

How parasitism affects critical patch-size in a host–parasitoid model: application to the forest tent caterpillar

C.A. Cobbold^{a,b,*}, M.A. Lewis^{b,c}, F. Lutscher^{b,d}, J. Roland^c

^aDepartment of Mathematics, University of Glasgow, University Gardens, Glasgow, G12 8QW, UK

^bDepartment of Mathematical and Statistical Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2G1

^cDepartment of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2G1

^dDepartment of Biological Sciences, University of Calgary, Calgary, Alberta, Canada T2N 1N4

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Abstract

Habitat structure has broad impacts on many biological systems. In particular, habitat fragmentation can increase the probability of species extinction and on the other hand it can lead to population outbreaks in response to a decline in natural enemies. An extreme consequence of fragmentation is the isolation of small regions of suitable habitat surrounded by a large region of hostile matrix. This scenario can be interpreted as a critical patch-size problem, well studied in a continuous time framework, but relatively new to discrete time models. In this paper we present an integrodifference host–parasitoid model, discrete in time and continuous in space, to study how the critical habitat-size necessary for parasitoid survival changes in response to parasitoid life history traits, such as emergence time. We show that early emerging parasitoids may be able to persist in smaller habitats than late emerging species. The model predicts that these early emerging parasitoids lead to more severe host outbreaks. We hypothesise that promoting efficient late emerging parasitoids may be key in reducing outbreak severity, an approach requiring large continuous regions of suitable habitat. We parameterise the model for the host species of the forest tent caterpillar *Malacosoma disstria* Hbn., a pest insect for which fragmented landscape increases the severity of outbreaks. This host is known to have several parasitoids, due to paucity of data and as a first step in the modelling we consider a single generic parasitoid. The model findings are related to observations of the forest tent caterpillar offering insight into this host–parasitoid response to habitat structure.

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1. Introduction

Landscape fragmentation is an increasingly important form of habitat disturbance that influences species dynamics. Its effects on landscape structure include decreased habitat area, increased edge length and altered distance between patches, all of which may affect species abundance and the population dynamics of residents of the habitat.

A number of insect species show population changes in response to habitat fragmentation. For example, outbreaks of the North American spruce budworm (*Choristoneura fumiferana*) are more severe in continuous forest compared to fragmented stands (Swetnam and Lynch, 1993; Mott, 1963). In contrast to the spruce budworm, forest tent caterpillar (*Malacosoma disstria*) outbreaks can last longer and are more frequent in forests fragmented by agricultural clearings (Roland, 1993). The mechanisms driving the outbreak response to fragmentation are poorly understood but may be a key to effective pest management. Natural enemies play an integral part in many insect systems, and therefore host–parasitoid interaction may be an important factor

*Corresponding author. Department of Mathematics, University of Glasgow, University Gardens, Glasgow G12 8QW, UK. Fax: +44 141 330 4111.

E-mail address: cc@maths.gla.ac.uk (C.A. Cobbold).

in determining insect outbreaks. The purpose of this study is to investigate how the coupling between host and parasitoid is affected by habitat patch-size.

Discrete time models are a natural framework for studying host–parasitoid insect systems, with species from temperate climates frequently exhibiting non-overlapping generations. While many researchers (Hassell and May, 1973; Hassell, 1978; May et al., 1981; Wang and Gutierrez, 1980; Umbanhowar and Hastings, 2002) since the initial model by Nicholson and Bailey (1935) have focussed on stabilising the host–parasitoid coexistence equilibrium in discrete time systems we provide a serious attempt to quantify population cycles, with respect to length and frequency. In natural insect systems, population cycles are common, and the peaks of these cycles are often associated with insect outbreaks. Rather than looking to stabilise this coexistence, our interest lies not only in the persistence of the host and parasitoid, but also in the factors which can lengthen and shorten these periodic insect outbreaks.

Spatial factors are also an important aspect determining outbreak characteristics in many insect systems. An extension of difference equations which are spatially, explicit and continuous, are integrodifference models. Integrodifference models describe a life cycle consisting of two distinct stages, a sedentary stage and a dispersal stage. Such models were initially applied to address questions of gene flow (Weinberger, 1982; Lui, 1982a,b) and have since been applied to ecological questions (Hardin et al., 1988, 1990; Kot et al., 1996; Neubert and Caswell, 2000; Lutscher and Lewis, 2004). Integrodifference equations are an ideal tool for investigating a spatially explicit host–parasitoid system. Two-species integrodifference models of predator–prey interactions have received increasing attention in recent years, with interest in questions of species invasion and spatial pattern formation (Neubert et al., 1995; Kot, 1992; Kot et al., 1996; Sherratt et al., 1997). Host–parasitoid extinction was studied in a spatially discretised integrodifference model by Allen et al. (2001). It was demonstrated that dispersal in space can have a stabilising effect on the populations. A natural progression from the work of Allen et al. (2001) is to examine the effects of habitat size.

The study of the critical patch-size necessary for species persistence was pioneered by Skellam (1951) in the context of a reaction–diffusion model. Critical patch-size has since been investigated for a single species integrodifference equation (Kot and Schaffer, 1986; Van Kirk and Lewis, 1997; Latore et al., 1998) and recently persistence in periodically spaced patches has been studied in the context of marine reserves (Botsford et al., 2001; Van Kirk and Lewis, 1997). Here, we address the two-species critical patch-size problem, and also numerically examine the response of population cycles to parasitoid behaviour. Temporal cycles have not

received much attention in the integrodifference framework, but the phenomenon is widespread and its mathematical development is applicable to the study of numerous insect assemblages. The model presented here is a spatial extension of an earlier host–parasitoid model (Cobbold et al., 2004).

We analyse the model in the context of a broad class of insect systems, however our system of interest is the forest tent caterpillar (*Malacosoma disstria*) and its parasitoid species, native to North America. Hence, we parameterise the model for this particular example.

During its periodic outbreaks, the high density of forest tent caterpillars causes mass defoliation of its host tree, the trembling aspen (*Populus tremuloides*). During a 1991 outbreak in Ontario, Canada, 1.9 million hectares of forest were defoliated (Anonymous, 1991). Such caterpillar attacks seldom result in tree death, but growth loss is common. Outbreaks occur approximately every 11 years, with outbreak densities typically maintained for 2–3 years, and up to 6 years (Roland, 1993). These prolonged outbreaks make tree death more likely. Outbreaks of this kind are common among defoliating insects, although the effects of the forest tent caterpillar are particularly devastating. The forestry implications of caterpillar control are significant: a one year reduction in outbreak duration can increase fibre production by as much as 10% over the course of a 10 year caterpillar cycle (Anonymous, 1991).

The forest tent caterpillar is attacked by a number of native host-specific fly and wasp parasitoids. These interactions are believed to play an important role in the oscillatory behaviour of these insect species.

In this paper, we formulate an integrodifference model describing host–parasitoid life-history. Section 3 is devoted to reviewing the dynamics of the non-spatial model. Sections 4 and 5 focus on the critical patch-size problem for which we perform a bifurcation analysis. Our objective is to gain understanding of how insect outbreaks are influenced by both habitat size and parasitism. In particular, we examine the interaction among parasitoid emergence time, parasitoid searching efficiency, dispersal, and patch size in ensuring host–parasitoid persistence.

2. Integrodifference model of forest tent caterpillar interaction with a generic parasitoid

Like many insect species, the forest tent caterpillar and its fly and wasp parasitoids have life cycles with one non-overlapping generation per year. We therefore formulate a discrete time model to capture the host–parasitoid dynamics. For simplicity we examine the effects of a single generic parasitoid species with the view of extending the model to a multi-parasitoid system in the future. To study critical patch-size, we

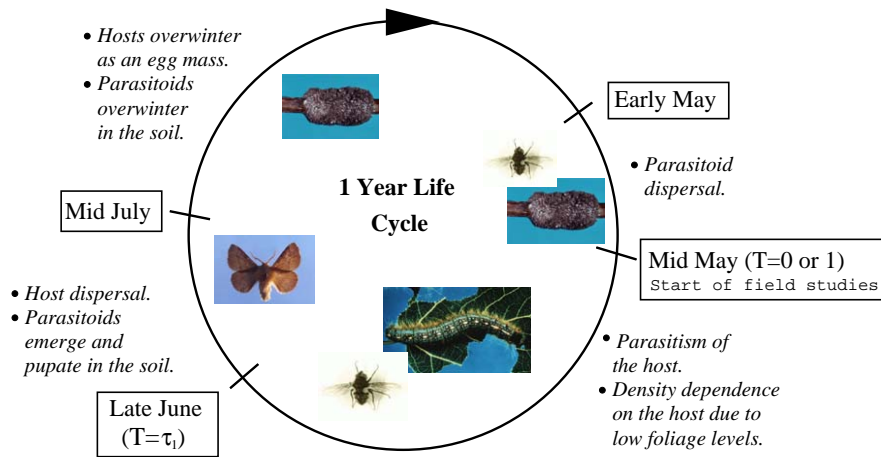


Fig. 1. Life cycle of the forest tent caterpillar and a generic parasitoid. Exact timing of events is determined by degree days.

introduce space by extending the model to a system of integrodifference equations that are discrete in time and continuous in space.

