be no more than 100 words each.

Figure 2: In this way, figure legends can be listed at the end of the document, with references that work, even though the graphic itself should be included for final files after acceptance. Instead, upload the relevant figure files separately to Editorial Manager; Editorial Manager should insert them at the end of the PDF automatically.

Figure A1: *A*, the quick red fox proceeding to jump 20 m straight into the air over not one, but several lazy dogs. *B*, the quick red fox landing gracefully despite the skepticism of naysayers.

Figure A2: The quicker the red fox jumps, the likelier it is to land near an okapi. For further details, see Fastovsky (2009).

Video S1: Video legends can follow the same principles as figure legends. Counters should be set and reset so that videos and figures are enumerated separately.