

Modeling Multi-Species Parasite Transmission

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Abstract

Some models are presented for the dynamics of a host population with two parasite species. The models differ in two main aspects: whether they include direct competition among parasites and whether the analysis is based on some approximation and which one. If the analysis is not constrained by a priori assumptions about parasite distributions, it is found that species coexistence is very unlikely without some kind of direct competition among parasites; on the other hand, coexistence generally occurs when inter-specific competition is lower than intra-specific, similarly to standard theory for free-living species. If hosts differ in their predisposition to infection, but not in an identical way towards the two parasite species, then species coexistence becomes feasible even if inter-specific competition is as strong as intra-specific; in this case, coexistence becomes easier as the variance in predisposition increases. These models do not yield universal predictions for patterns of parasite distributions; an analysis of the mechanisms of interaction in each specific system is necessary for that.

Introduction

Models for host-macroparasite interaction have a relatively long history, starting from the pioneering work of Kostizin¹ and with the two seminal papers by Anderson and May² making a strong impact also on the empirical research.^{3,4} On the other hand, very few authors have studied models with several species of parasites, despite the fact that parasite communities are routinely found and examined in empirical research. This is presumably due to the much higher complexity of the resulting mathematical models (see below) and the difficulties in extending to multi-species the approach (approximation via the negative binomial assumption) that has been so fruitful in the analysis of single species models.

None the less, several interesting models have been developed over the years. In this chapter, I will give a personal review of the subject, mainly focused on the subject of coexistence: what are the factors that lead to species coexistence? In so doing, I will quickly review some examples of dynamic models for two parasite species competition. In the final section, I briefly discuss whether these models give any general insight for parasite community ecology.

The models studied assume that parasites have only one host (i.e., they are monoxenic) and that infections occur through free-living larvae. I believe that most results would apply to more complex systems as well.

Simple Models for Multispecies Parasite Dynamics

The main difficulty in modeling parasite dynamics is that one cannot simply divide the host population into infected and not, but one has to describe and predict the distribution of para-

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sites among hosts, since the effect of parasites on hosts and on other parasite species depend on the number present in that host and perhaps also in features of their establishment. The typical approach used in one-species macroparasite models has been to choose a priori that the parasite distribution is negative binomial, generally (following Anderson and May²) with fixed aggregation parameter k , but also with a varying aggregation parameter^{5,6} and to then obtain an equation for the temporal dynamics of the mean parasite burden and, depending on the model, of other variables, such as host and/or free-living larvae density.

To my knowledge, the first model on two macroparasite species interacting with one host species has been proposed by Dobson.⁷ His model followed this approach, assuming that each parasite species follows the negative binomial distribution with fixed aggregation parameter (k_1 and k_2) and that the two distributions are independent; he then derived a model for the dynamics of the two parasite densities, assuming that the two species (and indeed all individual parasites) do not interact except in that each parasite contributes to the death of a host harboring both species. His main result is that there is an ample parameter region in which both species will coexist: the smaller the parameters k_i are (meaning the more aggregated their distributions), the larger the coexistence region will be.

That model has been extended to communities of parasites,⁸ to allow for interference or facilitation between parasites^{9,10} and to allow for logistic host growth.¹¹ The result about parasite coexistence has proved to be robust with respect to all these changes.

Even two species identical in all parameters and differing in just one (for instance, the rate of egg production) can coexist; thus a completely inferior competitor (the one with a lower egg production) can survive. This result is actually rather puzzling and seems to be in contrast with all the theory of competitive exclusion.¹² Competition theory does allow for several species to coexist on a single resource, for instance because of competitive balance shifts along a temporal cycle, or because of a colonization-competition trade-off in a metapopulation setting. In all cases, coexistence of competitors seems always to require the existence some trade-off between traits.

The problem seems to lie in the a priori assumptions made. It will be addressed here by examining conditions for coexistence in a model based only on explicit assumptions about the interaction mechanisms.

Structure and Parameters of Models

The models analyzed here concern the interaction of a host population with two species of monoxenic parasites with infections occur through free-living larvae. Differently from the models outlined in the previous section, the model considered here does not contain a priori assumptions about parasite distributions and allows for many types of competition among parasites in the same host. The model is deterministic, with main variables the density of hosts carrying i 1-parasites and j 2-parasites, denoted as $p_{ij}(t)$. Other authors^{13,14} start from a stochastic model, but then, to obtain analytic results, use some approximations leading to so-called hybrid models¹⁵ similar to those discussed here.

The system of differential equations satisfied by $p_{ij}(t)$ is rather cumbersome and can easily be obtained with some book-keeping: it is written explicitly in the Appendix. It can be derived by noting that $p_{ij}(t)$ may increase because some hosts that were carrying a different number of parasites switch to having exactly i 1-parasites and j 2-parasites ($p_{00}(t)$ increases also because of new births) and vice versa may decrease because some hosts carrying i 1-parasites and j 2-parasites switch to a different number of parasites (or die). Listing the possible transitions and their rates, as in the following Table 1, is then enough to specify the system:

In words, it is assumed here that adult parasites affect (additively) hosts' mortality and (multiplicatively) hosts' fertility. Moreover, parasites within a host interact directly by increasing (additively) the mortalities (according to the matrix τ that differentiates intra-species and inter-species effects), decreasing (multiplicatively) the fertilities (according to the matrix r) and decreasing the probability of establishment of an infecting larva (through the matrix γ). Finally, new infections occur through encounters (at rate β) with free-living larvae.

Table 1. List of the variables of the model and of the events being modeled together with their rates

Variable or Event	Host Transition	Rate or Symbol
Host density		$N = \sum_{i,j} P_{ij}$
Density of hosts carrying i 1-parasites and j 2-parasites		P_{ij}
Density of free-living stages of species 1 [2]		L_1 [L_2]
Birth from a host carrying i 1-parasites and j 2-parasites	$\emptyset \rightarrow (0,0)$	$b(N)(1 - \xi_1)(1 - \xi_2)^j$
Death of a host carrying i 1-parasites and j 2-parasites	$(i, j) \rightarrow \emptyset$	$d + \alpha_i i + \alpha_j j$
Density-dependence in host fertility (K carrying capacity of hosts)		$b(N) = b \left(\frac{d}{b} \right)^{N/K}$
Death of adult 1- [2-] parasites	$(i, j) \rightarrow (i - 1, j)$ $[(i, j) \rightarrow (i, j - 1)]$	$\sigma_1 + r_{\tau_{11}} + r_{\tau_{12}}$ $[\sigma_2 + r_{\tau_{21}} + r_{\tau_{22}}]$
Rate of parasite establishment	$(i, j) \rightarrow (i + 1, j)$ $[(i, j) \rightarrow (i, j + 1)]$	$\beta_1 L_1 \Psi_1 (1 - \gamma_{11})^i (1 - \gamma_{12})^j$ $[\beta_2 L_2 \Psi_2 (1 - \gamma_{21})^i (1 - \gamma_{22})^j]$
Birth from an adult 1- [2-] parasites	$\frac{d}{dt} L_1 = + \left[\frac{d}{dt} L_2 = + \right]$	$h_1 (1 - r_{11})^{i-1} (1 - r_{12})^j$ $[h_2 (1 - r_{21})^i (1 - r_{22})^{j-1}]$

The dynamics of free-living larvae has to be specified; new ones are produced from adult parasites (see Table 1), while they are removed through deaths (at rate δ_1 [or δ_2]) or encounters with hosts. One has then the differential equation

$$\frac{d}{dt}L_1 = b_1 \sum_{i,j} p_{ij} i(1-r_{11})^{i-1}(1-r_{12})^j - \delta_1 L_1 - \beta_1 L_1 N \quad (1)$$

and analogously for L_2 . A usual simplification² is the assumption of fast dynamics of larvae, so that they are at quasi-equilibrium with adult parasites. From (1), one obtains

$$L_1 = \frac{b_1 \sum_{i,j} p_{ij} i(1-r_{11})^{i-1}(1-r_{12})^j}{\delta_1 + \beta_1 N} \quad (2)$$

Finally, substituting (2) in the expression (Table 1) for the rate of adult parasite establishment, one obtains that, for a host carrying i 1-parasites and j 2-parasites, this is equal to

$$\varphi_1(1-\gamma_{11})^i(1-\gamma_{12})^j \quad \text{with } \varphi_1 = \frac{b_1 \psi_1 \sum_{k,l} k(1-r_{11})^{k-1}(1-r_{12})^l p_{kl}}{c_1 + N} \quad \text{and } c_1 = \delta_1 / \beta_1. \quad (3)$$

In the transitions listed, several relevant phenomena of host-parasite interactions have been neglected, such as nonlinear effects of parasite abundance on host mortality, facilitation of parasite establishment through parasite-caused impairment of immune response,¹⁶ context-dependent (through the sequence of infection by different species) parasite competition.¹⁷ The system is already complicated enough as it is and indeed it will be simplified to allow analysis; moreover, the main interest of the chapter lies in parasite competition rather than in facilitation.