The caterpillar and its parasitoids are univoltine, so we increment our model yearly in early May, when caterpillar hatch begins (Fig. 1). As the caterpillar population develops through 5 larval stages, density-dependent mortality from scramble competition can occur (Rossiter, 1995). Scramble competition for aspen foliage occurs in the fourth and fifth larval stage and is modelled using the Ricker Eq. (Ricker, 1954). By mid summer, the surviving caterpillars pupate, hatch, and the adult moths disperse to lay their eggs, which then overwinter. Newly emerged fly and wasp parasitoids overwinter in the soil and disperse in early spring to nectar feed and mate. Parasitism of the forest tent caterpillar can occur from early May onwards, before, during or after density-dependent host mortality, depending on the parasitoid species.

When parasitoids disperse in spring, forest tent caterpillar are either eggs or early instar larvae and are sedentary. When the adult forest tent caterpillar disperses as a moth in mid summer the parasitoids are in diapause and sedentary. During the winter period separating these two dispersal events both populations are in diapause. Thus, host and parasitoid development and interaction occurs from $T = 0$ to τ_1 and dispersal of the adult insects occurs from $T = \tau_1$ to 1 (cf. Fig. 1).

We let $H_t(X)$ be the density of the host population in year t at location X and $P_t(X)$ be the corresponding parasitoid density. We assume that parasitoids encounter their hosts randomly according to a Poisson distribution. The parasitoid has a searching efficiency a , giving a probability $e^{-aP_t(X)}$ of a host escaping parasitism. Two descriptions of parasitism were considered by Cobbold et al. (2004), clumped parasitoid attacks described by the negative binomial distribution and random attacks described by the Poisson distribution. Attacks on the forest tent caterpillar were best described by the Poisson

distribution. A more general description of parasitism is described by the negative binomial, which allows for clumping of parasitoid attack. Cobbold et al. (2004) analysed the non-spatial host–parasitoid model using this more general description of parasitism, the qualitative behaviour of the model was found to remain unchanged as the parameter describing clumping was varied. We do expect that the results that will be discussed in this paper will hold under the negative binomial model, this would broaden the class of insect systems for which the results can be applied.

Density-dependence in the host population affects the reproduction of parasitoids if a parasitised host dies before the parasite emerges from it. Therefore, it is the time of emergence rather than the time of parasitism that determines the effect of host density-dependence on parasitoid reproduction. We model this effect by inserting the term $e^{-\hat{\alpha}H_t(X)}$ into the parasitoid equation (1), where $\hat{\alpha}$ ranges from 0 to r/K . The case $\hat{\alpha} = 0$ describes the situation that parasitoids emerge before density-dependence acts on the host population. From each parasitised host there emerges one parasitoid. The other extreme $\hat{\alpha} = r/K$ describes the case that parasitoids emerge after density-dependence acts on the hosts. Only those host that survive can produce next-generation parasitoids. Intermediate values of $\hat{\alpha}$ describe concurrent parasitism and density-dependence. Once parasitoids have emerged from the host, the dynamics of the two populations decouple for the rest of the season. The equations for the vital dynamics ($H_{t+\tau_1}(Y)$ and $P_{t+\tau_1}(Y)$ in Eq. (1)) were introduced by Cobbold et al. (2004), a full discussion of the model and its application to the forest tent caterpillar can be found there. The host–parasitoid models by Beddington et al. (1975) and Wang and Gutierrez (1980) are special cases of this more general formulation.

Finally, we describe dispersal, the host and parasitoid densities at each spatial location X at the start of the next generation can be found by integrating over all

possible locations Y , from which the individual could have successfully dispersed. This yields

$$H_{t+1}(X) = \int_{\Omega} \overbrace{K_H(X, Y)}^{\text{Prob. of the host successfully moving from } Y \text{ to } X} \underbrace{H_t(Y) \times \overbrace{e^r}^{\text{Intrinsic growth}} \times \overbrace{e^{-rH_t(Y)/K}}^{\text{Prop. of hosts surviving density-dependence}} \times \overbrace{e^{-aP_t(Y)}}^{\text{Prob. of hosts not being parasitised}}}_{H_{t+\tau_1}(Y)=\text{Hosts at } Y \text{ which disperse at time } t+\tau_1} dY, \tag{1a}$$

$$P_{t+1}(X) = \int_{\Omega} \overbrace{K_P(X, Y)}^{\text{Prob. of the parasitoid successfully moving from } Y \text{ to } X} \underbrace{H_t(Y) \times \overbrace{e^{-\alpha H_t(Y)}}^{\text{Prop. of parasitised hosts surviving density-dependence}} \times \overbrace{(1 - e^{-aP_t(Y)})}_{\text{Probability of hosts being parasitised}}}_{P_{t+\tau_1}(Y) = \text{Parasitoids at } Y \text{ which disperse at time } t + \tau_1} dY. \tag{1b}$$

The functions, $K_H(X, Y)$ and $K_P(X, Y)$ are probability density functions with mean 0, variance σ_h^2 and σ_p^2 and describe dispersal kernels for the host and parasitoid populations respectively. They describe the probability of successful movement from location Y to location X . The spatial domain is denoted by Ω and includes only regions of suitable host habitat.

2.1. Parameterisation

2.1.1. Population dynamic parameters

The parameters describing forest tent caterpillar and parasitoid vital dynamics are from field data and the results are summarised in Table 1. (See Cobbold et al. (2004) for a detailed discussion of parameter estimation and data collection).

2.1.2. Dispersal parameters

Dispersal parameters (σ_h^2, σ_p^2) of the forest tent caterpillar and its parasitoids are considerably more difficult to estimate. In mark-recapture experiments, only 3/3000 adult parasitoids were recaptured (Roland and Taylor, 1995). They travelled up to 300 m from the release point, giving an idea of possible dispersal distance. The adult moth stage of the forest tent caterpillar has been recorded to travel on the order of 1 km or further. An estimate for parasitoid dispersal distance is 300–800 m depending on species (Roland and Taylor, 1997, 1995). To estimate σ_h^2 and σ_p^2 we assume that 90% of the host population travel within a 800–1000 m radius and that 90% of parasitoids disperse a distance of 300–800 m. Assuming a Gaussian dispersal kernel gives:

$$\sigma_h^2 \approx 0.235 - 0.367 \quad \text{and} \quad \sigma_p^2 \approx 0.058 - 0.235.$$

Adopting a Laplace distribution yields:

$$\sigma_h^2 \approx 0.241 - 0.377 \quad \text{and} \quad \sigma_p^2 \approx 0.060 - 0.241.$$

These distributions are compared in Fig. 2. Experimental data from a variety of insects show dispersal kernels with leptokurtic tails, consistent with the Laplace kernel (Makino et al., 1987; Taylor, 1978; Dobzhansky and Wright, 1943; Aikman and Hewitt, 1972). In the absence of further data, we assume a Laplace kernel for adult forest tent caterpillar dispersal. The Laplace kernel has a ‘fatter tail’ compared to the Gaussian kernel, which corresponds to rare long distant dispersal events such as those driven by wind for example. Mechanistically the Laplace kernel corresponds to random movement with a constant settling rate. Although these estimates of dispersal are very approximate, we feel, based on personal observation of flight of these insects, that they are reasonable and all our results can be easily interpreted for smaller or larger dispersal distances.

2.2. Non-dimensionalisation

A suitable non-dimensionalisation for the dynamics of the model is given by

$$h_t(X) = \frac{H_t(X)}{K}, \quad p_t(X) = aP_t(X), \quad \rho = Ka, \quad \alpha = \widehat{\alpha}K,$$

where $h_t(X)$ and $p_t(X)$ are the non-dimensionalised host and parasitoid densities, respectively. Initially we will consider a one-dimensional spatial domain of length L (km). Scaling the domain length to $x = X/L$ yields the following non-dimensional system of equations:

$$h_{t+1}(x) = \int_0^1 k_h(x, y) h_t(y) e^r e^{-rh_t(y)} e^{-p_t(y)} dy, \tag{2a}$$

$$p_{t+1}(x) = \int_0^1 k_p(x, y) \rho h_t(y) e^{-\alpha h_t(y)} (1 - e^{-p_t(y)}) dy. \tag{2b}$$

Table 1
Parameter values for the model kinetics, estimated from experimental data.

Parameter	Description and (units)	Parameter range	Typical value
r	Host intrinsic growth rate	0.05–0.9	0.7
K	Host carrying capacity (# of cocoons counted in a 15 min collection time)	200–300	260
a	Parasitoid searching efficiency (Area searched during a 15 min cocoon count per parasitoid)	0.009–0.033	0.031
$\hat{\alpha}$	Parasitoid mortality due to host density-dependent mortality (per host density)	$0-r/K$	$0.9r/K$

a and K are estimated using time linked cocoon counts of host and parasitoid densities taken over several years together with defoliation levels to estimate K . $\hat{\alpha}$ was found by experimentally isolating hosts at different densities and estimating the carrying capacity for each host larval instar. Lastly, an adult forest tent caterpillar lays an egg band containing 150–300 eggs and mortality is typically 98%, yielding our estimates of host growth rate r .

