

Effects of biological control on long-term population dynamics: identifying unexpected outcomes

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Summary

1. Attempts to control natural systems through management have often met with success but have also led to unexpected and often undesirable outcomes. Unfortunately, the ultimate result of such management programmes may not be apparent until long after the control efforts have begun. This is particularly true for forest-defoliating species that exhibit long-period cycles such as the invasive gypsy moth *Lymantria dispar*, which causes widespread damage in some years but is rare in other years.

2. We studied the effects of two commonly employed biocontrol agents on gypsy moth dynamics using a series of field-tested and empirically parameterized mathematical models, which allowed us to examine various potential control strategies and assess long-term effects.

3. In a non-spatial model, addition of either a manufactured version of the same baculovirus involved in natural epizootics, or a general bioinsecticide *Bacillus thuringiensis* var. *kurstaki* (Btk), which directly kills a fraction of the population, decreases the amplitude between boom and bust portions of the cycle.

4. However, ill-planned biocontrol applications can result in increased gypsy moth densities over the long term. Thus, control efforts may maintain pest populations at unexpectedly high numbers, which could result in constant forest defoliation.

5. In a spatial two-patch model, where one patch is sprayed and the other is left untreated, there is also considerable danger that migration between patches may drive the unsprayed population to levels that could result in constant forest defoliation.

6. *Synthesis and applications:* Perturbations to host–pathogen systems may have unexpected results, driving and maintaining populations at multiple levels including those far from desired management goals. It is often assumed that any control strategy that decreases pest populations in the short term is beneficial, but our results show that undesirable outcomes may often occur. The mechanisms we describe apply to many systems that undergo population cycles or outbreaks regulated by density-dependent processes, and in which disease or pesticide application is used for pest control. We suggest that successful management strategies should closely monitor population responses immediately following the control application to ensure that pest populations are not being maintained at artificially high levels compared with historic data.

Key-words: biocontrol, gypsy moth, host–pathogen interactions, *Lymantria dispar*, population dynamics, unexpected outcomes

Introduction

Efforts by managers to control natural systems, while often meeting with success (Hudson, Dobson & Newborn 1998; Roberts *et al.* 2001), may also lead to dramatic, unforeseen and undesirable consequences (Estes *et al.*

1998; Paine, Tegner & Johnson 1998; Roemer, Donlan & Courchamp 2002; Doak *et al.* 2008; Naficy *et al.* 2010). This is in contrast to agricultural systems, where management efforts frequently meet their goals (e.g. Hutchison *et al.* 2010; Wu 2010; Bell *et al.* 2012). Furthermore, the effects of management on natural systems may not be immediately apparent, and considerable time may elapse before the long-term effects of man-made perturbations become clear. This is particularly true for systems where

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decades of data need to be collected before patterns emerge. The development of data-parameterized and well-tested mathematical models allows us to ask how management strategies may affect the long-term dynamics of a system (e.g. decades into the future), identify potential risks or reveal unforeseen consequences before they occur.

Invertebrate pests, such as forest- and crop-defoliating insects, are regularly the focus of control efforts whose long-term effects may be unknown. Without management intervention, these populations often undergo dramatic multi-year oscillations in the form of boom and bust cycles (Anderson & May 1980; Bjørnstad, Robinet & Liebhold 2010). During the boom phase, widespread defoliation occurs, which causes substantial economic damage (Liebhold *et al.* 2000). Peak populations rapidly decline from outbreak levels due to increased mortality caused by pathogens or parasitoids (Liebhold & Kamata 2000). In an attempt to hasten these declines, there has been a great deal of effort and expense devoted to controlling population numbers when they reach the outbreak phase of the cycle (Podgwaite *et al.* 1984, 1992; Scriber 2001; Moreau *et al.* 2005; Maclauchlan *et al.* 2009). However, given that these fluctuations in population size occur approximately once a decade, the long-term multi-decadal effects of management strategies for these systems are not well known. Using a mechanistic model for the invasive gypsy moth *Lymantria dispar* that has been rigorously tested (Dwyer *et al.* 2000; Dwyer, Dushoff & Yee 2004; Elder, Dushoff & Dwyer 2008; Reilly & Hajek 2008; Bjørnstad, Robinet & Liebhold 2010), we show that the use of biocontrol efforts to manage these pests can sometimes have unexpected and undesirable outcomes. In fact, ill-informed biocontrol use could actually sustain long-term outbreaks. This can have important ecological and economic consequences for eastern deciduous forest stands where this invasive pest occurs (Doane & McManus 1981). While we examine these issues with the gypsy moth in mind, the results can be widely applied given the increased use of anthropogenic inputs for controlling and managing numerous populations.