The resulting system of differential equations is clearly very difficult to study, not least for its size: since the number of adult parasites in a host, i and j , can in principle be any number, it is a doubly infinite system; even if we restrict these numbers to a maximum, say 100, we would still have a system of 10,000 differential equations. The idea of simplifying the system by some kind of moment closure, either through a negative binomial assumption,⁷ or through a normal approximation,¹⁴ is clearly very appealing, although it is then necessary to understand whether the results are an artifact of the approximation.

A different approach is to limit the study to the computation of the invasion criteria for each species; these are sometimes possible to compute without any approximation.¹⁸ In this way it is not possible to infer the overall dynamics of the system, but at least one can compute exactly the parameter region that allow for species coexistence.

Invasion Criteria

While analyzing the dynamics of a complex nonlinear model, as generally is that including hosts and two parasite species, is very difficult, it is often possible to study the (linearized) dynamics close to an equilibrium. In particular, the computation of the invasion coefficient (i.e., the growth rate of one parasite species in a population close to the equilibrium where hosts coexist with a first population species) is sometimes feasible. Basically, this is an extension of the basic reproduction ratio (R_0) of a parasite in a parasite-free population, a quantity fundamental in models for microparasites,¹⁹ but that can be adapted for macroparasites as well.^{11,20}

In some cases it is then possible to characterize a quantity R_1^2 representing the basic reproductive ratio of parasite 2 invading a population at the equilibrium E_1 where hosts coexist with parasite 1. If $R_1^2 > 1$, the population of parasite 2 is able to initially increase and will establish itself; on the other hand, if $R_1^2 < 1$, that population will decrease and will eventually get extinct.

Coexistence will be deemed to occur when both R_1^2 and R_2^1 are greater than 1, i.e., when each parasite species is able to invade an equilibrium with only the other species present, together with

the host. This principle is well established in theoretical population biology and can be justified, under some technical assumptions, through persistence theory.²¹ One could extend the same principle to more than 2 species, through the computation of the invasion coefficient of parasite species n into an equilibrium with the first $n - 1$ present; however, this is generally very difficult because it requires finding explicitly an equilibrium with more than 1 parasite species.

Generally the basic reproduction ratio R_1^2 can be defined as the average number of established adult 2 parasites produced by a newly established parasite 2 during its expected life time.^{18,20} We can split this number in at least three components:

$$R_1^2 = (\text{average number of larvae produced over an adult parasite life time}) \cdot (\text{probability that larva is ingested by a host}) \cdot (\text{probability of a successful establishment}) \quad (4)$$

All these quantities will depend, according to the model used, on the features of the equilibrium E_1 since parasite survival and fertility may depend on how many 1 parasites are present in the same host (and perhaps also on host density); the probability that a larva is ingested by a host will depend on host density; the probability of a successful establishment may depend on host immune response, hence on the burden (as a surrogate of the host's previous exposure) of 1 parasites.

The Model without Direct Interactions

This has been the case mainly analyzed in the literature, mainly because it is the simplest, so that it can also serve as a reference for studying the effect of direct interactions. All the terms in Table 1 referring to parasite interactions, the matrices γ , r and τ are set equal to 0.

Pugliese¹⁸ computes the invasion coefficient for that case. As discussed above, this requires to obtain some features of the equilibrium with only 1 parasite species present and then to compute the component of formula (4) for the basic reproductive ratio R_1^2 .

Without repeating the technical steps presented there, we sketch the main ideas. First of all, at an equilibrium, if parasite interactions are neglected, the probability distribution of parasite burden follows some simple law, depending on hosts' age: precisely, if parasite infections occur one at the time and hosts do not differ in their resistance to infection, parasite distribution for each age is Poisson²² with mean

$$X(a) = \frac{\varphi}{\sigma + \alpha} (1 - e^{-(\sigma + \alpha)a}), \quad (5)$$

where σ and α are parasite mortality and parasite-induced host mortality (see Table 1) and φ is the equilibrium level of the parasite establishment rate (see Eqn. 3). Alternatively (generally data do not support the assumption of a Poisson distribution of parasite load, even when accounting for host's age^{23,24}), one can allow for multiple infections or heterogeneity in hosts' susceptibility to infection, obtaining mixtures of Poisson with levels of aggregation comparable to observed ones.²²

One can then compute the components of (4). Since $\gamma_{ij} = 0$, the probability of a successful establishment is equal to ψ_1 . Since larvae may either die (at rate δ) or be ingested by hosts (at rate βN), the probability of being ingested is $\frac{\beta N}{\delta + \beta N} = \frac{N}{c + N}$ with $c = \delta/\beta$ (see Eqn. 3) and N is host population size at equilibrium; when the equilibrium includes parasite species 1, this will be denoted as \bar{N}_1 .

The only part of (4) that requires lengthy computations is the average number of larvae produced over an adult parasite life time. First of all, one notes that in this model ($r_{ij} = 0$), fertility is constant (b_2); then one has

$$R_1^2 = \frac{b_2 \psi_2 \bar{N}_1}{c_2 + \bar{N}_1} T_1^2 \quad (6)$$

where T_1^2 represents the expected lifetime of a 2-parasite that has just infected an average host in a population at the equilibrium E_1 where hosts coexist with 1-parasites. This can be computed as the average of the expected lifetime of a 2-parasite establishing itself in a host of a given age and parasite

burden; the average will be weighed using the probability $\bar{N}_1(s) / \bar{N}_1$ of surviving to age s , (according to the stationary age density) and the Poisson assumption with (5) as its mean, or the somewhat more complicated distributions following from multiple infections, or heterogeneous hosts.

From the Poisson assumption, one obtains, after some algebra,

$$R_1^2 = \frac{b_2 \psi_2}{c_2 + \bar{N}_1} \int_0^{\infty} \frac{1 - e^{-(\alpha_2 + \sigma_2)s}}{\alpha_2 + \sigma_2} \bar{N}_1(s) ds. \quad (7)$$

Formula (7) shows that the reproduction ratio of parasite 2 increases with its fertility (b_2), with its probability of establishment (ψ_2), decreases with larval death rate (δ_2 through the parameter c_2), with its adult death rate (σ_2) and its induced host death rate (α_2). All this is rather intuitive and would not require modeling.

More interesting is the transformation of (7) into an expression containing the corresponding parameters for parasite 1; the expression is particularly simple if $c_1 = c_2$, which means that the parameters relative to the larval stages are the same for the two parasite species. One then obtains

$$R_1^2 = \frac{b_2 \psi_2}{b_1 \psi_1} \frac{\alpha_1 + \sigma_1 \int_0^{\infty} (1 - e^{-(\alpha_2 + \sigma_2)s}) \bar{\pi}_1(s) ds}{\alpha_2 + \sigma_2 \int_0^{\infty} (1 - e^{-(\alpha_1 + \sigma_1)s}) \bar{\pi}_1(s) ds}, \quad (8)$$

where $\bar{\pi}_1(s)$ represents the probability of surviving to age s , at the equilibrium E_1 of coexistence with parasite 1.