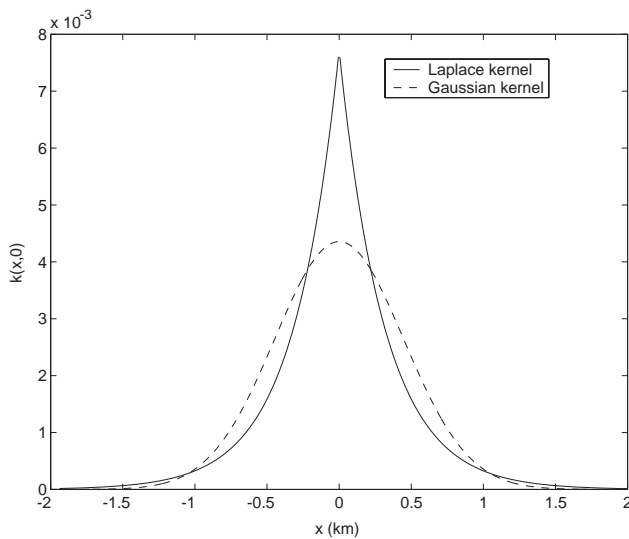


Fig. 2. Dispersal kernels used for both host and parasitoid populations. Individuals are released at 0 and the resulting probability density function (PDF) is plotted. The Laplace kernel has ‘fatter’ tails compared to the Gaussian kernel, but both give the same qualitative model results. The parameter used to generate these profiles is: $\sigma^2 = 0.2(\text{km}^2)$.

In the case of the Laplace kernel, we set $L_h = L\sqrt{\frac{2}{\sigma_h^2}}$ and $L_p = L\sqrt{\frac{2}{\sigma_p^2}}$, which gives,

$$k_h(x, y) = \frac{L_h}{2} \exp(-L_h|x - y|) \quad \text{and}$$

$$k_p(x, y) = \frac{L_p}{2} \exp(-L_p|x - y|).$$

L_h and L_p are the effective domain lengths and measure the domain length relative to dispersal distance. (L_h and L_p are used in calculations, however, figures illustrate the dimensional domain length L .)

3. Dynamics of the non-spatial system

Given that the forest tent caterpillar, like many host insects, is subject to attack from a number of specialist parasitoid species, it is interesting to examine the effect of parasitoid characteristics on host outbreaks. The behaviour of the non-spatial host–parasitoid system depends on both the strength of host density-dependent mortality experienced by the parasitoid (α), and on parasitoid searching efficiency (a). We first summarise the effects of parasitoid timing α , reported by Cobbold et al. (2004), extending the results presented by Neubert and Kot (1992).

3.1. Variation in parasitoid timing (α)

The non-dimensionalised non-spatial model has only three parameters: α, ρ and r and exhibits rich dynamics ranging from host–parasitoid extinction to a host–parasitoid limit cycle and even chaos. Fig. 3 summarises the behaviour of the model in $\rho - r$ parameter space and is a special case of the stability plots generated by Cobbold et al. (2004) and Neubert and Kot (1992). The timing of parasitism (α), often over looked in discrete time models, is shown to have a large affect on the population dynamics in host–parasitoid models, affecting persistence and the period and amplitude of temporal cycles.

The two extremes of parasitoid timing are parasitism followed by density-dependence ($\alpha = 0$) and density-dependence followed by parasitism ($\alpha = r$), these two cases are presented in Fig. 3a and b, respectively. For each stability plot, the central region (II) describes stable coexistence of the host and parasitoid. An increase in ρ leads to a loss of stability of the coexistence steady state via a Hopf bifurcation, a decrease in ρ leads to a transcritical bifurcation and an increase in r gives a period-doubling bifurcation. The effect of parasitoid emergence time α , is to deform the stability boundaries.

Consider fixed values for r and ρ marked by the \times in Fig. 3a and b. Increasing α from 0 to r changes the stable coexistence equilibrium to parasitoid extinction. This example demonstrates that the emergence time of the parasitoid has implications when evaluating a parasitoid as a biological control agent. (See Cobbold et al. (2004) for a more detailed discussion).

Biologically realistic parameter values for the forest tent caterpillar place the model in the region of parameter space where the host and parasitoid populations oscillate on a limit cycle irrespective of the value of α . Population cycles are consistent with the periodic outbreaks of the forest tent caterpillar. To validate the model for the forest tent caterpillar we fixed parameters using experimental data and calculated the correlation between the model and an independent historical time series (Cobbold et al., 2004). A 75–95% correlation between model and data was found. Simulations show differences between outbreak and non-outbreak host densities are at least 4–5 orders of magnitude, consistent with field observations for the forest tent caterpillar (Hodson, 1941).

The population cycles showed a decrease in period in response to an increase in α , furthermore the number of

years the host spends at high density decreased (results not shown, see Cobbold et al. (2004)). In summary, late emerging parasitoids were associated with less severe host outbreaks when compared to early emergers.

3.2. Variation in scaled parasitoid searching efficiency ($\rho = Ka$)

Parasitoid searching efficiency (a) can vary among parasitoid species. Searching efficiency incorporates a range of parasitoid attack strategies, such as ovipositing directly in or on the host versus ovipositing on damaged foliage which may be subsequently consumed by the host.

The effect of parasitoid searching efficiency on host-outbreak duration and frequency can be calculated from the model numerically (Fig. 4). Outbreak frequency is the period of the host cycle averaged over several periods. Outbreak duration is taken to be the proportion of one period for which the host density is above some arbitrary threshold, in this case 70% of K . Since the population cycles are a consequence of a Hopf bifurcation they are aperiodic and hence we also average the outbreak duration over several periods. Despite taking averages, we still find fluctuations in outbreak duration. This is a consequence of limit cycle deformation as ρ is changed. The population cycles make up discrete points on the limit cycle, the deformation of this cycle can push points that are initially near the outbreak threshold to move above or below. The model predicts that efficient searchers (large ρ) prolong outbreak duration, but reduce outbreak frequency. A single prolonged outbreak can be more severe than multiple short outbreaks over the same time frame, since the repeated annual foliage damage makes habitat dieback more likely.

It is somewhat counter intuitive that efficient searchers lead to more severe host outbreaks and, therefore, greater tree damage. Numerical simulations offer one explanation (Fig. 5). Parasitoids with large ρ rapidly suppress the host population causing parasitoid numbers to rapidly decline. Following the crash, the host population recovers faster than the parasitoid population allowing a long severe outbreak before parasitoids can control the hosts once more. Differences in ρ could occur in response to changes in the dominance by wasps (efficient) versus fly (inefficient) parasitoids.

In Section 4 we study the full spatial model (Eq. (2)) and investigate the effect of space on these population processes.

4. Dynamics of the spatial system: a single continuous forest

In sufficiently large domains, the behaviour of the spatial model is similar to the behaviour of the

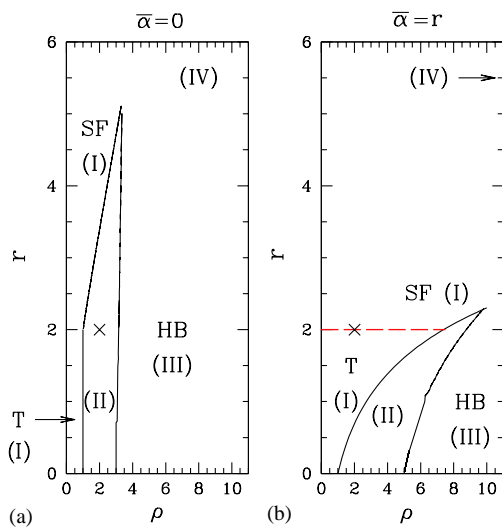


Fig. 3. $r - \rho$ -parameter space describing the stability of the host-parasitoid coexistence equilibrium. Region II marks stable host-parasitoid coexistence. As ρ decreases the equilibrium loses stability via a transcritical bifurcation T, resulting in parasitoid extinction. As ρ increases stability is lost through a hopf bifurcation HB, generating periodic cycles in the two populations. As r is increased a subcritical flip bifurcation SF, occurs leading to parasitoid extinction. Finally for large r and ρ chaotic behaviour occurs (IV). Plot (a) $\alpha = 0$, gives the special case studied by Beddington where parasitism is followed by host density-dependent mortality. Plot (b) $\alpha = r$, is the other extreme where density-dependence is followed by parasitoid emergence. The boundaries were calculated using a linear stability analysis by examining which parameters violated the Jury conditions. Changing α distorts the stability boundaries and can affect the persistence of the parasitoid species. For example, fix r and ρ (see \times), when $\alpha = 0$ the dynamics are in region II when $\alpha = r$ the dynamics are in region I.

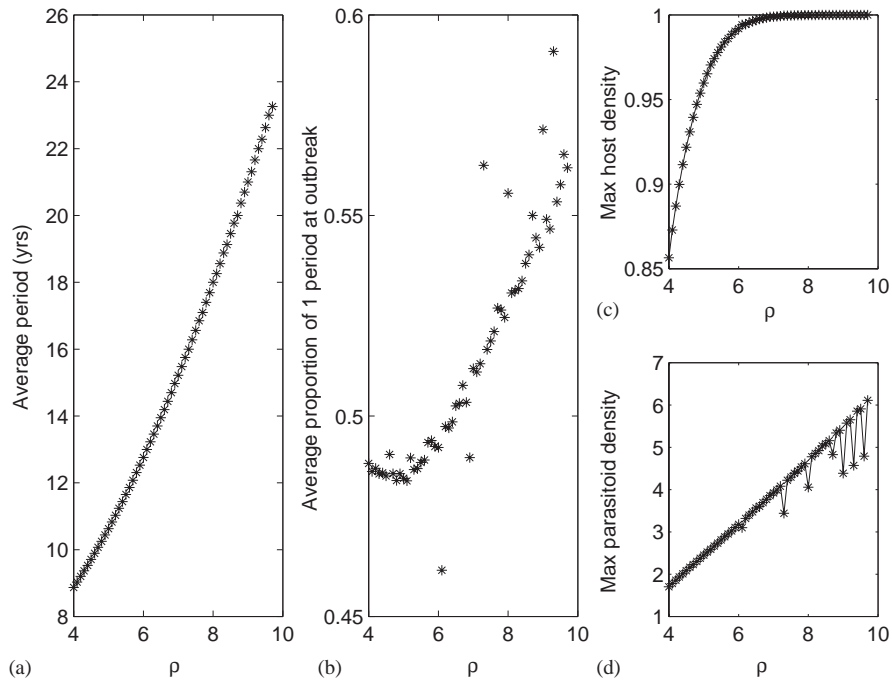


Fig. 4. Illustrating the period and outbreak-duration of oscillations in the host, as a function of ρ , scaled parasitoid searching efficiency. (a) The period of oscillations increases as a function of ρ , i.e. efficient parasitoids are associated with infrequent outbreaks. (b) The average proportion of one period spent at outbreak density ($h_t > 0.4$; for other threshold levels the trend remains unchanged) increases as a function of ρ . Host outbreaks are more severe under efficient parasitoids. (c) and (d), the maximum host and parasitoid density reached during a cycle increases with parasitoid searching efficiency. Parameter values used to generate these profiles are as follows: $r = 0.96$ and $\alpha = 0$. Initial conditions were $h_0 = 0.6$, $p_0 = 0.2$. Simulations were run for 7000 time iterations to ensure we are not observing transients, and the last 200 iterates were used to determine average period and outbreak duration.

