Template and Guidelines for Using LaTeX in

The American Naturalist

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Abstract

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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 denpendence 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 continumm 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

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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 Figure 1, and parameter explaination are in Table 1.
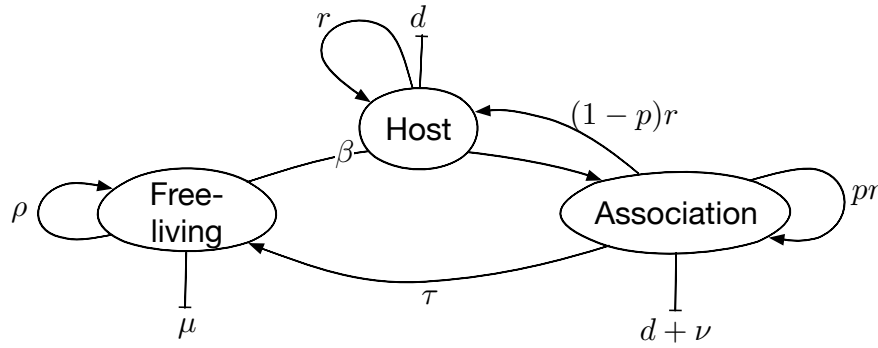

Figure 1: Model sketch

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

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

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

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

Mutant dynamics

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

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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

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

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

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

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

Three way trade-off

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

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

Results

Discussion

Conclusion

Acknowledgments

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.