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## Host control and nutrient trading in a photosynthetic symbiosis

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## HIGHLIGHTS

- We present a model of photosymbiosis, including nutrient trading between partners.
- Horizontal transmission determines symbiont distribution across host population.
- Host control of horizontal transmission is necessary to optimise host growth.
- We reproduce recent experimental results in the *P. bursaria*–*Chlorella* symbiosis.
- Intermediate levels of host control are an evolutionary stable strategy.

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## ABSTRACT

Photosymbiosis is one of the most important evolutionary trajectories, resulting in the chloroplast and the subsequent development of all complex photosynthetic organisms. The ciliate *Paramecium bursaria* and the alga *Chlorella* have a well established and well studied light dependent endosymbiotic relationship. Despite its prominence, there remain many unanswered questions regarding the exact mechanisms of the photosymbiosis. Of particular interest is how a host maintains and manages its symbiont load in response to the allocation of nutrients between itself and its symbionts. Here we construct a detailed mathematical model, parameterised from the literature, that explicitly incorporates nutrient trading within a deterministic model of both partners. The model demonstrates how the symbiotic relationship can manifest as parasitism of the host by the symbionts, mutualism, wherein both partners benefit, or exploitation of the symbionts by the hosts. We show that the precise nature of the photosymbiosis is determined by both environmental conditions (how much light is available for photosynthesis) and the level of control a host has over its symbiont load. Our model provides a framework within which it is possible to pose detailed questions regarding the evolutionary behaviour of this important example of an established light dependent endosymbiosis; we focus on one question in particular, namely the evolution of host control, and show using an adaptive dynamics approach that a moderate level of host control may evolve provided the associated costs are not prohibitive.

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## 1. Introduction

Endosymbiotic relationships are widespread in nature and play key roles in the functioning of many ecosystems (Esteban et al., 2010; Howells et al., 2012; Jeong et al., 2010; Johnson, 2011, 2011; Moorthi et al., 2009; Stoecker et al., 2009). Different symbioses have evolved many times throughout history; of particular note is the evolution of cellular organelles such as chloroplasts from a cyanobacteria–eukaryote symbiosis (Keeling, 2013). One well-

known example of endosymbiosis is the relationship between the ciliate *Paramecium bursaria* and the alga *Chlorella* (Karakashian, 1963). These organisms (Karakashian, 1963; Fujishima, 2009) and their close relatives (Esteban et al., 2010; Fenchel, 1980; Finlay et al., 1996) have been the focus of much study in both symbiotic and free-living contexts, and therefore provide an excellent model system for the study of alga–protist endosymbioses.

The primary benefit of an endosymbiotic relationship between a heterotrophic host and a photosynthetic symbiont (photosymbiosis) is thought to be nutrition (Johnson, 2011, 2011; Karakashian, 1963). The host obtains nutrients from its

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environment via phagotrophy—the engulfing of cells or particles and subsequent digestion within a vacuole. Free-living algae are also ingested in this manner, but not all digested; rather, some resist digestion long enough for a section of the digestive vacuole membrane to ‘pinch off’ and form a new, distinct vacuole. Known as the perialgal vacuole, this provides an alga with protection from digestion (Karakashian and Karakashian, 1973; Kodama and Fujishima, 2011), allowing it to take up residence within the host ciliate and carry out the usual unicellular life cycle of growth and cytokinesis (division). Such symbiotic algae are now dependent on their host for nutrients which are unobtainable via photosynthesis (in particular, nitrogen). In return for these nutrients, the symbiont releases a portion of its photosynthate into the host cytoplasm, resulting in a net gain of organic carbon for the host (Brown and Nielsen, 1974; Muscatine et al., 1967; Ziesenisz et al., 1981).

The consequence of this nutrient exchange is that the photosymbiosis exists on a context-dependent continuum whereby the nature of the interaction depends on the light level (Lowe et al., 2016). In low light, the correspondingly low photosynthetic output of the symbionts results in a net loss of nutrition for the host—this is effectively parasitism. As light increases, the increase in photosynthesis results in symbionts providing a net nutritional benefit to their host, yielding a mutualistic relationship.

A key step in the establishment of a permanent symbiotic relationship is the maintenance of a stable symbiont population (Muscatine and Pool, 1979). Clearly, if the host population grows more rapidly than the symbiont population, successive generations of host cells will become increasingly diluted until a completely aposymbiotic state is reached. This can occur when *P. bursaria* are grown in the dark (Karakashian, 1963). Conversely, if the symbiont population is the faster growing of the two, it will increase to the point of saturation, with severe consequences for the host—the symbionts have become parasites. Hence, if a host is to maintain a stable symbiont population it must carefully balance the gain and loss of symbionts so the two populations increase at approximately equal rates, either through controlling the rate of intake of new symbionts and the rate of removal (through expulsion or digestion), or by synchronising the cellular division cycles of the organisms. Both of these mechanisms could potentially lead to conflict between host and symbiont and the need for greater control by the dominant partner—presumed to be the host—to maintain the symbiosis.