non-spatial counterpart. In the other extreme when the suitable habitat domain is very small we may find extinction, giving rise to a critical patch-size problem. A natural question to ask is: what behaviour can be observed in smaller spatial domains? In this section we address the critical patch-size problem by numerically generating a bifurcation plot of the model for a fixed parameter set (Fig. 6). In the next section we look at some analytical results.

Consider the model on a one-dimensional spatial domain $\Omega = [0, L]$ of suitable habitat. Insects that disperse and remain within Ω survive and reproduce there. Those leaving Ω land in unsuitable habitat and die. We refer to L as the forest size and use this as a parameter in our bifurcation analysis. The spatial average of the host and parasitoid densities over the habitat Ω are used as bifurcation variables.

To numerically construct a bifurcation diagram, we first discretise Eq. (2) in space using 33 grid points yielding a set of coupled difference equations. These equations are coupled via the discretised redistribution kernel which is obtained by approximating the integral using Simpson's rule. To ensure the accuracy of this discretisation, spatial grids containing up to a 161 points were also considered and bifurcation results were compared to numerical simulations of the integrodiffer-

ence model using a fast Fourier transform on a spatial grid containing on the order of 2000 points (Andersen, 1991; Brewster and Allen, 1997). Thirty three grid points proved sufficient for good numerical accuracy while maintaining speed of calculation. The AUTO package (Doedel et al., 1991) is used to generate the bifurcation diagram (Fig. 6).

The bifurcation plot demonstrates that domain size can significantly influence population dynamics (Fig. 6). Small patch sizes (region A, Fig. 6) result in host and parasitoid extinction. Host dispersal out of the habitat patch reduces the host population to a level too small to persist and consequently the parasitoid population is driven to extinction.

In slightly larger patches (region B, Fig. 6) a host-only equilibrium is established. Parasitoid absence can be explained by host dispersal: loss through the boundary and are large enough to drive host numbers below those required to sustain the parasitoid population. Isolated patches of this type could provide a refuge for host insects. This in fact has been observed by Roland and Taylor (1995) who found that some isolated aspen stands supported caterpillars but remained uninfested by particular parasitoids species.

When larger patch sizes are considered (region C, Fig. 6), the host and parasitoid populations coexist. A

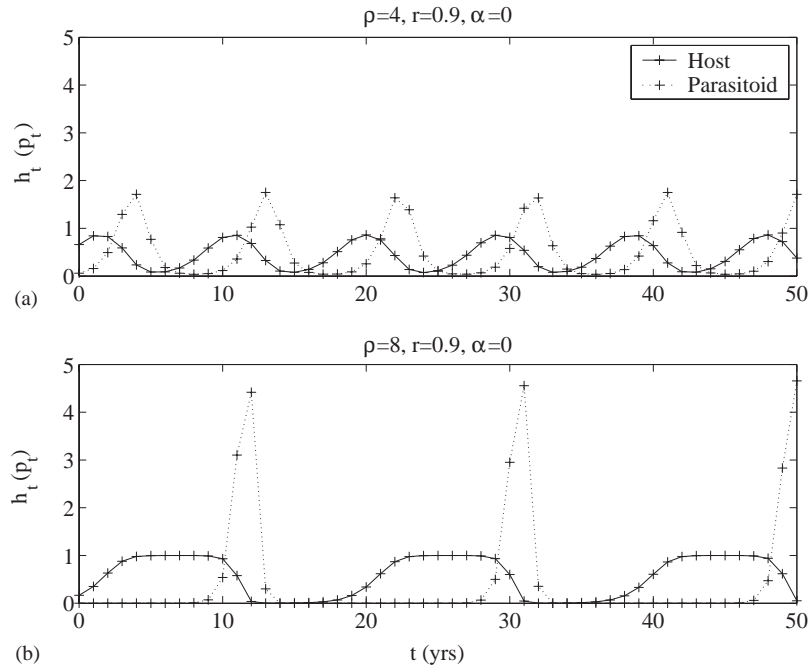


Fig. 5. Temporal evolution of the non-spatial model using two scaled parasitoid searching efficiencies (a) $\rho = 4$ and (b) $\rho = 8$. When parasitoid searching efficiency is high host outbreaks are longer but less frequent. The parameter values used to generate these profiles are as follows: $r = 0.9, \alpha = 0, \rho = 4$ or $\rho = 8$ (consistent with experimentally estimated values for the forest tent caterpillar system). Initial conditions were $h_0 = 0.6, p_0 = 0.2$. Simulations were run for 7000 time iterations to ensure we are not observing transients, and last 50 time iterates were plotted.

further increase in domain size moves the dynamics into region D, here the system undergoes a Hopf bifurcation, leading to temporal oscillations in both host and parasitoid densities. These oscillations are equivalent to the periodic outbreaks observed in many insect populations. We illustrate the temporal oscillations in Fig. 7. For small spatial domains there is little spatial variation in the host and parasitoid distributions, spatial oscillations become apparent for sufficiently large L as seen in Fig. 7.

5. Critical patch size problem: analytical classification of forest size

In Section 4, we only allowed the spatial parameter L , to vary and demonstrated the existence of critical patch sizes for host–parasitoid persistence. We now generalise these results by presenting two analytical methods to calculate critical patch size as a function of model parameters. The first method involves converting a linearised system of equations to a boundary value problem which can then be used to derive a stability boundary separating stable equilibria. The second method uses the formulation of a caricature model which is spatially implicit. Stability boundaries, and hence critical patch sizes of the spatially implicit system, are then determined using the Jury conditions. We show

that the two methods are related and agree numerically. The two approaches both have merits and pitfalls which we will discuss. The implications of these analytical expressions are then presented in Section 5.3.

5.1. Boundary value problem

We analytically classify forest size according to the presence and absence of host and parasitoid by using and extending results from Kot and Schaffer (1986), Van Kirk and Lewis (1997) and Lutscher and Lewis (2004).

5.1.1. Critical patch size problem 1: host persistence

We first consider the boundary dividing regions A and B in Fig. 6 to determine the minimum domain size that permits host growth. We linearise (Eq. (2)) about the trivial equilibrium $(h^*(x), p^*(x)) = (0, 0)$, yielding:

$$h_{t+1}(x) = \int_0^1 k_h(x, y)e^r h_t(y) dy, \tag{3a}$$

$$p_{t+1}(x) = 0. \tag{3b}$$

The parasitoid equation vanishes, so the problem becomes one-dimensional. The stability of the trivial equilibrium is determined using linear operator theory. We consider the eigenvalues (λ) of Eq. (3), by looking for solutions of Eq. (3) of the form $h_t(x) = \lambda^t \phi_h(x)$. This

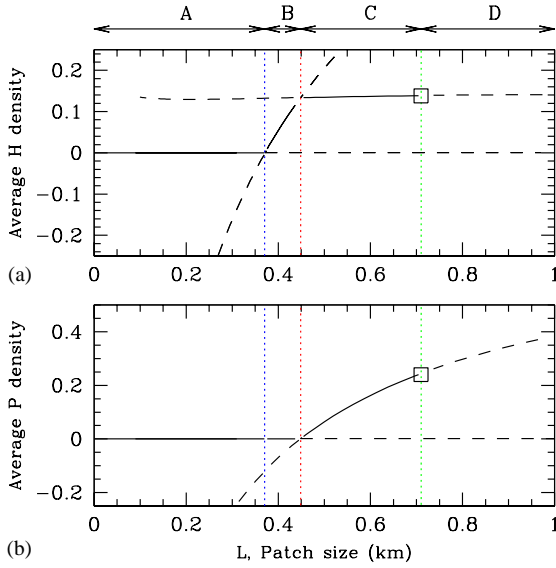


Fig. 6. Bifurcation diagram of the full spatial model, with the spatial average of (a) host and (b) parasitoid populations (averaged over L) plotted against patch size (L). The plots were generated using the AUTO package by discretising space into 33 grid points and applying Simpson’s rule to approximate the integration. The solid lines indicate stable steady states and the dashed lines are unstable equilibria. The dotted lines indicate a bifurcation. In region A, where both host and parasitoid are extinct, a combination of dispersal and resource limitation prevent species persistence. As the domain is increased we observe a stable host-only steady state in region B. The hosts are still at a sufficiently low density that they cannot support a parasitoid population. Increasing L further gives region C, where host and parasitoid coexist. For large domains we pass through a Hopf bifurcation, marked with the box (\square), indicating periodic temporal oscillations (region D). Parameter values used to generate this figure are: $\sigma_h^2 = 0.25$, $\sigma_p^2 = 0.01$, $\alpha = 0$, $\rho = 8$, $r = 0.96$.

yields the eigenvalue problem

$$\lambda \phi_h(x) = \int_0^1 \frac{L_h}{2} \exp(-L_h|x-y|) e^r \phi_h(y) dy. \quad (4)$$

By repeatedly differentiating Eq. (4) we obtain a boundary value problem which can be solved analytically, where the boundary conditions are found by solving the eigenvalue equation at the two end points of the domain, $x = 0$ and 1 . The differential equation we obtain is given by

$$\phi_h''(x) = -L_h^2 [(1/\lambda) e^r - 1] \phi_h(x), \quad (5)$$

with flux boundary conditions

$$L_h \phi_h(0) - \phi_h'(0) = 0, \quad \text{and} \quad L_h \phi_h(1) + \phi_h'(1) = 0. \quad (6)$$

(See Van Kirk and Lewis (1997) for a detailed derivation and discussion of this class of equation).

