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

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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

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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 temporate 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

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