Formula (8) shows clearly a principle: a parasite that is superior to the resident one (higher fertility and lower death rate and induced host death rate) will always be able to invade and will never be invaded by other. Mutual invasibility can occur only if there exists a trade-off between traits, namely one parasite has a higher fertility (say $b_2 > b_1$), but suffers also from a higher mortality or higher damages caused to its host ($\alpha_2 + \sigma_2 > \alpha_1 + \sigma_1$). When a trade-off occurs, Pugliese¹⁸ shows that coexistence is possible but only when the parameters are very precisely balanced: for given values of $\alpha_2 + \sigma_2 > \alpha_1 + \sigma_1$, there exists a very narrow interval of values b_2 (with $b_2 > b_1$) that gives rise to coexistence.

This conclusion is in strong contrast with that obtained by Dobson⁷ and others,⁹⁻¹¹ that parasite coexistence is easy and is especially facilitated by aggregation in parasite distribution. Given that the model with single infections and homogeneous hosts gives rise to very little aggregation (which is caused by the mixture of Poisson with different mean, because of hosts' age), it may be not surprising that coexistence is very unlikely in this model.

In Pugliese¹⁸ the issue was tackled by analyzing models including mechanisms that built more aggregation into parasite distributions. Precisely, two models were analyzed: one with multiple infections of larvae (with a Poisson distribution of mean λ), the other with heterogeneity in hosts' susceptibility to infection, i.e., ψ is not constant among hosts, but has a distribution with means $\bar{\psi}_1$ and $\bar{\psi}_2$ for the two parasite species.

In both models, the invasion coefficient can be computed from (4) along lines similar to those leading to (7) and (8). The computations are more involved and are not reported here. Eventually, one arrives at an expression of the type

$$R_1^2 = \frac{b_2 \bar{\psi}_2}{b_1 \bar{\psi}_1} F(\alpha_2, \sigma_2, \alpha_1, \sigma_1) \quad (9)$$

where the function F depends on all details of the model, but has two fundamental properties:

- a. F equals 1 if all parameters are the same ($F(\alpha, \sigma, \alpha, \sigma) = 1$), which means that if two parasite species differ only in their fertility, the one with higher fertility outcompetes the other;

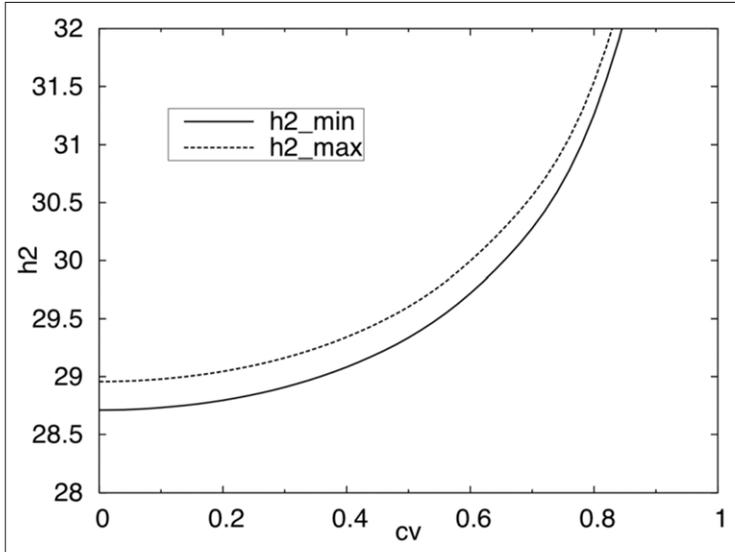


Figure 1. The values of h_2 as a function of the coefficient of variation in host susceptibility for which a second parasite species could coexist with a first parasite species. Other parameter values are $\alpha_1 = 5$, $\alpha_2 = 0.5$, $\sigma_1 = \sigma_2 = 2$, $h_1 = 65$, $c_1 = c_2 = 1$, $d = 0.5$, $b = 1$, $K = 1000$. Figure adapted from *Theoretical Population Biology*, vol. 57, pp. 145-165, Figure 6, © 2000 Elsevier, with permission.

- b. F is decreasing with α_2 and σ_2 (the reproductive ratio decreases, if a parasite suffers higher mortality, or induces a higher death rate on the host) and is increasing with α_1 and σ_1 (it is easier for a parasite to invade, if the resident parasite suffers higher mortality, or induces a higher death rate on the host).

These two properties imply that a trade-off between fertility, on the one hand and parasite- or host-induced mortality, on the other hand, is necessary for two parasites to coexist.

The coexistence region could be examined only by numerically computing the function F in (9). It was found (see Fig. 1) that the width of the coexistence region was basically independent of the degree of aggregation induced by the model: one could assume a very large heterogeneity in host susceptibility and thus a very aggregated parasite distribution, but still the potential for parasite coexistence was very limited, basically the same as with homogeneous hosts and little aggregation.

The rationale for the difference in this result from what obtained by Dobson is discussed at length in Pugliese.¹⁸ Basically, Dobson⁷ assumes that parasite distributions are aggregated and independent. On the other hand, if aggregation arises from the fact that some hosts are more susceptible to infection (from whichever parasite species), it is clear that both species of parasites will be found in the most susceptible hosts, so that parasite distribution will be positively correlated; the stronger is host heterogeneity (and thus parasite aggregation), the more positive the correlation will be. Indeed, Dobson and Roberts,⁹ studying a negative binomial approximation with fixed correlation coefficient, show that positive correlation coefficients hinder coexistence.

Clearly, things would be different if some hosts were more susceptible to parasites of species 1 and others to parasites of species 2; this is explored in references 13-14 (see below), but it is a different explanation: coexistence arises because of differential host susceptibility, not because of aggregation per se.

Competition among Parasites

The results obtained in the previous section are very elegant mathematically, providing a subtle reason for coexistence among parasites without direct interactions: the shift in the age-dependence of host mortality when at equilibrium with either parasite species. On the other hand, they are somewhat disconcerting biologically, because coexistence is very unlikely, while routinely parasites of several species are found in the same host populations and individuals.²⁵ Moreover, it refers to any kind of parasites: even parasites colonizing different organs could coexist only under very restrictive conditions, which seems plain nonsense.

The point is that in the model the only density-dependence mechanism, that keeps parasite load from growing to infinity, is the induced host mortality. Hence, parasite density at equilibrium will be at a sufficient high level to overall induce a significant host mortality. In turn, the high level of host mortality will make it very difficult for a second parasite species to invade, unless it has a higher reproduction number than the resident one and then displace it.

In short, to make a realistic multiparasite model, it is essential to introduce competition between parasites, whether they are of the same species or of different ones. In Table 1, three levels of competition are considered, translated as rates depending on the number of parasites in a host: parasite mortality will increase, while parasite fertility and probability of successful establishment will decrease.

Empirical evidence exist for all these facts;^{26,27} the number of parasite in a host may be relevant because of its impact on host resources available for other parasites, or because of the immune response induced in the host; in the latter case, it might be better modeling immune response, as depending on the history of infection of individual hosts,²⁸ rather than on the current parasite load, but this would be rather more complex and current parasite load may be a reasonable proxy for history of infection.

Explicit mechanisms of parasite competition have been introduced in models for competition between two parasite species by Bottomley et al,^{13,14} using the methods developed by Isham and coworkers.^{22,29} They consider separately the effect of parasite load on probability of establishment and on parasite fertility; here I consider the same cases, neglecting the effect on parasite mortality, mainly because of the mathematical complications of this. First, I use the same approach as in previous Section, that leads to an exact computation of the invasion coefficient, hence to finding the conditions for coexistence as mutual invasibility, only for the case of competition acting on parasite fertility. Then, I show the approach by Bottomley et al^{13,14} that involves the computation of approximate equations for the first two moments of parasite distribution, thus yielding conditions for coexistence but also the dynamic pattern of parasite densities.

Parasite Fertility Depending on Available Resources

Let r_{ij} measure the effect of the load of parasite species j on the fertility of parasite species i ; precisely, I assume (see Table 1) that the fertility of one parasite of species 1, living in a host that harbors i parasites of species 1 and j of species 2, is $b_1(1 - r_{11})^{i-1}(1 - r_{12})^j$. Note that I use a multiplicative effect (and not an additive one) of parasites, to avoid the fertility becoming negative at high parasites load; as long as $i r_{11}$ and $j r_{12}$ are not too large, that expression can be approximated as $b_1(1 - (i - 1) r_{11} - j r_{12})$, yielding a more usual expression.

