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Processes leading to the coexistence of a host and its parasitoid in homogeneous environments: The role of an infected dormant stage

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ABSTRACT

Theoretical studies have usually been used to explain host–parasitoid persistence in conditions of spatial heterogeneity or in homogeneous environments with specific conditions. In shallow estuaries where spatial heterogeneity is prevented by tides and river input, a common host–parasitoid system (dinoflagellate-*Amoebophrya* spp.) is able to persist even in the absence of specific conditions described in the literature. Recent observations have revealed that the cyst stage (during which the dinoflagellate host can survive in difficult environmental conditions in a dormant stage) can be infected by the parasitoid. The encystment/excystment process is suspected to be the basis for the long-term persistence of the system. In this work, the coexistence of *Amoebophrya* spp. and their hosts in homogeneous environments has been tested with an individual-based model of host–parasitoid interactions. Three processes that enable the coexistence were introduced into our model: (1) modifications in infection parameters, (2) a tritrophic food web and (3) a host encystment–excystment process. The persistence of the system was obtained in mixed conditions in all cases; however, the conditions required to obtain persistence with the infection parameter modifications were unrealistic. The tritrophic food web scenario produced short, stable, 10-d-long cycles in which the control of the parasite population in the environment was difficult to observe. The excystment process appears to be responsible for the interannual persistence of the system. Durable cycles with periods of 50 d were produced despite the unstable conditions. Moreover, these cycles did not depend on the proportion of infected cysts as long as a portion of the cysts remained healthy.

1. Introduction

Parasitism is one of the key types of interactions that can occur between two organisms. A specific category of parasite known as a parasitoid kills its hosts to survive and reproduce. Mechanisms allowing the host–parasitoid system to persist have been most studied in the insect community (Hassell et al., 1991a,b; Kraaijeveld and Godfray, 1997; Stiling, 1987). In these systems, experimental and theoretical studies generally predict unstable dynamics without incorporating external interactions or specific conditions in homogeneous environments into the relevant models (Getz and Mills, 1996; May and Hassell, 1981). Some heterogeneity is needed to enable these systems to persist, a feature that has been principally explained by patchy population distributions and different behvioral patterns of the host and parasitoid (Auger et al., 2000; Coats and Bockstahler, 1994; Hassell and May, 1988; Hassell et al., 1991a,b; Hassell, 2000; Murdoch and Briggs, 1996).

However, several of these persistent host–parasitoid systems have been found in mixed environments. Samples taken from mixed shallow estuaries have contained Syndiniales *Amoebophrya* spp., obligate parasitoids of dinoflagellates (Chambouvet et al., 2008; Coats et al., 1996). *Amoebophrya* species are widespread intracellular parasites that can infect more than 40 free-living dinoflagellate species (Park et al., 2004; Salomon et al., 2009). However, most isolated parasitoid strains are very specific and can infect only a few species or strains of host species. The infection begins when a dinospore (a biflagellate free-living form of *Amoebophrya* spp.) encounters and penetrates its host. Inside the host cell, the parasites develop into trophonts and use the cellular material of the host to grow. The trophont develops in the nucleus or in the cytosol of the host (depending on the species of host). Infection prevents host division and always leads to cell death. Maturation takes approximately two days and produces a multinucleate and

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multiflagellate stage known as a vermiform. After maturation, the vermiform ruptures through the host cell membrane and produces dozens to thousands of dinospores by cytokinesis after a short time (less than 1 h) (Chambouvet et al., 2008; Coats and Park, 2002). A more in-depth description of the life cycle of *Amoebophrya* spp. was produced by Cachon (1964), Cachon and Cachon (1987) and Coats and Bockstahler (1994).

The conditions in which *Amoebophrya* and its host interact in mixed estuaries are, in theory, incompatible with the persistence of the system. Above all, the high infectivity and reproductive output of *Amoebophrya* should not allow the host population to maintain itself in the water column. The host can develop each year because it produces cysts that can survive for several years in the sediment. Cysts accumulate in the sediment and germinate in favorable conditions. The dinospores cannot survive without their hosts, yet hosts and parasitoids are observed every year. A more recent study (Chambouvet et al., 2011) suggested that parasitoids such as *Amoebophrya* spp. could infect their dinoflagellate hosts just before encystment (in the planozygote stage) and enter into dormancy within the host. The cyst stage represents a survival stage for both the host and the parasitoid that might be responsible for the long-term persistence of the system.