The operator presented in Eq. (4) is compact the kernel is positive, hence the eigenvalue determining stability is always positive (Krasnoselskii, 1964). Loss of stability can therefore only occur through $\lambda = +1$ in this

discrete dynamical system. Setting $\lambda = +1$ will indicate the location of the stability boundary separating host extinction from host persistence. We solve the boundary value problem (Eqs. (5) and (6)) using half angle formulae. We obtain an expression for critical domain length as a function of host per capita growth rate e^r , and variance in host dispersal distance σ_h^2 (see Van Kirk and Lewis (1997) for a discussion).

$$L_{AB}(r) = \frac{\sqrt{2\sigma_h^2} \tan^{-1}[1/\sqrt{e^r - 1}]}{\sqrt{e^r - 1}}. \quad (7)$$

The dimensional parameter L_{AB} , is the critical patch size (in km) separating patches of host extinction (region A, Fig. 6) from those of host persistence (region B). Eq. (7) shows that host persistence is independent of parasitoid densities.

5.1.2. Critical patch size problem 2: parasitoid persistence

The next critical patch size problem we study answers the question, when parasitoids persist in a patch. We calculate the stability boundary separating regions B and C in Fig. 6. This problem proves to be more difficult. We linearise (Eq. (2)) about the heterogeneous equilibrium, $(h^*(x), 0)$, and as before set $h_t(x) = \lambda^t \phi_h(x)$ and $p_t(x) = \lambda^t \phi_p(x)$, giving an eigenvalue problem,

$$\begin{aligned} \lambda \phi_h(x) = & \int_0^1 k_h(x,y) [(e^r e^{-rh^*(y)} \\ & - rh^*(y) e^r e^{-rh^*(y)}) \phi_h(y) \\ & - (h^*(y) e^r e^{-rh^*(y)}) \phi_p(y)] dy, \end{aligned} \quad (8a)$$

$$\lambda \phi_p(x) = \int_0^1 k_p(x,y) \rho h^*(y) e^{-\alpha h^*(y)} \phi_p(y) dy. \quad (8b)$$

We notice that the parasitoid (8b) decouples; since we are concerned only with conditions for parasitoid persistence, it is sufficient to study only this equation. We repeatedly differentiate Eq. (8b) to obtain the following Sturm Liouville problem with spatially varying coefficients:

$$\phi_p''(x) = -L_p^2 [(1/\lambda) \rho h^*(x) e^{-\alpha h^*(x)} - 1] \phi_p(x), \quad (9a)$$

$$L_p \phi_p(0) - \phi_p'(0) = 0 \quad \text{and} \quad L_p \phi_p(1) + \phi_p'(1) = 0. \quad (9b)$$

The spatial dependence of the coefficients $h^*(x)$, prevents us from being able to solve the boundary value problem. However, we can show there exists a constant \bar{h} which gives the true solution to (9a) (see Appendix A for details). We therefore approximate the coefficients ($h^*(x)$) by constants, yielding an equation analogous to Eq. (5). So our goal is to find the constant which best approximates \bar{h} . A natural choice of constant is the spatial average of $h^*(x)$, $h_{av} = \frac{1}{|\Omega|} \int_{\Omega} h^*(x) dx$. When the spatial variation in $h^*(x)$ is small it is clear why we

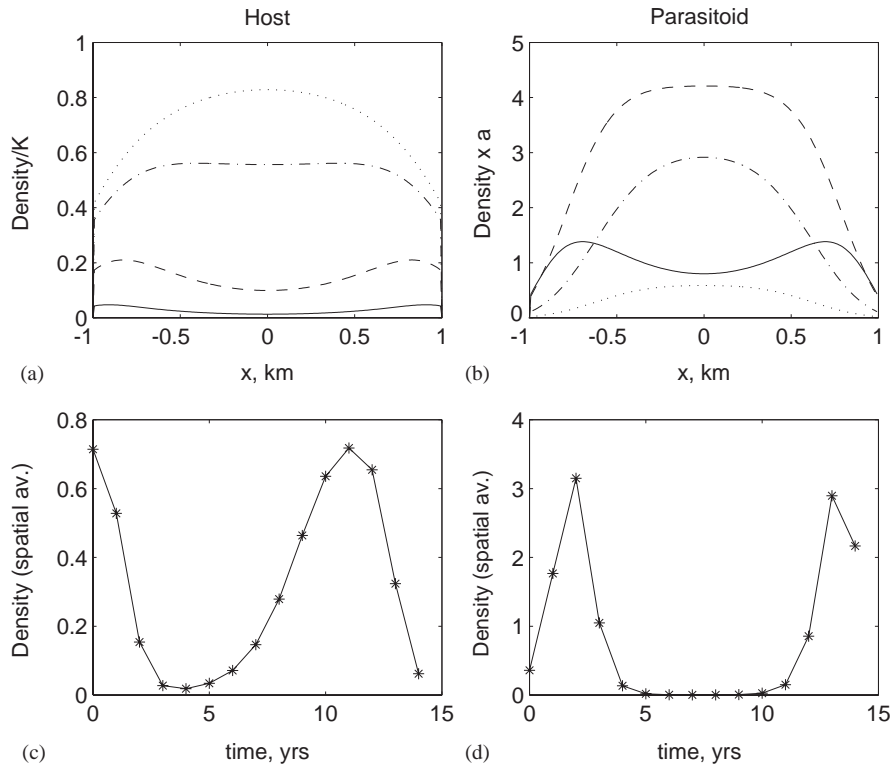


Fig. 7. (a)–(b) The evolution in time of the spatial distribution of the host and parasitoid populations respectively. (c)–(d) illustrate the spatial average of the host and parasitoid density respectively, plotted over time. The first time point ($t = 1$) corresponds to the dotted line in (a)–(b), the dot–dash line corresponds to $t = 2$ and the dash line corresponds to $t = 3$, finally the solid line is $t = 4$, we would like to plot more, however the plot becomes difficult to read. The populations are undergoing temporal oscillations consistent with periodic host outbreaks. The spatial distributions show spatial variation, in particular we observe a non-concave shape to the profiles. The parameters used to generate these profiles are $r = 0.96$, $\rho = 8$, $\alpha = 0$, $\sigma_h^2 = 0.25$, $\sigma_p^2 = 0.01$, with a Laplace dispersal kernel. The simulation was run for 200 time iterates, with the final 13 plotted.

would expect such an approximation to work. Van Kirk and Lewis (1997) numerically showed that this approximation also works well even when h_{av} and $h^*(x)$ differ quite significantly.

Calculating h_{av} is done using the “average dispersal success approximation” S_h (Van Kirk and Lewis, 1997), details are given in Appendix B. In summary,

$$\bar{h} \approx h_{av} = \frac{\ln S_h}{r} + 1, \quad \text{where } S_h = 1 - \frac{1 - \exp(-L_h)}{L_h}. \tag{10}$$

This approximation improves as domain size L increases.

Using the approximation in (10), we can now solve the modified Sturm Liouville problem,

$$\phi_p''(x) = -L_p^2 \left[(1/\lambda)\rho\bar{h}e^{-x\bar{h}} - 1 \right] \phi_p(x), \tag{11a}$$

$$L_p\phi_p(0) - \phi_p'(0) = 0, \quad \text{and} \quad L_p\phi_p(1) + \phi_p'(1) = 0. \tag{11b}$$

The problem is now reduced to one equivalent to Van Kirk and Lewis (1997), yielding an implicit function of

dimensional domain length L_{BC} ; we note that \bar{h} is also a function of L_{BC} ;

$$\tan \left(L_{BC} \sqrt{\frac{\rho\bar{h}e^{-x\bar{h}} - 1}{2\sigma_p^2}} \right) = \frac{1}{\sqrt{\rho\bar{h}e^{-x\bar{h}} - 1}}. \tag{12}$$

The domain length necessary for parasitoid persistence is $L > L_{BC}$, and is dependent on both the host and parasitoid parameters. In Section 5.3 we discuss this relationship.