Alga-protist endosymbioses have been addressed only briefly in the mathematical literature; see Momeni et al. (2011) for a review. There has been much emphasis on potential mechanisms for cell-cycle synchronisation in *Chlorella-Hydra* symbioses (Taylor et al., 1989; McAuley and Darrah, 1990) and *Chlorella*-ciliate symbioses (Stabell et al., 2002), while others focus on the role of nutrient trading (Flynn and Mitra, 2009; Hallock, 1981) in more general photosymbioses. Conditions determining the evolution of an obligate endosymbiosis were investigated in Law and Dieckmann (1998), Weisbuch and Duchateau (1993), and Yamamura (1996). A relevant recent paper modelled the *P. bursaria-Chlorella* symbiosis, showing how the combination of dynamic nutrient trading and differences in growth rates between partners yield a steady symbiotic population, but neglected to incorporate the potentially significant effects of symbiont intake and removal (Iwai et al., 2015). To the best of our knowledge, the present work represents the first attempt to provide a comprehensive ecological model encapsulating the many facets of symbiosis across a range of environmental conditions.

In this paper we develop a model to illustrate the mechanistic basis for a photosymbiotic relationship and the configuration of the resultant mixotrophic holobiont. We describe host-symbiont interactions by a deterministic system of ordinary differential equations, incorporating the vertical transmission of symbionts via

host cytokinesis and the horizontal transmission of symbionts via ingestion from, and egestion into, the environment. The above discussion on host-symbiont cell-cycle synchronisation forms the basis of a key assumption; namely that on the timescale of our model, host and symbiont cytokinesis is almost concurrent, in that daughter cells have a symbiont load equal to that of their mother cell. This has been directly observed in *P. bursaria* (Takahashi et al., 2007), and is in contrast to asynchronous cell cycles, for example, in which daughter cells have a symbiont load half that of their mother cell. The interplay between horizontal and vertical transmission of symbionts selects a particular symbiont distribution across the host population. We investigate how this distribution responds to different environmental conditions, in particular light levels, and how host control mechanisms may evolve. Note that our model is constructed in reference to the specific relationship between *P. bursaria* and *Chlorella*, but is readily reparameterised so as to be applicable to other photosymbioses. Hence we formulate our model using the language of a general symbiotic relationship between a heterotrophic host and a phototrophic symbiont, and parameterise it using data available in the literature on the *P. bursaria-Chlorella* symbiosis.

The paper is organised as follows. In Section 2 we derive our model. Incorporating nutrient trading and limitation allows us to formulate the host growth rate in terms of symbiont load and nutrient availability, highlighting the different strategies available to the host. This leads to the inclusion of general host control mechanisms, with particular attention paid to their impact on symbiont distribution via horizontal transmission. In Section 3 we perform numerical simulations of our model, highlighting the roles played by host control and irradiance in determining population equilibria. We then employ adaptive dynamics to illustrate how host control is able to evolve in Section 4. We conclude by discussing our findings and intentions for future investigation in Section 5.

## 2. The model

We describe the distribution of symbionts among the host population by defining the time-dependent set of variables  $\phi = (\phi_0, \phi_1, \dots)^T$ , where each entry  $\phi_k(t)$ ,  $k \in \mathbb{N}_0$ , of the column vector  $\phi$  represent the concentration of hosts with  $k$  symbionts at time  $t$ . We assume that the composition of the population changes due to the following processes:

- Cytokinesis of host cells, at rate  $c_k$ : We assume that the host and symbiont cell cycles are synchronised so as to be concurrent on the appropriate timescale; thus a host containing  $k$  symbionts divides into two hosts that each contain  $k$  symbionts. Also, we suppose that host cytokinesis is mediated by total host population density.
- Death of host cells, at rate  $d_k$ : Host death is independent of population density.
- Symbiont gain via ingestion of free-living potential symbionts, at rate  $g_k$ .
- Symbiont loss, at rate  $l_{kk}$ . We assume hosts lose symbionts at a rate proportional to their symbiont load.

Note that the first process encodes vertical transmission of symbionts, while the third and fourth encode horizontal transmission via the free-living population.

Empirical evidence supports the hypothesis of cell cycle synchrony; Takahashi et al. (2007) found that symbionts divided only when host cytoplasmic streaming ceased, which occurred just prior to host division. Each symbiont divided approximately once, resulting in two daughter cells with symbiont loads approximately

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