A test of heterogeneous mixing as a mechanism for ecological persistence in a disturbed environment

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SUMMARY

Persistence is a central issue in population ecology with important implications for population management. Most theoretical studies have focused on continually interacting populations, even though many systems are subject to ecological disturbances which confound analysis of persistence. In this paper, we use a combination of a simple parasite–hyperparasite model with disturbances and field data to investigate the factors contributing to the observed persistence of the parasite population. The field data are taken from a two-year experiment (including five growing seasons) investigating the use of the mycoparasite *Sporidesmium sclerotivorum* as a persistent biological control agent of *Sclerotinia minor*, an economically important fungal parasite of lettuce. We show that the standard assumption of homogeneous mixing fails to predict the observed persistence of the parasite population. We demonstrate that allowing for heterogeneous mixing prevents the fade-out predicted in the homogeneous mixing case. The implications of the results for broad classes of host–parasite systems are discussed.

1. INTRODUCTION

Of central importance in population ecology are the questions of invasion and persistence (Anderson & May 1986). Persistence is particularly influenced by seasonality and disturbances (Allen *et al.* 1993; Bolker & Grenfell 1995; Grenfell *et al.* 1995). Moreover, ecological disturbances are an inherent property of many plant, microbe and invertebrate populations, but this feature has received little attention (Barlow 1993; Hanski *et al.* 1993; Shaw 1994; Carroll *et al.* 1995). Most ecological and epidemiological models describe systems with continuous, uninterrupted interactions between populations (Murray 1989). Alternatively, birth rates are allowed to vary seasonally (Anderson & May 1981), or equivalently, the infection term is seasonally forced in epidemiological models (London & Yorke 1973; Bolker & Grenfell 1993).

Invasion and persistence have been well studied for homogeneously mixed populations (Anderson & May 1986; Heesterbeek & Roberts 1995), but recent work has questioned this standard assumption (D'Amico *et al.* 1996; Gubbins & Gilligan 1996; Kneil *et al.* 1996). Theoretical studies have begun to focus on the role of spatial heterogeneity on the persistence of continuously interacting populations (Hassell *et al.* 1991; Bolker & Grenfell 1995; Mollison & Levin 1995). The effects of various other heterogeneities in transmission have also been considered, for example age structure (Bolker & Grenfell 1993) and social or genetic heterogeneity (Anderson & May 1991). However, the interaction between spatial heterogeneity and disturbances and their influence on persistence has been neglected to date.

The success of biological control is intimately linked to invasion and persistence (May & Hassell 1988). However, few field trials provide long enough time series data to investigate persistence. One such data set involves a two-year experiment (including five growing seasons) investigating the use of the mycoparasite *Sporidesmium sclerotivorum* Uecker, Ayers & Adams as a persistent biological control agent of *Sclerotinia minor* Jagger, an economically important fungal parasite of lettuce (Adams & Fravel 1990). In this paper, we use a combination of a simple parasite–hyperparasite model with disturbances and Adams & Fravel's (1990) field data to investigate the factors contributing to the observed persistence of the parasite population. In particular, we analyse the roles played by spatial heterogeneity and disturbances in the system. Spatial heterogeneity is incorporated in the model by relaxing the standard assumption of homogeneous mixing to allow for heterogeneous mixing of the populations (Liu *et al.* 1987).

2. THE BIOLOGICAL SYSTEM

The models are tested using data from a field trial for the biological control of an economically important fungal plant parasite, *S. minor*, by the fungal hyperparasite *S. sclerotivorum* (Adams & Fravel 1990). *Sclerotinia minor* is an ecologically obligate plant pathogen that infects lettuce plants from soil-borne sclerotia. Sclerotia of *S. minor* are produced on and within the leaves, stem and upper portion of the roots of lettuce plants (Adams 1986) and on previously infected lettuce tissue returned to the soil after harvest (Dillard & Grogan 1985). *Sporidesmium sclerotivorum* is a

naturally occurring hyperparasite of sclerotia and has been widely used as a potential biological control agent (Adams & Fravel 1990).

Adams & Fravel (1990) carried out a two-year experiment investigating the use of *S. sclerotivorum* as a persistent biological control agent of *S. minor*. In May 1987 field plots measuring 3 m by 3 m were treated with a single preparation of inoculum of *S. sclerotivorum* at rates of 0.2, 2 and 20 kg ha⁻¹ (corresponding to levels of 0.08, 0.8 and 8 spores g⁻¹ soil). Five successive lettuce crops (comprising three autumn and two spring crops) were grown in the field plots between September 1987 and November 1989. There were five replicates of each treatment. Soil samples were taken at two-week intervals and assayed for the number of *S. minor* and *S. sclerotivorum*. The mean data from this trial are used to test the model.