The boundary value method presented here has the advantage that we can obtain an exact solution for L_{AB} , the critical host patch size, and a good approximation to L_{BC} , the parasitoid critical patch size. However, we are restricted to using a Laplace dispersal kernel, which may not be appropriate for all insect species. We will now follow another approach to analytically calculate an approximation to L_{AB} and L_{BC} . The second approach uses a spatially implicit caricature model, which does not give exact solutions, but works for general kernels. In Section 5.2, we illustrate the approach using the Laplace kernel so we can compare the two methods.

5.2. Average dispersal success approximation

In Section 5.1 the average dispersal success approximation is used to approximate the spatial equilibrium. In this section we will use this approximation to construct a system of spatially implicit equations describing host–parasitoid interaction. Van Kirk and Lewis (1997) showed that in the case of a single population such a spatially implicit approximation captured the bifurcation structure of the full spatial model very well. We will numerically demonstrate that the same is true of the two species model,

$$h_{t+1} = S_h h_t e^r e^{-rh_t} e^{-p_t}, \tag{13a}$$

$$p_{t+1} = S_p \rho h_t e^{-\alpha h_t} (1 - e^{-p_t}), \tag{13b}$$

where $S_h = 1 - \frac{1 - \exp(-L_h)}{L_h}$ and $S_p = 1 - \frac{1 - \exp(-L_p)}{L_p}$ (average dispersal success for host and parasitoid, respectively) describe the effect of space on the population densities. (See Lutscher and Lewis (2004) for a general exposition of the theory for structured populations.)

Eqs. (13) arise from the average dispersal success approximations of Section 5.1 and Appendix B. The spatially implicit model is consistent with the assumptions used in the analysis of the explicit model (2) in Section 5.1. Namely, the host-only steady state ($h = 1 + \ln(S_h)/r, p = 0$) of the average dispersal success model is the same as the average host density h_{av} used to approximate $h^*(x)$, the spatially dependent host-only equilibrium of (2). Eqs. (13) can be arrived at by spatially averaging the full model and applying the method presented in Appendix B.

5.2.1. Critical patch size problem 1: host persistence

The stability boundaries for host–parasitoid persistence can be determined by using the eigenvalues of model (13) and applying the Jury conditions (Jury 1964, 1974) (See Kot (2001) for a general discussion of the stability theory for discrete time models). To examine host persistence, we look at the Jacobian matrix of Eq. (13) linearised about the steady state ($h = 0, p = 0$). The parameter regions for which the steady state is stable ($\lambda < 1$) are separated from regions of instability ($\lambda > 1$) by the boundary,

$$\lambda = S_h e^r = 1, \quad \text{or} \quad 1 - e^{-r} = \frac{1 - \exp(-L_{AB}\sqrt{2}/\sigma_h)}{L_{AB}\sqrt{2}/\sigma_h}. \tag{14}$$

Eq. (14) depends on the same parameters that appeared in the stability boundary calculated using the boundary value approach (7). The expressions themselves are quite different, however, in Section 5.3 we demonstrate that the two methods give virtually the same boundary curve.

5.2.2. Critical patch size problem 2: parasitoid persistence

Next we characterise the domain length L_{BC} , which separates a host-only equilibrium from host–parasitoid persistence. The system is linearised about ($h = 1 + \ln(S_h)/r, p = 0$) and the stability boundary is calculated, yielding:

$$\frac{S_p \rho e^{-\alpha}}{S_h^{\alpha/r}} = 1 - \frac{S_p \rho \ln(S_h) e^{-\alpha}}{S_h^{\alpha/r}}, \tag{15}$$

where $S_i = 1 - \frac{1 - \exp(-L_i)}{L_i}$ and $L_i = \frac{L_{BC}\sqrt{2}}{\sigma_i}$.

The transcendental equation (15) has a similar parameter relationship as the stability boundary generated via the boundary value approach. In Section 5.3, we demonstrate that the average dispersal success approach works well for the Laplace kernel, as well as other kernels.

5.3. Conclusions from the stability boundary analysis

Sections 5.1 and 5.2 provide equations for the stability boundaries separating host extinction from host persistence (L_{AB} Eqs. (7) and (14)), and host only equilibria from host–parasitoid coexistence (L_{BC} Eqs. (12) and (15)). We use these results to study the impact of dimensional patch size (L), dispersal (σ_h, σ_p), scaled parasitoid searching efficiency (ρ) and emergence time (α) on the parasitoids ability to coexist with the host. In Fig. 9, we show the effects of α and ρ relative to r on coexistence. We observe that the boundary value approach and the average dispersal success formulation give virtually indistinguishable stability curves. Moreover, we have generated points on the stability boundary by numerical simulation of the full model, verifying the accuracy of our approximations (Fig. 9a).

5.4. Variation in dispersal (σ_h, σ_p)

The parameter scaling in Section 2.2 shows that increasing dispersal distance of either the host or parasitoid is equivalent to increasing critical patch size. The relationship is of the form

$$\frac{L}{\sqrt{\sigma_{h/p}^2}} = \text{constant}.$$

We have assumed that dispersal of the other population is fixed here. We now consider a fixed habitat size L and examine the trade-off between host and parasitoid dispersal necessary for coexistence. The stability boundary is shown in Fig. 8. We see that for large host dispersal, the parasitoid must disperse less than the host; while for small host dispersal, shorter or longer parasitoid dispersal both allow coexistence. When host dispersal is large, the loss through the boundary is high. While there are sufficiently many hosts at the centre of

the domain to support a parasitoid population, this is not the case near the edge.

If we consider a fixed host and parasitoid dispersal and reduce the domain size L , the maximum parasitoid dispersal that ensures coexistence is reduced, thus longer dispersing parasitoids are driven to extinction. In the Roland and Taylor (1997) study of the forest tent caterpillar it was shown that one of its farthest dispersing parasitoids *A. aldrichi*, does poorly in fragmented stands measured at a 425 m scale, while *C. malacosomae* a shorter dispersing species, responded to forest structure at a much finer scale. The interaction between host and parasitoid dispersal is not the only explanation for this finding, as these parasitoids also differ in timing and searching strategy and the habitat was part of large matrix of forest. This is however, an insightful example of how dispersal and habitat size influence parasitism in a real system.

5.4.1. Variation in parasitoid emergence time (α)

Recall that α ranges between 0 and r . We introduce the new parameter $\bar{\alpha} = \alpha/r$, the proportion of the host density-dependent phase occurring prior to parasitoid emergence or equivalently, the fraction of host density-dependent mortality experienced by the parasitoid. Density-dependent mortality of the host and subsequent parasitoid mortality is linearly dependent on the host growth rate (r), so by scaling out r from the parameter α we can compare the effect of parasitoid timing under different host growth rates. The parameter $\bar{\alpha}$ varies between 0 and 1. Fig. 9a shows the L_{BC} stability curve for several values of $\bar{\alpha}$. The L_{BC} stability curve shifts up the domain length axis (L) in response to increases in $\bar{\alpha}$.

Thus, early emerging parasitoids can persist in a smaller domain than can later emergers. By avoiding density-dependent mortality of their host, early emerging parasitoids have increased survival. Fewer hosts and a corresponding smaller domain are then required for parasitoids persistence.

To put this result in a biological context, consider *Arachnidomyia* (= Sarcophaga) *aldrichi* (Sarcophagidae), a dominant, late emerging pupal fly parasitoid on forest tent caterpillars. The model predicts that this species would require a relatively large stand of aspen forest to persist. Observational studies lend some support to this theory, in that the rates of parasitism by this fly increase with increased proportion of the landscape that is covered by forest; a pattern that is particularly apparent when forest cover is measured at a coarse spatial scale (>800 m). As well, the dominance by *A. aldrichi* within the parasitoid community varies geographically, with greater dominance in Ontario (Sippell, 1957) compared to in Alberta (Parry, 1995), a

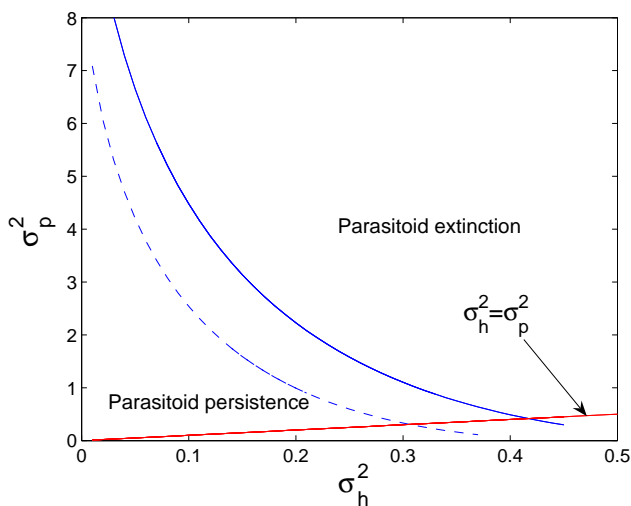


Fig. 8. In $\sigma_h - \sigma_p$ -space, for a fixed domain length $L = 0.7$ km (solid line) (and $L = 0.6$ km dash line) we plot the stability boundary L_{BC} , separating parasitoid persistence and extinction. When host dispersal is high, the parasitoid can also persist with a shorter dispersal distance. The parameters used in this plot are: $\rho = 8$, $r = 0.96$, $\alpha = 0$.