The aim of this paper was to study the effects of different processes that allow the coexistence of hosts and parasitoids (dinoflagellates and *Amoebophrya*, respectively) in a homogeneous environment. Three main processes were studied: the modification of infection parameters, the control of the parasite by grazers and the excystment process. An individual-based model (IBM) approach was developed to simulate short synchronous dynamics, thus overcoming the problem of rapid parasite generation time in a non-IBM model (Salomon and Stolte, 2010); in particular, a parasite maturation time was introduced into a phytoplankton ecophysiological model. The individual approach ensures that complex behaviors and intracellular process modifications can be introduced into the model. The representation of the parasitoid–host dynamics (*Amoebophrya* spp./dinoflagellate host) was primarily validated with experimental data from Coats and Park (2002) in an initial basic configuration. Three different hosts (*Akashiwo sanguinea*, *Gymnodinium instriatum* and *Karlodinium veneficum*) were used in the validation process. Subsequently, using the best simulated host–parasitoid couple, different processes that enabled coexistence were studied in three different model configurations: the basic configuration (validated with experimental data) with different parameterizations (model A), a configuration with a parasite grazer (model B; tritrophic model) and a configuration with hosts and parasites produced by cysts (model C). The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual and agent-based models (Grimm et al., 2006, 2010).

2. Materials and methods

2.1. Purpose

The purpose of this model was to introduce a precise and unbiased maturation time with stochastic and changing biological processes (i.e., infection) into an ecophysiological model of the host and to simulate infection dynamics.

2.2. Entities, state variables, and scales

Host cells were individually simulated in a fixed volume of water and characterized by their cell age (d), size (cm), carbon mass (pmol C host^{-1}), infected state (true or false), number of infections, infection time (d) and type of death (natural or parasite-induced mortality). Depending on the model configuration, parasites concentrations (*Par* – parasites ml^{-1}), grazers concentrations (*G* – grazers ml^{-1}) and non-individual host concentrations (H_e – hosts ml^{-1}) were also simulated. The time step used in the model is 30 s. Simulations length ranged from 3.5 d to 150 d.

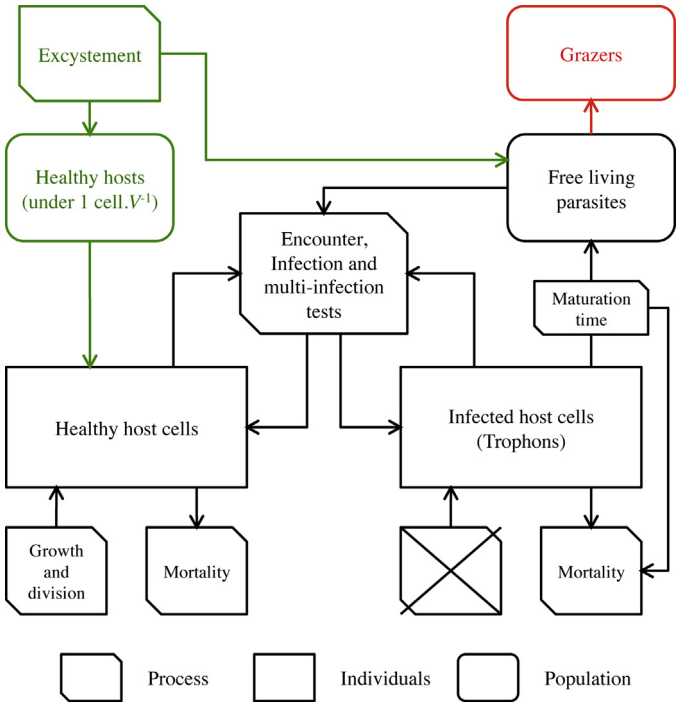

Fig. 1. Schematic diagram of the IBM model structure at each time step. Each part of the model that is interacting with another part of the model during a time step is represented by its category. Squares represent individually simulated host cell populations (either healthy or infected). Squares with rounded corners represent population variables that were not individually simulated. Squares with cut corners represent all biological and physical processes linking to and interacting with individual and population-level variables. Black compartments represent model A, black and red compartments represent model B and black and green compartments represent model C.

2.3. Process overview and scheduling

After initialization, at every time step (30 s), each host cell undergoes an infection test and is subjected to growth and mortality processes. The parasite concentration is modified by parasite mortality and the number of infections. If a host cell becomes infected, its infected state changes, its growth stops and the parasite responsible for the infection is removed from the water concentration. At each time step until maturation, an infected cell can be re-infected (multi-infection) and subjected to the same mortality process as that of a healthy cell (i.e., density-dependent mortality with a carrying capacity). As soon as the maturation time is reached, the infected cell dies and produces p_{out} parasites. The model is summarized in a schematic diagram (Fig. 1).

2.4. Design concepts

The main parameters and state variables (carbon mass, maximum growth rate, maturation time) of host cells are randomly drawn from an empirical range of values (population parameter ±12.5%) of a uniform distribution at the initiation and during cell division to represent inter-individual variability. This assigned randomization avoids a numerical synchronization of cells (Hellweger and Kianirad, 2007; Kreft et al., 1998).