Materials and methods

STUDY SYSTEM

Like many forest defoliators, the gypsy moth is univoltine (i.e. one generation per year) and has an obligatory overwintering diapause phase. When temperatures rise in the spring, neonates hatch from egg masses laid the previous year. After hatching, larvae go through five to six instars, depending upon the sex of the moth, during which defoliation and horizontal disease transmission occur. We refer to the period of time in which disease transmission occurs as the within-season larval period (Dwyer *et al.* 2000; Elder, Dushoff & Dwyer 2008; Bjørnstad, Robinet & Liebhold 2010). After emerging from pupation, the adults, which do not feed, mate and the resulting egg masses enter diapause until the next spring (Leonard 1981). For modelling purposes, the period of adult activity and the overwintering of eggs are considered to occur between seasons of the larval period.

Over the long term, the gypsy moth exhibits classic boom and bust cycles. The collapse of gypsy moth populations following a boom is driven by a fatal host–pathogen interaction that occurs during the within-season larval period (Elkinton & Liebhold 1990; Dwyer *et al.* 2000). The pathogen *Lymantria dispar* nucleopolyhedrovirus (LdNPV), which is a member of the Baculoviridae and co-occurs naturally with the gypsy moth, is encapsulated in a protein coat or an occlusion body. Each occlusion body contains multiple copies of the virus. After hatching, some neonates consume LdNPV occlusion bodies that have overwintered on the egg mass (Podgwaite *et al.* 1979; Murray & Elkinton 1989, 1990). The virus replicates in the host and eventually causes liquefaction of the host's tissues (Miller 1997; Reilly & Hajek 2008). The occlusion bodies from the infected larvae are released and contaminate the leaf tissue on which the host dies. During this time, uninfected larvae grow to larger instars. The later-instar larvae become infected if they consume foliage on which recently released occlusion bodies reside, producing a second wave of infection (Woods & Elkinton 1987). The virus is transmitted horizontally between individuals with little evidence for direct vertical (transovarial) transmission from parent to offspring (Murray *et al.* 1991). Once pupation occurs, transmission stops. After disease transmission has ceased, a proportion of the virus survives the winter and provides the inoculum for infecting neonate larvae in the next season.

BIOCONTROL AGENTS

Given the destructive nature of defoliator outbreaks, considerable effort has been spent looking for ways to control the boom phase of the population. This is true for the gypsy moth (Podgwaite *et al.* 1992) as well as other widespread defoliators (Podgwaite *et al.* 1984; Maclauchlan *et al.* 2009). *Bacillus thuringiensis* (Bt), in particular Bt var. *kurstaki* or Btk, represents a popular biocontrol agent given the broad spectrum of leaf-eating caterpillars that it can attack and potentially control (Scriber 2001). Bt occurs naturally in the soil and is a facultative insect pathogen that can be mass-produced as a bacterial insecticide spray. After ingesting the spores, larvae die either from the action of the Bt toxins or by infection. Unlike baculoviruses, Bt does not create natural epizootics and subsequent waves of infection are not produced after application (Khetan 2001). In this respect, spraying Bt can be considered equivalent to spraying a chemical insecticide. It simply kills a certain percentage of susceptible larvae. However, since Bt is detrimental only to Lepidoptera and because it has a relatively short environmental persistence, it is considered to be more environmentally friendly than chemical insecticides and is increasingly taking their place in spray programmes (Ritter 2010).

Given the risk that Bt poses to non-target Lepidoptera, particularly endangered or threatened species, interest in finding a species-specific biocontrol agent that could be easily mass-produced has been high. Baculoviruses meet these criteria (Doane & McManus 1981). To control gypsy moth populations, the U.S. Forest Service began marketing a powder containing the baculovirus LdNPV under the name Gypchek. Since it is species-specific, Gypchek is often used in habitats where sensitive populations of non-target Lepidoptera are found (Doane & McManus 1981). Gypchek essentially enhances the amount of pathogen in the system. Unlike Bt, Gypchek creates waves of infection after spraying, similar to those seen in naturally occurring epizootics. While Gypchek is specifically formulated for the gypsy moth, other baculoviruses exhibit promise in controlling numerous

outbreking pests (Doane & McManus 1981; Podgwaite *et al.* 1984; Moreau *et al.* 2005; Maclauchlan *et al.* 2009). Thus, baculoviruses represent a viable, though currently more expensive, alternative to Bt without many of the corresponding concerns.