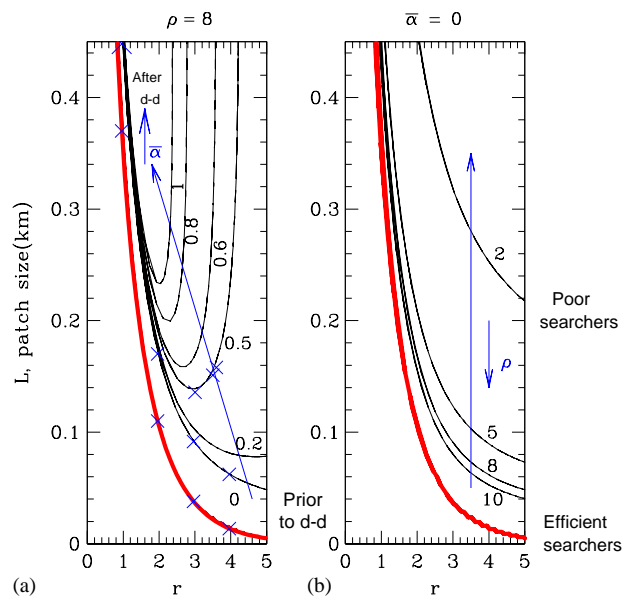


Fig. 9. Stability boundaries in $r - L$ space for the host–parasitoid system (r , host growth rate, L , patchsize in Km). The thick solid line is the L_{AB} stability boundary. Above the line the hosts persist, below we have extinction. The stability boundary from both the average dispersal success model and the boundary value approach are plotted, but the curves are indistinguishable. The thin solid lines indicate the L_{BC} stability boundary. Above the thin lines the parasitoid can persist, below we have parasitoid extinction. (a) shows thin lines for a range of parasitoid emergence times $\bar{\alpha}$: 0, 0.2, 0.5, 0.6, 0.8, 1; where 0 corresponds to parasitoid emergence prior to density-dependent host mortality and 1 corresponds to emergence after density-dependence. Bifurcation points (\times) were found by simulation of the full model and show that the analytical stability boundaries have extremely good agreement with the true bifurcation points. (b) shows the effect of varying ρ , scaled parasitoid searching efficiency. The thin lines are plotted for $\rho = 2, 5, 8, 10$. Poorer searchers require a larger domain to survive, or smaller average dispersal distance to persist. The dispersal parameters used to generate these figures are: $\sigma_h^2 = 0.25$, $\sigma_p^2 = 0.01$.

pattern generally correlated with more contiguous forest stands in the former, and smaller stands interspersed with agricultural matrix in the latter.

It seems reasonable that the higher the host fecundity, r , the smaller the patch size required for parasitoid survival. This is the case for early emergence ($\bar{\alpha} = 0$). As $\bar{\alpha}$ increases however, the $r-L$ -parameter space for coexistence shrinks and at higher values of r the parasitoid cannot survive in any size patch. An explanation for this result is that large r leads to heavy density-dependent mortality of the host, which in turn affects the parasitoid population. Thus, larger domains can prevent host overcrowding up to a point, but at high r the resulting parasitoid mortality is too high for the parasitoids to persist. The overcompensatory nature of the Ricker density-dependence is acting. The U -shape prediction from the analysis is verified against numerical simulation as indicated by the crosses in Fig. 9.

When $\bar{\alpha}$ is small, parasitoids emerge very shortly after host density-dependent mortality begins and parasitoid survival is high. In this case the U -shape behaviour of the stability boundary occurs only at very large r . Early emerging parasitoids can therefore persist in a smaller domain than late emerging parasitoids. Those parasitoids emerging early from third and fourth instar larvae (e.g. *Aleiodes malacosmatos*), in fact are most effective relative to the later emerging flies, in smaller patches (Roland and Taylor, 1997; Rothman and Roland, 1998).

5.4.2. Variation in scaled parasitoid searching efficiency ($\rho = Ka$)

Fig. 9b illustrates the effects of ρ on the stability boundaries. Decreasing ρ results in the need for larger domain sizes for parasitoid persistence. More efficient searchers can invade and coexist in smaller stands of aspen than poorer searchers. This result follows quite naturally from the biology. Parasitoids such as the wasp *Aleiodes malacosmatos* and the fly *Carcelia malacosomae* (Tachinidae) that tend to be very good searchers and attack forest tent caterpillar hosts directly, are most effective in more fragmented forest stands (Roland and Taylor, 1997). In contrast, other fly parasitoids are less efficient at finding hosts, such as *Patelloa pachypyga* (Tachinidae) and *Leschenaultia exul* (Tachinidae) that lay first instar fly maggots that must subsequently find and penetrate host pupae; these species are most dominant in larger forest patches (Roland and Taylor, 1997).

The stability boundary calculations enable us to examine the trade-off between searching efficiency and emergence time required for parasitoid persistence in a fixed habitat size (Fig. 10). By fixing r and L we plot ρ as a function of $\bar{\alpha}$. The profile describes the stability boundary separating parasitoid persistence from a host only equilibrium. Above the curve the model predicts

host–parasitoid coexistence. Fig. 10 illustrates the predictions for two parasitoid species A and B which differ only in emergence time. Species A emerges early and B emerges late. For a host growth rate of $r = 0.96$, both species A and B can persist with the host. If we now consider a habitat with $r = 2.96$, then only species A , the early emerging parasitoid persists, a consequence of density-dependence affecting later parasitoids. If we increase the searching efficiency of B we find that it too can then persist with the host.

In summary, theoretical predictions suggest early emerging parasitoids are less susceptible to changes in host growth rate. Increasing parasitoid searching efficiency can compensate for the effects of late emergence; however, the later the parasitoid emerges the more efficient it needs to be to guarantee persistence with the host. Our model illustrates that host outbreak dynamics are potentially sensitive to the type of parasitoid species present in the system.

We have considered the effects of a single parasitoid species, parasitoid interaction in a multi-parasitoid community are likely to affect these theoretical predictions, although the extreme cases where parasitoid abundance is dominated by one species could be described by this model. Our results suggest that it is necessary to study the effect of forest management practices on both the host and parasitoid populations and not just the host species.

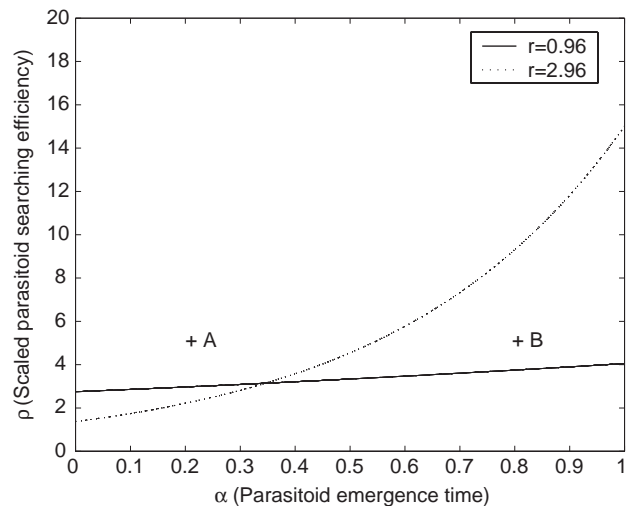


Fig. 10. The stability boundary separating the host only steady state from stable host–parasitoid coexistence for a fixed domain length L , at two host growth rates $r = 0.96$ and 2.96 . Above the curves parasitoids persist in the system. When host growth rate is low, higher searching efficiency is required for early-emerging parasitoids to persist. Points A and B represent two parasitoid species which differ only in emergence time. An early emerging parasitoid, species A, persists under varied host growth rates. Species B only persists when host growth is low, or if searching efficiency is sufficiently high. The parameter values used to generate these profiles are: $\sigma_h^2 = 0.25$, $\sigma_p^2 = 0.01$, $L = 0.7$.

6. Discussion

Forest fragmentation has implications for biodiversity and species and habitat conservation. We have examined the effects of a major component of habitat fragmentation, namely patch size, on the dynamics of host–parasitoid interaction. These interactions typically result in temporal cycles of the insect populations. We developed a simple integrodifference model which considers a single isolated patch of habitat. Varying patch size alone and allowing complete mortality outside of the habitat is the classical setting for studying critical patch size and represents the ‘extreme’ or ‘worst’ case scenario for habitat fragmentation. In contrast to considering the effect of very small patches of habitat, when we consider a large contiguous habitat, the model essentially reduces to a non-spatial system. We have demonstrated that in this scenario, the timing of parasitoid emergence from the host and searching efficiency of the parasitoid can be influential in determining the frequency and severity of host outbreaks.

The non-spatial model shows that increases in parasitoid searching efficiency induce less frequent, but longer host outbreaks, early emergence of the parasitoid has a similar affect on increasing outbreak severity. In systems where multiple specialist parasitoid species parasitise the same host species the relative abundance of the parasitoid types may be crucial in determining the severity of host outbreaks.

The sensitivity of insect outbreaks to parasitoid behaviour also holds in a spatially explicit setting. The critical patch-size necessary for host–parasitoid persistence increases as a function of α , the timing of parasitism, thus later emerging parasitoids require larger habitat for survival. This phenomenon is driven by host loss through the patch boundary. The boundary conditions considered in this paper allow free movement out of the habitat into the surrounding hostile matrix. In natural populations, this simplistic model of no edge effects is likely to be unrealistic. Field observations for the forest tent caterpillar for example, have found the adult moths fly loops out from the forest edge and then return with some eventually leaving the forest entirely. Van Kirk and Lewis (1999) derived a dispersal kernel from a random walk that allowed for some probability of not moving at the habitat edge. We have not studied this kernel here, but our analysis can easily be applied to such a kernel and we hypothesise that the critical patch size for host–parasitoid persistence would decrease. Thus, persistence under mixed boundary conditions would guarantee persistence when edge responses reduce flux from the boundary. Our estimate of critical patch size can therefore be regarded as conservative.