Most of the analysis outlined for the model without direct interactions still applies. One can use (4) to find the invasion coefficient for species 2 in a population where the host coexists with species 1. In the equilibrium with only species 1, equation (5) still holds; in this case, however, the average number of larvae produced by an adult parasite is not simply the product of the fertility rate times its expected lifetime, because the fertility depends on the number of other parasites present. The computations (that will be presented elsewhere) can be performed easily using functional-analytic methods.³⁰ The final result can be written as

$$R_1^2 = \frac{b_2 \psi_2}{c_2 + \bar{N}_1} \frac{1}{\alpha_2 + \sigma_2} \int_0^\infty (1 - e^{-(\alpha_2 + \sigma_2)s}) \exp\left\{-\frac{\varphi_1}{\alpha_1 + \sigma_1} (1 - e^{-(\alpha_1 + \sigma_1)s})\right\} r_{21} \bar{N}_1(s) ds, \quad (10)$$

or, if $c_1 = c_2$, as

$$R_1^2 = \frac{h_2 \psi_2}{h_1 \psi_1} \frac{\alpha_1 + \sigma_1 \int_0^\infty (1 - e^{-(\alpha_2 + \sigma_2)s}) \exp\{-\frac{\varphi_1}{\alpha_1 + \sigma_1} (1 - e^{-(\alpha_1 + \sigma_1)s})\} r_{21}(s) ds}{\alpha_2 + \sigma_2 \int_0^\infty (1 - e^{-(\alpha_1 + \sigma_1)s}) \exp\{-\frac{\varphi_1}{\alpha_1 + \sigma_1} (1 - e^{-(\alpha_1 + \sigma_1)s})\} \bar{\pi}_1(s) ds}, \tag{11}$$

where φ_1 is the rate at which (at equilibrium) new 1-parasites establish themselves (see Eqn. 3), while $\bar{\pi}_1(s)$ is as in (8).

Expressions (10) and (11), that extend (7) and (8), are rather cumbersome, but one can easily use it on a computer to find the parameter values that allow for coexistence, i.e., those for which both $R_1^2 > 1$ and $R_2^2 > 1$ (see Figs. 2 and 3).

Moreover, one can easily understand some particular cases:

if all parameters of the two parameter species are identical, then $R_1^2 = 1$; hence, if $r_{21} < r_{11}$ (i.e., interspecific is lower than intraspecific competition), $R_1^2 = 1$. One then obtains in this context the classical result that two competing species that have the same demographic parameters but use somewhat different resources can always coexist.

In the extreme case where $r_{21} = 0$ (i.e., the presence of species 1 has no effect on parasites of species 2) and $\alpha_1 = 0$ (hence population density is at its carrying capacity, K , independently of the presence of parasites), expression (10) simplifies to

$$R_1^2 = \frac{h_2 \psi_2}{c_2 + K} \frac{K/L}{\alpha_2 + \sigma_2} \int_0^\infty (1 - e^{-(\alpha_2 + \sigma_2)s}) \pi(s) ds$$

where L is the average length of host life. In this case, $R_1^2 > 1$ is simply the condition for species 2 to be able to persist with the host at its carrying capacity. Then two species that do not interact and do not increase host mortality can always coexist, provided each can persist with the host.

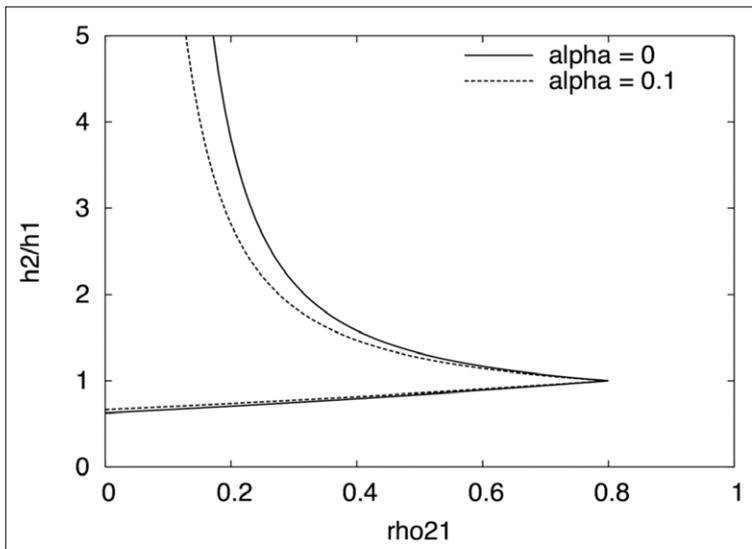


Figure 2. The region in the parameter space ($r_{21} = r_{12}$, h_2/h_1) that allows species coexistence (to the left of the chevron-shaped curves) for $\alpha_1 = \alpha_2 = 0$ (solid curve) or $\alpha_1 = \alpha_2 = 0.1$ (dashed curve). Other parameter values are $r_{11} = r_{22} = 0.8$, $h_1 = 4$, $c_1 = c_2 = 1$, $d = 0.5$, $b = 1$, $K = 1000$.

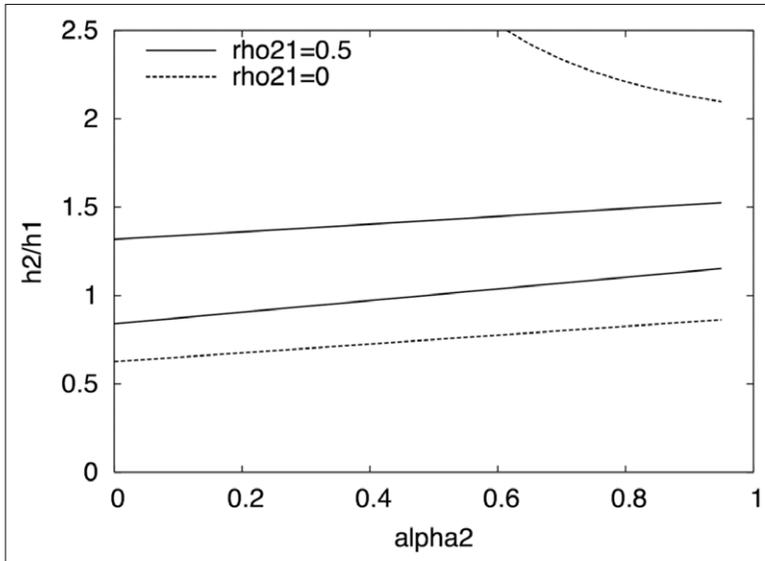


Figure 3. The region in the parameter space $(\alpha_2, h_2/h_1)$ that allows species coexistence (between the curves) for $r_{12} = r_{21} = 0.5$ (solid curve) or $r_{12} = r_{21} = 0$ (dotted curve). Other parameter values are $r_{11} = r_{22} = 0.8$, $a_1 = 0$, $\sigma_1 = \sigma_2 = 2$, $h_1 = 4$, $c_1 = c_2 = 1$, $d = 0.5$, $b = 1$, $K = 1000$.

Generally, if $\alpha_1 = 0$, computations are easier, since the presence of parasites does not affect host demography. Then (10) can be written as

$$R_1^2 = \frac{h_2 \psi_2}{c_2 + K} \frac{K/L}{\alpha_2 + \sigma_2} \int_0^\infty (1 - e^{-(\alpha_2 + \sigma_2)s}) \exp\left\{-\frac{q_1}{\sigma_1} (1 - e^{-\sigma_1 s}) r_{21}\right\} \pi(s) ds.$$

Figure 2 shows how the coexistence region depends on the ratios of parasite fertilities and the strength of their interspecific competition. In the figure, the two parasite species have the same value of all parameters except the fertility h_i and have a common inter-specific competition coefficient $r_{21} = r_{12}$. It can be seen that, when inter-specific competition is very low, the two species will coexist for almost all feasible fertility values; on the other hand, the ratio of fertilities must become very close to 1 for the two species to coexist, as the inter-specific competition coefficient approaches 0.8, the value of the intra-specific competition coefficient. When $r_{21} = r_{12} = r_{11} = r_{22}$, coexistence is impossible, as seen in Figure 2 and shown by (11). It can also be seen from Figure 2 that the coexistence regions are similar for $\alpha_1 = 0$ and $\alpha_1 = 0.1$ (a rather strong parasite-induced mortality, comparing with the other parameter values).