3. THE MODEL

To analyse the effects of heterogeneous mixing in a disturbed environment, we use a simple predator–prey model (May 1981). The generic structure for this system is

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K} \right) - Xf(P, X), \quad (1)$$

$$\frac{dX}{dt} = gXf(P, X) - hP,$$

where P is the parasite (the pathogen, *S. minor*) density and X is the hyperparasite (the biological control agent, *S. sclerotivorum*) density. In the absence of the hyperparasite, the parasite population grows logistically with carrying capacity, K , and a growth rate, r ; g is the number of hyperparasites produced per parasite infected and h is the hyperparasite death rate.

We consider two forms for the functional response of the hyperparasite to changes in parasite density, $f(P, X)$. The first assumes that the populations mix homogeneously and $f(P, X)$ takes the form of the simple Lotka–Volterra type of functional response (May 1981),

$$f(P, X) = bP, \quad (2a)$$

where b is the transmission parameter. This response corresponds to mass action transmission. Spatial homogeneity is an implicit assumption for homogeneous mixing. Heterogeneous mixing, and hence spatial heterogeneity, can be allowed for simply by letting the incidence rate vary as powers of P and X (Liu *et al.* 1987). Then

$$f(P, X) = bP^m X^{n-1}, \quad (2b)$$

where the mixing parameters, m and n , are real and positive.

4. SEASONALITY AND DISTURBANCES

Examination of the data shows discontinuities in the population dynamics, with disturbances due to cropping (presence of the crop followed by intercrop periods), and a pulsed input to the *S. minor* population

Figure 1. Experimental time series data from Adams & Fravel (1990) used to test the model. (a) Logarithm of parasite density (sclerotia of *S. minor* g⁻¹ soil) against time (weeks). (b) Logarithm of hyperparasite density (spores of *S. sclerotivorum* g⁻¹ soil) against time (weeks). Data set shown is that with medium initial hyperparasite density, $X_0 = 0.8$ spores g⁻¹ soil. Planting of the lettuce crop is marked by a hollow triangle, and harvesting is indicated by a solid triangle.

at harvest as infected lettuce tissue is returned to the soil (Adams 1986) (figure 1). To include the pulsed input at harvest, we let

$$r = r_1 + r_2 \sum_{n=1}^5 \delta(t - t_n), \quad (3)$$

where $\delta(t - t_n)$ is a delta function representing a pulse at the n th harvest at $t = t_n$. The birth term, r , has two components: the continuous addition (r_1) of sclerotia (see section 2) and a pulse (r_2) of sclerotia at harvest ($t = t_n$) when infected lettuce plants are disked into the soil.

The rate of infection of *S. minor* by *S. sclerotivorum* depends on temperature (Adams & Ayers 1980), which affects the ability of *S. sclerotivorum* to control *S. minor* (Adams & Fravel 1990). This is apparent from the data which show seasonal variations in the rate of infection by the hyperparasite: periods of rapid infection are followed by periods with low levels of infection (figure 1). Accordingly, we allow the infection rate to vary seasonally,

$$b = b(t) = b_0(1 + b_1 w(t)), \quad (4)$$

where $w(t)$ is a forcing function. We use a generic form for $w(t)$,

$$w(t) = \begin{cases} 1 - \theta^{2a} & 0 \leq \theta < 1, \\ (\theta - 2)^{2a} - 1 & 1 \leq \theta < 3, \\ 1 - (\theta - 4)^{2a} & 3 \leq \theta < 4, \end{cases} \quad (5)$$

where $\theta = (4/T) \bmod (t - \phi, T)$, $T = 52$ weeks, $\phi = 12$ weeks and q is a positive integer. This function captures a range of shapes from (approximately) sinusoidal ($q = 1$) through to a square wave (q , large). After exploratory analysis, the value of the shape parameter, q , was fixed at $q = 3$.

5. PARAMETER ESTIMATION

The models were fitted to three data sets from Adams & Fravel (1990). Each data set has a different initial hyperparasite density (X_0) designated: low, $X_0 = 0.08$ spores g^{-1} soil; medium, $X_0 = 0.8$ spores g^{-1} soil; high, $X_0 = 8$ spores g^{-1} soil. Because there is an apparent jump from the first to the second data point in the parasite population, the initial parasite population (P_0) was treated as a parameter to be estimated, and was varied to obtain an optimal fit. The parameters in the model were estimated by least-squares minimization using FACSIMILE (Anon. 1995). The goodness of fit was tested by examination of the residual plots and by the consistency and convergence of the parameter estimates for small differences in initial estimates (Gubbins & Gilligan 1996). The consistency of the parameter estimates across the three data sets was inspected since, other things being equal, differences in X_0 would not be expected to affect parameters in the model. The change in deviance for hierarchically related models was also examined (Aitkin *et al.* 1989; Ross 1990) to test for redundant parameters.