Truely isolated habitat patches, such as studied in the critical patch-size problem, occur rarely for these insect

populations. More naturally, one would expect a network of patches connected by interpatch dispersal. Integrodifference models for single and structured species on finitely many or infinitely many periodically spaced patches have been formulated by Van Kirk and Lewis (1997), Botsford et al. (2001), and Lutscher and Lewis (2004). The average dispersal success in those cases increases compared to a single patch, since individuals leaving one patch may end up in another patch, and consequently still contribute to offspring production. Since an increased average dispersal success translates into increased overall growth rates, we expect that a population can survive in networks of patches, even if some or all individual patches are smaller than the critical patch-size. Studying such networks in the framework of integrodifference equations is an important next step to understanding the effects of fragmentation on population dynamics.

The paucity of dispersal data for our study species, the forest tent caterpillar, implies that our assumed dispersal kernel may also be subject to error. Lockwood et al. (2002) examined the effect of five dispersal kernels on the average dispersal success for a single population. There was little difference in average dispersal success among kernels, however the laplace kernel gave the lower bound on critical patch size and the gamma distribution gave an upper bound. Thus, in systems for which there is reason to expect dispersal to be concentrated at sites some distance from the point of release, as observed with seed shadows generated in some plant systems, then in such cases our estimate of critical patch size may no longer be conservative.

We assumed one specific form of host density-dependence, namely overcompensatory Ricker density-dependence because our study system shows this response. Overcompensation is not necessary for the prediction that later emerging parasitoids require larger critical patch size for persistence, only some form of host induced parasitoid mortality is required. However, the prediction that for high host growth rates, late emerging parasitoids may not be able to persist at all (see the U shape in Fig. 9), is a consequence of the overcompensatory dynamics. Bellows (1981) describes methods for estimating the functional form of density-dependence from data. An extension of the work is to generalise the results presented here to compensatory and undercompensatory dynamics. The theta-Ricker model of density-dependence has a free parameter to describe compensation and would be a logical choice for extending this work to a wider class of host–parasitoid systems.

6.1. Application to the forest tent caterpillar

In this paper, we parameterised the model for our system of interest, the forest tent caterpillar and its

parasitoids. The community of parasitoid species differs among geographical regions, as do the frequency and duration of forest tent caterpillar outbreaks (Cooke, 2001). The model predicts that it is possible to have small regions of habitat that support only hosts. Thus, the model indicates that fragmentation has the potential to exacerbate host outbreaks by providing refuges. Empirical studies have found that some sites do harbour forest tent caterpillar in the absence of parasitoids.

Moreover, the theory suggests that late emerging parasitoids such as *Arachnidomyia aldrichi* require a large habitat and should not persist in small isolated stands as found in highly fragmented forests. Roland and Taylor (1995) have shown that *A. aldrichi* appears fairly insensitive to inter-patch distance, which may help this species to persist in small isolated aspen stands. However, not all late emerging parasitoids possess the same resilience to patch isolation, one reason for this is differing dispersal patterns.

The critical patch-size problem suggests that parasitoid searching efficiency (a , or scaled searching efficiency $\rho = Ka$), and emergence time (α), have opposing effects on forest tent caterpillar outbreaks. Later emerging parasitoids in the model require an increased searching efficiency to successfully persist in an isolated patch. Interestingly, the three latest-emerging parasitoids *A. aldrichi*, *P. pachygyga* and *C. malacosomae* have quite different searching strategies. *A. aldrichi* lays first-instar maggots that must search and find host pupae, *P. pachygyga* lays eggs on foliage which must be subsequently ingested by feeding caterpillars, and *C. malacosomae* oviposits directly on the host. Among these three, and consistent with model predictions, it is the more efficient searcher, *C. malacosomae*, that persists best at low host density (Parry, 1995) and persists best in small forest patches (Roland and Taylor, 1997). We cannot compare our critical patch size estimates directly to data because we do not have sufficient information on dispersal. However, the survival of later emerging parasitoids places an upper bound on critical patch size, suggesting a focus for parasitoid dispersal studies.

In the introduction we noted that spruce budworm outbreaks also respond to habitat structure. We have not attempted to parameterise the model for this insect, however, the spruce budworm is also univoltine and is subject to parasitism. A High rate of parasitism of mature larvae by the wasp *Meterorus trachynotus* (Viereck) was seen in declining budworm populations in Maine and New York (Kucera and Orr, 2004). The spruce budworm is known to have a very high reproductive capacity (r). A large value of r , together with late emerging parasitoids (large α) place our model in a region of parameter space where very large habitat regions are necessary for coexistence of the host and parasitoid (See Fig. 9a for large values of r). This result

partially depends on the budworm exhibiting over-compensatory density-dependent mortality, which is possible given that foliage availability is frequently a limiting factor for outbreaks and the tree size within a stand is important for achieving budworm outbreaks. Bird predation is very high in spruce budworm populations and is a factor which also needs to be considered, but certainly the budworm is amenable to the general framework and techniques presented here.

Acknowledgments

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Appendix A. The existence of a constant solution for a Sturm Liouville problem

There is a constant \bar{h} such that if $h^*(y)$ is replaced by \bar{h} the eigenvalues of the operator L do not change, where L is given by

$$\lambda\phi(x) = \int_0^1 K(x, y)f(h^*(y))\phi(y) dy = L\phi(x). \quad (16)$$

To prove this, we first notice that

$$\begin{aligned} & \underbrace{\min_z f(h^*(z)) \int_0^1 K(x, y)\phi(y) dy}_{=L_{\min}\phi(x)} \\ & \leq \int_0^1 K(x, y)f(h^*(y))\phi(y) dy \\ & \leq \underbrace{\max_z f(h^*(z)) \int_0^1 K(x, y)\phi(y) dy}_{=L_{\max}\phi(x)}. \end{aligned} \quad (17)$$

This holds for every function ϕ and f . Therefore, the operators are ordered as follows: $L_{\min} \leq L \leq L_{\max}$ and thus, L is a positive operator. Krasnoselskii (1964) proved that the corresponding dominant eigenvalues of these operators satisfy: $\lambda_{\min} \leq \lambda \leq \lambda_{\max}$.

If we now consider the operator $c \int_0^1 K(x, y)\phi(y) dy$, which exists for each c . We can say that there exists some c such that $\lambda_c = \lambda$ where $c = f(\bar{h})$. In summary, there is a constant \bar{h} which satisfies Eq. (16).

Appendix B. Estimating h_{av}

Our goal is to estimate h_{av} , the spatial average of the host only steady state $h^*(x)$:

$$h_{av} = \frac{1}{|\Omega|} \int h^*(x) dx.$$

We do not know the function $h^*(x)$ explicitly; however we have an implicit equation for $h^*(x)$:

$$\begin{aligned} h^*(x) &= \int k_h(x, y) h^*(y) e^f e^{-rh^*(y)} e^0 dy \\ &= \int k_h(x, y) f(h^*(y)) dy. \end{aligned} \quad (18)$$

Using an approach developed by Van Kirk and Lewis (1997) we can now estimate h_{av} . By the mean value theorem there exists some $\hat{h}(y)$ such that:

$$f(h^*(y)) - f(h_{av}) = f'(\hat{h}(y))(h^*(y) - h_{av}). \quad (19)$$

Substituting Eq. (19) into Eq. (18) yields the following expression:

$$\begin{aligned} h^*(x) &= f(h_{av}) \underbrace{\int k_h(x, y) dy}_{=s_h(x)} \\ &\quad + \int k_h(x, y) f'(\hat{h}(y))(h^*(y) - h_{av}) dy. \end{aligned} \quad (20)$$

When the spatial variation in $h^*(y)$ is small, then $h^*(y) \approx h_{av}$ and therefore the last term in Eq. (20) is very small, so we may neglect it. It turns out that we may neglect this term even when the spatial variation in $h^*(y)$ is large. Large spatial variation will occur, for example, when edge effects are severe. In this case, the edges will be characterised by low population size (i.e. $h^*(y) - h_{av} < 0$) and correspondingly high growth rate ($f'(\hat{h}(y))$), giving a large negative product $f'(\hat{h}(y))(h^*(y) - h_{av})$. In the interior, the converse is true, i.e. $h^*(y) - h_{av} > 0$, $f'(\hat{h}(y))$ is low, and the product is small and positive. Since the edge area is small relative to the interior, the sum of few edge and many interior products is small and can be neglected. The larger the domain, the smaller the term we neglect. Van Kirk and Lewis (1997) demonstrate numerically that this holds.

Neglecting the last term of Eq. (20) yields

$$h^*(x) \approx f(h_{av}) s_h(x). \quad (21)$$

It remains to calculate h_{av} . By taking the spatial average of Eq. (21), we obtain an estimate of h_{av} :

$$\bar{h} = f(\bar{h}) S_h \quad \text{where } S_h = \frac{1}{|\Omega|} \int_{\Omega} s_h(x) dx. \quad (22)$$

Adopting a Laplace dispersal kernel, we can calculate the average dispersal success function S_h , exactly:

$$S_h = 1 - \frac{1 - \exp(-L_h)}{L_h}.$$

Taking the function f as described in (18), Eq. (22) can be solved for h_{av} to give:

$$h_{av} = \frac{\ln S}{r} + 1.$$

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