Figure 2 compares parasite species differing in only one demographic parameter; in Figure 3, the case of a trade-off between fertility and parasite-induced mortality is analyzed, as in Ref. 18. One can again see the strong influence of the interspecific competition coefficient $r_{12} = r_{21}$ on the width of the coexistence region, although coexistence becomes anyway more difficult when the competitor is extremely lethal.

The trade-off between fertility and parasite-induced mortality was shown¹⁸ to be sufficient for species coexistence, in absence of intra- or inter-specific competition, although the rates had to be balanced very carefully. One may wonder whether this can happen also with inter-specific competition equal to the intra-specific one. However, repeating the computations shown in Figure 3 with $r_{12} = r_{21} = r_{11} = r_{22} = 0.8$, one sees that coexistence is impossible for any values of α_2 or h_2/h_1 . Vice versa, one finds a region where both $R_1^2 < 1$ and $R_2^2 < 1$, i.e., both monospecific equilibria are uninvadable. Namely, a (narrow) parameter region may exist where, even if inter-specific

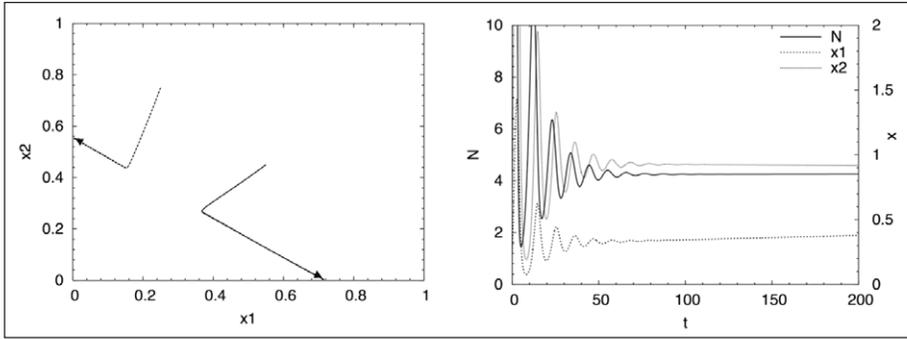


Figure 4. Simulations of the system in the variables p_{ij} , with equal inter-specific and intra-specific competition coefficients. In the left panel, parameter values are $r_{11} = r_{22} = r_{12} = r_{21} = 0.5$, $\alpha_1 = 0.1$, $\alpha_2 = 0.5$, $\sigma_1 = \sigma_2 = 2$, $h_1 = 4$, $h_2 = 4.55$, $c_1 = c_2 = 1$, $d = 0.5$, $b = 1$, $K = 1000$. Axes represent average parasite loads, $X_1 = \sum_{i,j} ip_{ij}/N$ and $X_2 = \sum_{i,j} jp_{ij}/N$. The solid line shows a simulation starting from (0.55, 0.45), the dotted line one starting from (0.25, 0.75). In both cases $N(0) = 800$. In the right panel, parameter values are the same except $r_{11} = r_{22} = r_{12} = r_{21} = 0.01$, $h_2 = 4.492$. On the x-axis, time; on the y-axis, host population density (scale on the left) $N = \sum_{i,j} p_{ij}$ and average parasite loads (scale on the right) X_1 and X_2 .

competition is exactly equal to intra-specific one (and could even be slightly lower), the system exhibits competitive exclusion dependent on initial densities, as it happens for Lotka-Volterra systems when inter-specific competition is higher than the intra-specific one.

In Figure 4, two contrasting examples are shown of simulations with inter-specific competition exactly equal to intra-specific one; in the left panel, competition is rather strong ($r_{11} = r_{22} = r_{12} = r_{21} = 0.5$) and values of α_i and b_i have been found, for which both exclusion equilibria are attractive, as discussed above; in the right panel, competition is very low ($r_{11} = r_{22} = r_{12} = r_{21} = 0.01$) and values of α_i and b_i have been found that allow for species coexistence, like in the case without competition.

The simulations in the left panel of Figure 4 show a very simple behavior, typical of two-dimensional Lotka-Volterra competition systems: fast convergence to a one-dimensional manifold connecting the equilibria and then slow convergence to an equilibrium, along the manifold. In this case then parasite competition follows the standard patterns of competition theory and it becomes reasonable the search for some simple approximating system.

In the simulation shown in the right panel of Figure 4, after some initial oscillations host population and parasite loads approach a stable coexistence equilibrium. It may be noted that the population density reached (around 4) is extremely lower than the carrying capacity (1,000); this is not meant to be realistic and is due to the choice of very high induced mortalities and the very low level of parasite competition.

The previous analysis can be applied, in a relatively simple way, when parasite resource competition affects only parasite birth rate. Judging from preliminary simulations, it seems likely, that similar results will hold also when parasite competition increases death rates (through parameters r of Table 1) or decreases establishment probability (through parameters γ of Table 1). The computations outlined in this Section do not easily extend however, since parasite distribution will not be Poisson for fixed age (as in (5)), so that no explicit formulae can be found, although the ideas of invasion criteria still apply.

Instead, normal approximations can be obtained,¹⁴ as shown in the following Section.

Normal Approximations

Bottomley et al^{13,14} have studied parasite competition through normal approximations. The idea is very simple: from the equations in the variables p_{ij} , or directly from computations of the

possible instantaneous changes in parasite load, one can find equations satisfied by the first moments of the parasite distributions (means, variances, covariances...). Unfortunately, as usual in most complex models in ecology, the equations for lower moments have terms including higher moments; to obtain a closed low-dimensional system, one then needs some form of "moment closure".³¹ A simple approach is the normal approximation,²² i.e., to assume that higher moments can be expressed in terms of the first and second moments, according to the same relations that hold for a normal distribution. The assumption may not seem very adequate for parasites, since normal distributions are continuous and include a negative part; the negative binomial distribution used since Anderson and May² does not have these problems, but cannot be easily generalized to two or more variables;¹⁰ moreover, Bottomley et al¹⁴ show, through simulations, that the normal approximation works reasonably well, as long as parameter values are not extreme.

The use of the normal approximation requires a correction in the laws used for density-dependence. Precisely, it becomes more convenient assuming that parasite fertility decreases with the number of parasites according to an additive law $b_1(1 - (i-1)r_{11} - jr_{12})$ and similarly the probability of establishment is $\psi_1(1 - ir_{11} - jr_{12})$. For the rule to be reasonable, it should be assumed that fertilities (or probability of establishment) are 0 when the quantities are negative. The following analysis is feasible only without that restriction; however, as long as the parameters r and γ are not too large, ignoring the restriction does not make a big difference.¹⁴

The equation (1) for the larvae still hold, together with the quasi equilibrium approximation (2) that, with the change to the additive law, changes (3) into

$$\varphi_1 = \frac{b_1 \psi_1 N (\langle x_1 \rangle - r_{11} \langle x_1^2 \rangle - \langle x_1 \rangle - r_{12} \langle x_1 x_2 \rangle)}{c_1 + N} \quad (12)$$

where x_i is the i -parasite load and $\langle \rangle$ represents the average.