6. RESULTS

The models with and without homogeneous mixing were fitted to the data (figure 2; table 1). Parameter estimates were consistent across the three data sets (table 1). The homogeneous mixing model led to under-estimation and fade-out of the *S. minor*

population (figure 2a). This did not occur in the heterogeneous mixing case (figure 2b) for which $m > 1$, $n < 1$ (table 1). Approximate *F*-tests (Aitkin *et al.* 1989; Ross 1990) indicated a significant ($\alpha = 0.01$) reduction in deviance (table 1) for heterogeneous mixing over homogeneous mixing.

The influence of the delta function pulses and seasonal forcing were separately tested for the models with homogeneous and heterogeneous mixing. The absence of pulses led to systematic error when estimating the parasite population during the early cycles of infection ($t < 60$ weeks) (figure 3a). After this, the fit matches the data, but does miss the sharp increases in the *S. minor* population immediately after harvest (figure 3a). Omitting seasonal forcing led to under-estimation of sclerotia densities (figure 3b), although the parasite population does not fade out. Approximate *F*-tests indicated a significant ($\alpha = 0.01$) reduction in deviance for the models with both pulses and seasonal forcing over those omitting one of these features. We conclude that heterogeneous mixing, seasonal forcing and delta function pulses are necessary to capture all the dynamical features of the parasite data.

7. DISCUSSION

In this paper, we used a combination of a simple parasite–hyperparasite model with disturbances and independently collected field data to investigate the factors that contribute to the observed persistence of the parasite population. Examination of the data showed discontinuities in the population dynamics, with disturbances due to cropping and a pulsed input to the *S. minor* population at harvest. The data also showed seasonal variations in the rate of infection by the hyperparasite and, accordingly, the infection rate was allowed to vary seasonally. Model fitting and

Figure 2. Fit of the parasite–hyperparasite model, (1)–(5), to the data set with medium initial hyperparasite density, $X_0 = 0.8$ spores g^{-1} soil. (a) Homogeneous mixing, $f(P, X) = bP$, with pulsed inputs and seasonal forcing. (b) Heterogeneous mixing, $f(P, X) = bP^m X^{n-1}$, with pulsed inputs and seasonal forcing. The solid line (—) is the least-squares fit and the points (●) are the data from Adams & Fravel (1990). Planting of the lettuce crop is marked by a hollow triangle, and harvesting is indicated by a solid triangle.

Table 1. *Parameter estimates for the model, (1)–(5), with pulsed inputs and seasonal forcing*

parameter	model					
	homogeneous mixing, (2a)			heterogeneous mixing, (2b)		
	$X_0 = 0.08$	$X_0 = 0.8$	$X_0 = 8$	$X_0 = 0.08$	$X_0 = 0.8$	$X_0 = 8$
P_0	0.828	0.909	0.692	0.758	0.886	0.868
r_1	0.042	0.081	0.061	0.061	0.053	0.070
r_2	4.072	2.158	3.578	1.217	1.385	3.396
K	0.399	0.552	0.775	0.676	0.680	0.616
b_0	1.319	1.364	1.401	1.076	1.340	1.290
b_1	0.900	0.914	0.882	0.791	0.837	0.778
m	—	—	—	1.590	1.471	1.290
n	—	—	—	0.870	0.927	0.933
g	0.259	0.207	0.161	0.215	0.174	0.159
h	0.007	0.006	0.007	0.013	0.007	0.011
RSS ^a	72.76	51.16	80.20	43.80	38.06	69.87
df ^b	84	84	83	82	82	81

^a residual sum of squares; ^b degrees of freedom.

Figure 3. Fit of the parasite–hyperparasite model, (1)–(5), to the data set with medium initial hyperparasite density, $X_0 = 0.8$ spores g^{-1} soil. (a) Heterogeneous mixing, $f(P, X) = bP^m X^{n-1}$, without the delta function pulse at harvest ($r_2 = 0$) and with seasonal forcing. (b) Heterogeneous mixing, $f(P, X) = bP^m X^{n-1}$, with the delta function pulse at harvest and without seasonal forcing ($b_1 = 0$). The solid line (—) is the least-squares fit and the points (●) are the data from Adams & Fravel (1990). Planting of the lettuce crop is marked by a hollow triangle, and harvesting is indicated by a solid triangle.

parameter estimation demonstrated that both seasonal forcing and pulses were necessary to capture all the dynamical features of the parasite data (figure 3). A further mechanism that may contribute to the observed persistence is spatial heterogeneity. This was incorporated in the model by relaxing the standard assumption of homogeneous mixing to allow for heterogeneous mixing of the populations.

