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 principle, is the transition from independent replicators to associations, and this process has been foundational to the origin and diversity of complex life on Earth. Two kinds of major transitions are recognised: ″fraternal″ transitions and ″egalitarian″ transitions (Queller, 2000) . ″Fraternal″ transitions involve related independent entities and are often promoted by collaboration among kin (Nowak et al., 2010). In contrast, the ″egalitarian″ transitions involve unrelated independent entities, and it remains a challenge to understand how they come together and form tight associations (Tarnita et al., 2013). Intuitively, conflict may prevail in such a relationship as these entities can replicate independently. Even when some form of dependence evolves, 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 proteobacteria and archaea in forming eukaryotes, show a complete renunciation of independent replication and full cooperation from both parties. However, in the evolutionary transition process, it is natural that dependency may not evolve synchronously from both parties, and uncooperative behaviour such as exploitation and harmful effects exerted by one party might be common. Studying the major evolutionary transitions thus involves evolution along at least two continuums simultaneously (Estrela et al., 2016) . The first continuum involves independent reproduction ranging from complete renouncement of independent reproduction (i.e. becoming a tight association) to retaining a full level of independent reproduction (i.e. full independent entity). The second continuum is the well-known mutualism-parasitism continuum. A key question then becomes - if obligate symbiosis evolves more easily from free-living organisms 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 focuses 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 works of the mutualism-parasitism continuum (ref). In particular, if cooperation cannot be maintained, cheaters who do not contribute to the benefit of the association will prosper (Szathmáry and Smith, 1995). These cheaters are parasites if harm to the partners is considered, whereas they are commensal if no harm is induced or if harm is not considered in the study.

Few studies actually consider the evolution of renouncement of independent reproduction. Nguyen and Van Baalen (2020) 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, ignores the effect of symbionts on their hosts and assumes that host dynamics is a fixed parameter. **?** 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 a free-living organism to an obligate symbiont, considering the effect that the symbiont has on its host. Work by (**?**) assumes a trophic relationship between the host products and the free-living symbionts. However, in principle, the effect can be on the continuum from negative, suggesting parasitism, to 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 decouple. Particularly, at a rate τ, new free-living organisms are born, and we call this rate bound reproduction. With probability p, symbionts reproduces together with their host at rate r, making rp the vertical transmission rate. Symbionts only have effect on hosts' mortality at a rate ν, where ν can be positive, suggesting parasitic relationship, or negative, suggesting mutualistic relationship. Hosts have their own dynamics; they reproduce at rate r. At rate $(1-p)r$, new hosts are produced from associations. Both hosts and associations have natural mortality rate at d, and compete with all hosts and associations at rate γ. Description of the system dynamics are in Figure 1, and parameter explaination are in Table 1.

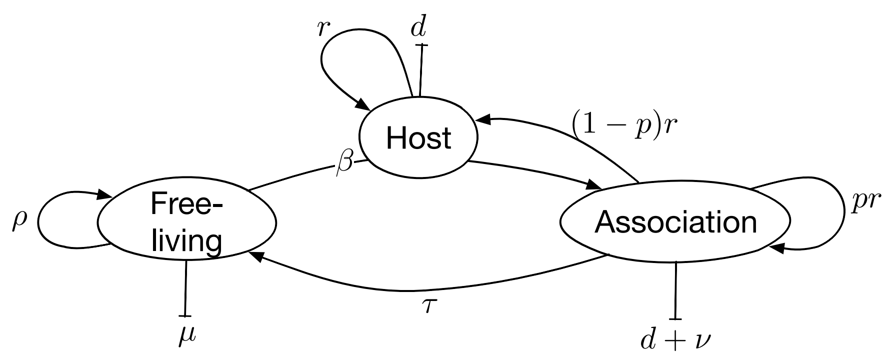

Figure 1: Model sketch

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

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

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

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

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

Mutant dynamics

We consider the evolution of three traits: independent reproduction ρ, bound reproduction τ, and effect of the symbiont on the host ν. A rare mutant, with trait values ρ_m, τ_m, and ν_m arises 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 ν. 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 ν, it gain additional energy on the total budget, although this increase is limited to a value of ν_{max}. On the other hand, if the symbiont provides some kind of protection, i.e. negative ν, then it rips off some energy from the total budget. We assume that the protection value is always smaller than the natural death $\nu < d$ because if negative value $\nu > d$ then it becomes additional reproduction to the association.

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

Evolutionary Stable Strategy – ESS

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, **?**).

Appendix A: Additional Methods and Parameters

Further insights

Literature Cited

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Szathmáry, E., and J. M. Smith. 1995. The major evolutionary transitions. Nature 374:227–232.

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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 **?**.

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.