It is also easy writing an equation for the total host density N

$$N' = N(b(N) - d - \alpha_1 \langle x_1 \rangle - \alpha_2 \langle x_2 \rangle) \quad (13)$$

One can then write equations for $\langle x_i \rangle$ obtaining

$$\begin{aligned} \langle x_1 \rangle' &= \varphi_1 (1 - \gamma_{11} \langle x_1 \rangle - \gamma_{12} \langle x_2 \rangle) - \sigma_1 \langle x_1 \rangle - \rho_{11} \langle x_1^2 \rangle - \rho_{12} \langle x_1 x_2 \rangle - \alpha_1 \langle x_1^2 \rangle \\ &\quad - (b(N) - \alpha_1 \langle x_1 \rangle - \alpha_2 \langle x_2 \rangle) \langle x_1 \rangle \\ \langle x_2 \rangle' &= \varphi_2 (1 - \gamma_{21} \langle x_1 \rangle - \gamma_{22} \langle x_2 \rangle) - \sigma_2 \langle x_2 \rangle - \rho_{22} \langle x_2^2 \rangle - \rho_{21} \langle x_1 x_2 \rangle - \alpha_2 \langle x_2^2 \rangle \\ &\quad - (b(N) - \alpha_1 \langle x_1 \rangle - \alpha_2 \langle x_2 \rangle) \langle x_2 \rangle. \end{aligned} \quad (14)$$

Competition at Establishment. No Induced Mortality

In the case where the parasites donot induce mortality ($\alpha_i = 0$) and parasite competition acts only by reducing the probability of establishment ($r_{ij} = \tau_{ij} = 0$), equations (14) become a closed system. In fact, N is then fixed at the carrying capacity K with $b(K) = d$ and (14) reduces (dropping for ease of notation the brackets) to

$$\begin{aligned} X_1' &= \frac{b_1 \psi_1 K x_1}{c_1 + K} (1 - \gamma_{11} X_1 - \gamma_{12} X_2) - (\sigma_1 + d) X_1 \\ X_2' &= \frac{b_2 \psi_2 K x_2}{c_2 + K} (1 - \gamma_{21} X_1 - \gamma_{22} X_2) - (\sigma_2 + d) X_2 \end{aligned} \quad (15)$$

Equations (15) have exactly the form of a Lotka-Volterra competition system. Hence, according to the values of the coefficients, one can have the four possible outcomes: equilibrium coexistence of the two species, competitive exclusion of species 1, competitive exclusion of species 2, contingent competitive exclusion (either species may be excluded depending on initial densities).

First of all, it is necessary to assume that each parasite species alone is able to persist with the hosts at the carrying capacity K . This condition can be written in terms of basic reproductive numbers as

$$R_0^1 = \frac{b_1 \psi_1 K}{(c_1 + K)(\sigma_1 + d)} > 1 \quad \text{and} \quad R_0^2 = \frac{b_2 \psi_2 K}{(c_2 + K)(\sigma_2 + d)} > 1. \tag{16}$$

Then, the conditions for coexistence are

$$\frac{\gamma_{21}}{\gamma_{11}} < \frac{1 - (R_0^2)^{-1}}{1 - (R_0^1)^{-1}} \quad \text{and} \quad \frac{\gamma_{12}}{\gamma_{22}} < \frac{1 - (R_0^1)^{-1}}{1 - (R_0^2)^{-1}} \tag{17}$$

In case R_0^1 and R_0^2 are much larger than 1, conditions (17) simply mean that inter-specific competition is lower than intra-specific one.

If both conditions are reversed (intra-specific competition lower than inter-specific one), one obtains contingent competitive exclusion.

Finally, if one of (17) holds and the other not, strict competitive exclusion of one species occurs.

Note that, while (15) are obtained from (14) without approximations, still they are not exact for the complete system because they have been derived neglecting the constraints (see above) that only the positive values of $b_1(1 - (i - 1)r_{11} - jr_{12})$ and $\psi_1(1 - i\gamma_{11} - j\gamma_{12})$ had to be considered.

Competition Acting on Parasite Fertility

One has to add equations for the second moments, since they appear in right hand sides of (14) unless $r_{ij} = 0$.

Using as variables the variances and covariance ($V_1 = \langle x_1^2 \rangle - \langle x_1 \rangle^2$, $V_2 = \langle x_2^2 \rangle - \langle x_2 \rangle^2$, $C_{12} = \langle x_1 x_2 \rangle - \langle x_1 \rangle \langle x_2 \rangle$), one obtains, after some lengthy calculations, equations satisfied by them, involving the third moments. The normal approximation allows to write the third moments in terms of the first two, using the relation

$$\langle UVW \rangle = \langle UV \rangle \langle W \rangle + \langle UW \rangle \langle V \rangle + \langle VW \rangle \langle U \rangle - 2 \langle U \rangle \langle V \rangle \langle W \rangle \tag{18}$$

exact if (U, V, W) follows a multivariate normal distribution.

The expressions in the general model are very complex and add little insight, though they could be used for numerical computation. I restrict to the case of competition acting only on parasite fertility, the case analyzed above through invasion coefficient and also studied^{13,14} through normal approximations.

First of all, φ_1 and φ_2 are given by (12) that is rewritten now, using V_1, V_2 and C_{12} as

$$\varphi_1 = \frac{b_1 \psi_1 N}{c_1 + N} (x_1(1 + r_{11}) - r_{11}(V_1 + x_1^2) - r_{12}(C_{12} + x_1 x_2)) \tag{19}$$

and analogously for φ_2 . Then equations (14) can be rewritten for this case as

$$x_1' = \varphi_1 - \sigma_1 x_1 - \alpha_1 V_1 - b(N)x_1 + \alpha_2 x_1 x_2 \tag{20}$$

Finally, writing the equations for the second moments and applying also (18), one obtains:

$$V_1' = \varphi_1 - \sigma_1(2V_1 - X_1) + \alpha_2 X_1^2 X_2 - (V_1 - X_1^2)b(N) \tag{21}$$

$$C_{12}' = -(\sigma_1 + \sigma_2)C_{12} - \alpha_1 X_1(C_{12} + X_1 X_2) - \alpha_2 X_2(C_{12} + X_1 X_2) - (C_{12} - X_1 X_2)b(N) \tag{22}$$

Equations (13) – (20) – (21) – (22) (with the analogous ones for x_2 and V_2) are a closed system describing parasite competition. One can use them to find the equilibrium with only one species present and then find the invasion conditions for the second species; mutual invasibility could then be considered as denoting coexistence. Unfortunately, analytical computations are still rather difficult and it is generally necessary to resort to numerical computations.

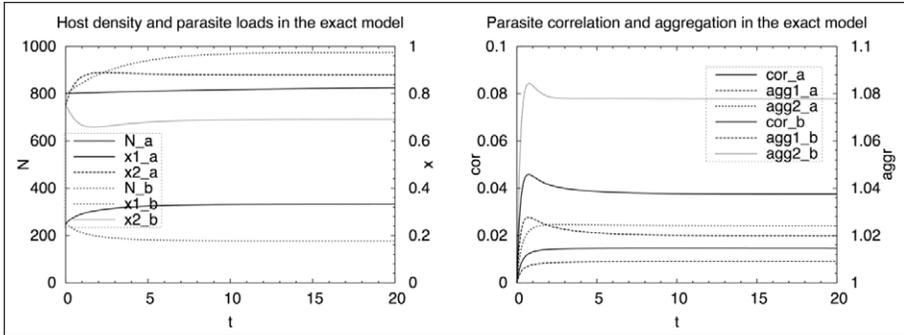


Figure 5. Host density and parasite loads vs time (left panel); correlation between the distribution of the two species and aggregation (= variance/mean) of each vs time (right panel) in two simulations of the infinite system. Simulation “a” has $b = 0.2$, $d = 0.1$; simulation “b” has $b = 1$, $d = 0.5$. All other parameter values are the same: $r_{11} = r_{22} = 0.8$, $r_{12} = r_{21} = 0.4$, $\alpha_1 = \alpha_2 = 0.01$, $\sigma_1 = \sigma_2 = 2$, $h_1 = 4$, $h_2 = 5$, $c_1 = c_2 = 1$, $K = 1000$. Initial conditions are $N(0) = 800$ and Poisson independent distribution for each parasite of means 0.25 and 0.75, respectively.

The normal approximation works effectively only when host death rates are small.¹⁴ In the limiting case where $\alpha_1 = \alpha_2 = 0$ and also $b(N) = d$, at equilibrium $x_1 = V_1$ and $C_{12} = 0$; then, using these relations in (20), the equations for x_1 and x_2 take the Lotka-Volterra form (15) and one can easily analyze them.

One can also compare numerically system (13) – (20) – (21) – (22) with the exact system presented in the Appendix; two examples of this comparison are shown in Figures 5 and 6.