Under the standard assumption of homogeneous mixing, the model failed to predict the observed persistence of the parasite population. Making the simple change to allow for heterogeneous mixing improves the fit of the model and, more importantly, prevents fade-out (figure 2; table 1). Moreover, the

parameter estimates (table 1) obtained are biologically plausible. The infection term, $f(P, X) = bP^m X^{n-1}$, increases faster than linearly with parasite density, P ($m > 1$; table 1), implying that when a hyperparasite encounters one parasite, it is likely to encounter another one; that is, the parasite population is aggregated. This agrees with observations in the field: *S. minor* is found in aggregations in soil after infected lettuce plants are disked into the soil (Adams 1986). Estimates of $n < 1$ (table 1) are consistent with only a proportion of the hyperparasites being able to infect their parasites.

The simple change from homogeneous to heterogeneous mixing introduces only two extra parameters,

but improves the fit of the model and prevents fade-out. As our analysis has shown, the two mixing parameters are both biologically meaningful and readily estimated from the data. Although it still hides much of the spatial dynamics of the system, heterogeneous mixing provides a method of analysing the dynamical effects of spatial heterogeneity without recourse to explicitly spatial data. Another simple method for analysing the effects of heterogeneity in host–parasite systems relates to the square of the coefficient of variation of the distribution of parasites (CV^2): if $CV^2 > 1$, the parasite is able to regulate the host population (Hassell & Pacala 1990; Pacala *et al.* 1990). This rule can be partitioned into density dependent and independent components, allowing a more detailed analysis of the heterogeneities (see Hassell & Pacala 1990 for details). In contrast, with heterogeneous mixing though, this approach requires data on the spatial distribution of parasites. The relative simplicity and robustness in estimation of the mixing parameters or CV^2 contrasts with the difficulties of measuring the diffusion constant in reaction-diffusion models (Murray 1989; Dwyer 1992) or the coupling in meta-population models (Kareiva 1990; Bolker & Grenfell 1995).

Many different models have been proposed that include spatial heterogeneity, but without producing a unified cohesive theory (Kareiva 1990; Barlow 1995). As a result, models have had little impact on experimental work on the effects of spatial heterogeneity on natural communities and, equally, experiments have had little effect on theory (Kareiva 1990). This reflects the difficulties in testing explicitly spatial models and the effort necessary to collect sufficient spatial and temporal data. An important technique that overcomes these difficulties is to use relatively simple models, such as one including heterogeneous mixing, that can be tested against experimental time series data. However, it remains to relate the mixing parameters to the spatial structure of heterogeneous populations.

We have used only elementary methods in model fitting here with an assumption of independent errors due to measurement variability. Further work is under way to explore the effects of refined techniques that take account of auto-correlation, non-normal errors and unequal variances. The results presented in this paper open up possibilities for analysis involving experimental and simulated manipulation of populations to investigate biological mechanisms for the interaction between disturbances and spatial heterogeneity.

We thank P. B. Adams and D. R. Fravel for providing us with their data. This work was funded by the Biotechnology and Biological Sciences Research Council (BBSRC), which we gratefully acknowledge. We also thank Adam Kleczkowski and Jonathan Swinton for helpful comments on the manuscript.

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Received 30 August 1996; accepted 1 October 1996

APPENDIX. SUMMARY OF PRINCIPLE VARIABLES AND PARAMETERS

variable	description	dimensions
P	parasite density	[sclerotia g ⁻¹ soil]
X	hyperparasite density	[spores g ⁻¹ soil]
parameter	description	dimensions
r_1	parasite birth rate (continuous)	[time] ⁻¹
r_2	parasite birth rate (pulsed)	[time] ⁻¹
κ	parasite carrying capacity	[sclerotia g ⁻¹ soil]
b_0	mean infection rate of parasite by hyperparasite ^a	[spores g ⁻¹ soil] ⁻¹ [time] ⁻¹
b_1	amplitude of seasonal forcing	(dimensionless)
w	seasonal forcing function	(dimensionless)
q	shape parameter for forcing function	(dimensionless)
m	parasite mixing parameter	(dimensionless)
n	hyperparasite mixing parameter	(dimensionless)
g	hyperparasite birth rate	[spores g ⁻¹ soil] [sclerotia g ⁻¹ soil] ⁻¹
h	hyperparasite death rate	[time] ⁻¹

^a dimensions for b_0 are given for the homogeneous mixing response, (2a).