From the figures it can be seen, first of all, that, in both cases, simulations converge quickly to a coexistence equilibrium (inter-specific competition is half the intra-specific one). Moreover, the same qualitative trends exist for both exact and approximate models; increasing host death and birth rate (while maintaining all other parameters) results in decreased parasite loads, hence in higher host density. Similarly, parasite aggregation and correlation increase with host death and birth rate, since in these models parasite aggregation (and correlation) results from the hidden variable age: for each given age, parasite distributions are Poisson (no aggregation) and independent, but differ in their means; the mixture of these distributions results into a (little) aggregated distribution.

On the other hand, the absolute values predicted for parasite loads are rather different, especially for the more abundant species (2) and so is host density, since it will suffer from parasite-induced mortality. It must be remembered, however, that a multiplicative law for parasite fertility is used in the exact model and an additive law in the normal approximation; the latter results in a lower fertility when there are at least 3 parasites in a host, so it is no wonder that they yield quantitative different results.

Competition and Host Heterogeneity

As can be seen from Figures 5 and 6 (right panels), the previous models yield a very low correlation between parasite distribution and a very low aggregation in each. Then, on the one hand, one could feel justified in assuming a priori that parasite distributions are independent; on the other hand, it seems necessary to allow for some aggregation in the distributions, to have a model closer to reality. The approach by Dobson⁷ and others¹¹ is to use independent negative binomial distributions for each species, or with a fixed correlation coefficient.^{9,10}

Bottomley et al^{13,14} have instead modeled a mechanism that produces parasite aggregation, studying its effects on species coexistence, according to the detailed assumptions used. Precisely, they assume that the parameter ψ (establishment probability) is not a constant, but varies among

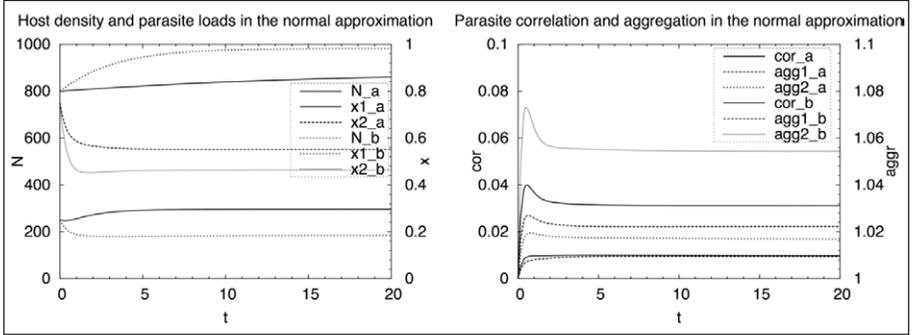


Figure 6. Host density and parasite loads vs time (left panel); correlation between the distribution of the two species and aggregation (= variance/mean) of each vs time (right panel) in two simulations of the approximating system (13)-(20)-(21)-(22). Simulations “a” and “b”, parameters and initial conditions as in Figure 5.

hosts according to some given distribution (like in Fig. 1); the equations for the second moments will then involve mean and variance of this distribution. Note that, since ψ is a probability, it must lie between 0 and 1, so that its variance cannot be large; however, it is also possible to assume that the encounter rates of hosts with larvae (parameter β in Table 1) is variable among hosts; by a redefinition of parameters one can include this variation in ψ and then its variance can take any value, as will be assumed here.

If some hosts have a higher predisposition to infection (measured by their value of ψ), they are more likely to get infected, so that a correlation will build up between ψ and parasite load x . The covariance between ψ and x , $C_{\psi x}$ will then be a variable of the system.

To keep things simple, I will restrict the analysis to the case where parasites do not induce mortality ($\alpha_i = 0$) and parasite competition acts only by reducing the probability of establishment ($r_{ij} = \tau_{ij} = 0$). Then, host population density is fixed at K and equations for parasite loads x_i do not depend on variances (see (15)).

The resulting competition system will assume given (different distributions) for ψ_1 and ψ_2 , summarized by their means $\bar{\psi}_1$ and $\bar{\psi}_2$, variances V_1^ψ and V_2^ψ and covariance ($C^{\psi\psi}$). Variables of the system will be parasite loads (x_1 and x_2) and the covariances between ψ_i and x_j ($C_{ij}^{\psi x}$). Through some steps,¹⁴ one arrives at the following system of equations

$$\begin{aligned} \frac{d}{dt} X_1 &= \frac{b_1 K}{c_1 + K} X_1 (\bar{\psi}_1 - \gamma_{11} (C_{11}^{\psi x} + \bar{\psi}_1 X_1) - \gamma_{12} (C_{12}^{\psi x} + \bar{\psi}_1 X_2)) - (\sigma_1 + d) X_1 \\ \frac{d}{dt} C_{11}^{\psi x} &= \frac{b_1 K}{c_1 + K} X_1 (V_1^\psi - \gamma_{11} (\bar{\psi}_1 C_{11}^{\psi x} + V_1^\psi X_1) - \gamma_{12} (\bar{\psi}_1 C_{12}^{\psi x} + V_1^\psi X_2)) - (\sigma_1 + d) C_{11}^{\psi x} \\ \frac{d}{dt} C_{12}^{\psi x} &= \frac{b_2 K}{c_2 + K} X_2 (C^{\psi\psi} - \gamma_{21} (\bar{\psi}_2 C_{11}^{\psi x} + C^{\psi\psi} X_1) - \gamma_{22} (\bar{\psi}_2 C_{12}^{\psi x} + C^{\psi\psi} X_2)) - (\sigma_2 + d) C_{11}^{\psi x} \end{aligned} \quad (23)$$

with analogous equations for x_2 , $C_{21}^{\psi x}$ and $C^{\psi x}$.

In order to study coexistence in model (23), one can, as discussed above, compute the equilibrium E_i with only one species present and find the conditions for invasion from the other species. As shown in Bottomley et al,¹⁴ this can be written as reproduction numbers

$$R_1^2 = \frac{b_2 K}{c_2 + K} \frac{\bar{\psi}_2 - \gamma_{21} (C_{21}^{\psi x} + \bar{\psi}_2 x_1)}{\sigma_2 + d} \Bigg|_{E_1} = R_0^2 \left[1 - \gamma_{21} \left(\rho \frac{c v_2^\psi}{c v_1^\psi} \left(\frac{1 - (R_0^1)^{-1}}{\gamma_{11}} - x_1 \right) + x_1 \right) \right] \Bigg|_{E_1} \quad (24)$$

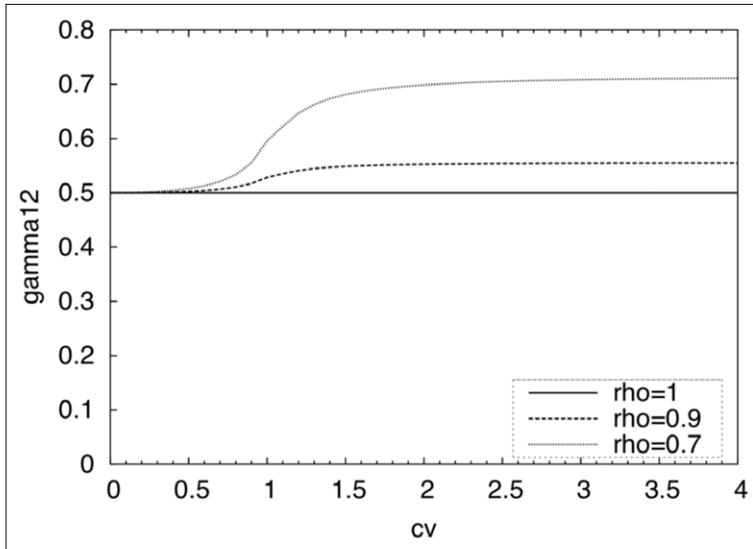


Figure 7. The maximum value of inter-specific competition $\gamma_{12} = \gamma_{21}$ that allows for coexistence, vs $cv_1^{\psi} = cv_2^{\psi}$, for different values of ρ . Other parameter values are $\gamma_{11} = \gamma_{22} = 0.5$, $\alpha_1 = \alpha_2 = 0$, $\sigma_1 = \sigma_2 = 2$, $h_1 = h_2 = 15$, $c_1 = c_2 = 1$, $K = 1000$, $d = 0.5$.

where all quantities are computed at the equilibrium E_1 . Moreover, R_0^2 and R_0^1 are the basic reproduction number given in (16), using the means of ψ_1 and ψ_2 , ρ is the correlation coefficient between ψ_1 and ψ_2 and cv_i^{ψ} are the coefficients of variation (= standard deviation/mean) of ψ_i .

The interest of the analysis of this model lies mainly in understanding the role of ρ , cv_1^{ψ} and cv_2^{ψ} . In fact, high values of cv_1^{ψ} and cv_2^{ψ} correspond to highly aggregated parasite distributions at equilibrium; indeed, Dobson⁷ had found that aggregation promotes parasite coexistence.

One can start the analysis by a simple case: when $\rho = 1$, cv_1^{ψ} , cv_2^{ψ} the conditions for coexistence $R_2^2 > 1$ and $R_1^1 > 1$ become identical to the conditions (17) found without heterogeneity. Hence, when there is perfect correlation among hosts between predispositions to each parasite species, a high aggregation (as long as it is the same in both species) has no effect on coexistence. This conclusion is similar to what found by Pugliese¹⁸ in the exact invasion analysis of a model without direct interactions (see Fig. 1). When cv_1^{ψ} and cv_2^{ψ} are different, the conclusion is not as straightforward; one can see that the invasion of a parasite is hampered, if its variation in predisposition is much larger than that of the resident parasite, while is facilitated if its much lower; on the whole, still aggregation does not promote parasite coexistence.

Decreasing the correlation ρ among host predisposition to parasites makes coexistence easier; this can be seen from (24), since the coefficient of ρ is negative. Intuitively, it is clear that, if some hosts are more predisposed to parasite 1 and others to parasite 2, parasite coexistence becomes easier.

Less intuitive is the fact that there is an interaction between the effects of the two parameters. When $\rho < 1$ and $cv_1^{\psi} = cv_2^{\psi}$, increasing the coefficients of variations (still keeping $cv_1^{\psi} = cv_2^{\psi}$) makes it easier satisfying the invasion conditions. This follows indirectly from (24), since higher cv_1^{ψ} results in lower x_i at equilibrium. Hence, in these circumstances the conclusion that aggregation promotes coexistence may be justified. A quantitative example is shown in Figure 7; it can be seen that an imperfect correlation in predisposition ($\rho < 1$) and high coefficients of variation allow for the coexistence of parasite species that are identical in all demographic parameters, but with inter-specific competition higher than intra-specific one; the effect is not very large, though, unless correlation is rather low.

Table 2. Summary of models examined in this chapter

Biological Assumption	Mathematical Method	Mechanisms of Coexistence
No direct interactions. Induced mortality ⁷	Assumption of independent negative binomial distributions	Aggregation of parasite distributions
As above ⁹	Negative binomial distributions with fixed correlation coefficient	As above and favored by negative correlation coefficient
As above ¹⁸	Exact computation of invasion coefficients	Trade-off fertility-survival, with subtle effects on host mortality schedules that can allow coexistence
Competition at establishment. No induced mortality ¹³	Normal approximations	Inter-specific competition lower than intra-specific
As above with variance in predisposition to infection ¹³	Normal approximations	Imperfect correlation between predisposition to infection from the different parasite species
Density-dependence in parasite fertility. ¹³ Induced mortality allowed (this chapter)	Normal approximations. ¹³ Exact computation of invasion coefficients (this chapter)	Inter-specific competition lower than intra-specific

Conclusions

Several models for parasite competition have been presented. All are rather complex and do not allow for an easy analysis. For this reason, only some special cases have been considered in this chapter and more extensive analyses would be necessary before drawing clear conclusions. In Table 2 I present a summary of the models considered and the mechanisms yielding coexistence in each.

Still, it is possible to state some general, though preliminary, results. Parasite coexistence generally requires intra-specific competition; if parasite populations are controlled only indirectly through their effects on hosts (through mortality or fertility) and do not compete directly for host resources, then at equilibrium host density will be severely reduced and parasite coexistence would require precise balances of demographic parameters that appear rather unlikely. Such a trade-off between parasite fertility and survival (including the host's) would result in a coexistence of metapopulation type, with one species quicker at reaching new hosts and another surviving longer on the colonized ones.

On the other hand, if parasite populations are controlled by their competition for host resources, or other types of interactions among them, then coexistence occurs as long as inter-specific competition is lower than intra-specific one, following a dynamics reminiscent of Lotka-Volterra equations.

A specific feature of host-parasite interactions is host predisposition for infection, that is generally considered the most relevant mechanism generating aggregated parasite distributions, a feature universally observed in empirical surveys.²⁴ If there exists only a generic predisposition for all parasite species, then this has no effects on the feasibility of parasite coexistence. On the other hand, if the predisposition to different parasite species differs among hosts, then coexistence becomes more likely, as quite obvious intuitively; in this case, a higher variance in predisposition generates both a higher aggregation in parasite distribution and a larger parameter region for coexistence; in this limited sense, it may be stated that aggregation promotes coexistence.

Are there general predictions about patterns that can be observed in natural population? At this level of generality, it seems very difficult; for instance, predictions about correlations between different parasite species depend on the mechanisms allowing for coexistence. Positive (but low) correlation coefficients are produced simply by the mixture of hosts of different age (and other groups); strong intra-specific competition, coupled with a low inter-specific one, will make them more positive, as well as a strong variance in generic predisposition to infection. On the other hand, predisposition to different parasite species differing among hosts will force towards negative correlation.

Finally, the dynamics exhibited by the models displayed in this chapter is very simple: quick convergence towards an equilibrium. This indeed is a typical behavior of competition systems and one may wonder whether interactions with hosts can modify this. The examples shown in this chapter have considered a rather limited parameter range, that allowed for a low-dimensional truncation of the infinite system and/or for a reasonable normal approximation. It is known, on the other hand, that host-parasite interactions may induce cycles, especially when parasites affect host fertility;² although variance in host predisposition to infection and parasite competition decrease the likeliness of cyclic behavior.³² Simple dynamics with quick convergence to equilibrium has been the rule in the examples examined for this chapter; however, it seems likely that more extensive numerical explorations will uncover examples of complex dynamics in host-2 parasite systems.

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Appendix. The Model Analyzed

The system in the variables $p_{ij}(t)$ arising from the assumptions shown in Table 1 is:

$$\begin{aligned}
 p'_{ij}(t) &= \varphi_1(1-\gamma_{11})^{i-1}(1-\gamma_{12})^j p_{i-1,j}(t) + \varphi_2(1-\gamma_{21})^i(1-\gamma_{22})^{j-1} p_{i,j-1}(t) + (i+1)(\sigma_1 + \tau_{11}(i+1) + \tau_{12}j) p_{i+1,j}(t) \\
 &\quad + (j+1)(\sigma_2 + \tau_{21}i + \tau_{22}(j+1)) p_{i,j+1}(t) - [\varphi_1(1-\gamma_{11})^i(1-\gamma_{12})^j + (1-\gamma_{21})^i(1-\gamma_{22})^j \\
 &\quad + i(\sigma_1 + \alpha_1 + \tau_{11}i + \tau_{12}j) + j(\sigma_2 + \alpha_2 + \tau_{21}i + \tau_{22}j) + d] p_{i,j}(t) \\
 p'_{00}(t) &= (\sigma_1 + \tau_{11}) p_{1,0}(t) + (\sigma_2 + \tau_{22}) p_{0,1}(t) - (\varphi_1 + \varphi_2 + d) p_{0,0}(t) + b(N) \sum_{i,j} p_{i,j}(t) (1-\xi_1)^i (1-\xi_2)^j
 \end{aligned}$$

where $\varphi_1 = \beta_1 L_1 \psi_1$ and, by convention, $p_{-1,j}(t) = p_{i,-1}(t) = 0$.

The system is completed by equations (1) for L_1 and L_2 .

In the quasi-equilibrium approximation, L_1 and L_2 are given by (2) and $\varphi_1 [\varphi_2]$ by (3).