THE MODELS

To examine how the addition of Gypchek and Bt affect the long-term population dynamics of the gypsy moth, we employed a well-tested mechanistic model of gypsy moth dynamics (Dwyer, Dushoff & Yee 2004). The basic structure of the model, which we have modified to explore our questions, has been shown to successfully explain many aspects of the population dynamics of natural gypsy moth populations (Dwyer *et al.* 2000; Dwyer, Dushoff & Yee 2004; Elderd, Dushoff & Dwyer 2008; Bjørnstad, Robinet & Liebhold 2010). As compared to models that describe patterns in ecological data such as phenomenological models (Bolker 2008), the model used in our analysis allows us to directly manipulate processes that drive the long-term dynamics. Using the model, we can ask how various management practices affect the future dynamics of the system.

The model divides each gypsy moth generation into a within-season component when defoliation and infection take place and a between-season component when reproduction and overwintering occur. The modified biocontrol model allows us to examine how differences in the amount of pathogen sprayed and the threshold population sizes that trigger a spray event affect long-term dynamics. We also explore how within-season timing of the biocontrol application affects population dynamics using a computationally intensive suite of delay-differential equations. Our results show that within-season timing of the application does not matter (see Fig. S11, Supporting Information) given standard model assumptions. Thus, we do not touch on these results further. Additionally, using standard methods (Dennis *et al.* 2001; Abbott & Dwyer 2007), we consider whether the time series associated with various biocontrol efforts would continue to exhibit the chaotic oscillations generally observed in gypsy moth populations (see Chaotic Dynamics in Supporting Information). We summarize the model below and present the full model details in the Supporting Information.

WITHIN-SEASON DYNAMICS

To model the within-season dynamics, we begin with two delay-differential equations (Dwyer *et al.* 2000; Dwyer, Dushoff & Yee 2004):

$$\frac{dS}{dt} = -\bar{v} \left[\frac{S(t)}{S(0)} \right]^V P(t)S(t) \quad \text{eqn 1}$$

$$\frac{dP}{dt} = \bar{v} \left[\frac{S(t-\tau)}{S(0)} \right]^V P(t-\tau)S(t-\tau) - \mu P(t) \quad \text{eqn 2}$$

where S and P represent the susceptible host larvae and pathogen, \bar{v} is the mean transmission rate, and V is the squared coefficient of variation of the transmission rate, t is time, τ is the delay between consuming a lethal dose of the virus and death of the larva, and μ represents the degradation rate of the virus in the environment. The model assumes that individuals vary in degree of virus susceptibility such that, as the season progresses, the most susceptible hosts die first. The dynamics due to differences

in susceptibility are captured by $\left[\frac{S(t)}{S(0)} \right]^V$ where $S(0)$ represents susceptibles at time 0. This ratio declines as the number of susceptibles decreases during the epizootic and effectively scales the transmission rate \bar{v} .

Using eqns 1 and 2, we can derive the burnout approximation (Dwyer *et al.* 2000), which is the fraction of infected individuals over the course of an epizootic as $t \rightarrow \infty$:

$$I_T = 1 - \left\{ 1 + \frac{\bar{v}V}{\mu} [N_T I_T + \eta Z_T] \right\}^{-1/V} \quad \text{eqn 3}$$

where N and Z represent the host population and pathogen, respectively, at generation T and η is the relative susceptibility of the neonates as compared to the later instars. The burnout approximation assumes that epizootics are not cut short by the end of the larval season, but due to the lack of infected individuals in the population (Fuller, Elderd & Dwyer 2012).

BETWEEN-SEASON DYNAMICS

The between-season equations track both the host N and the pathogen Z during the overwintering period (Dwyer, Dushoff & Yee 2004).

$$N_{T+1} = \lambda N_T (1 - I_T) \left[1 - \frac{2abN_T}{b^2 + N_T^2} \right] \quad \text{eqn 4}$$

$$Z_{T+1} = \gamma N_T I_T + \xi Z_T \quad \text{eqn 5}$$

$$I_T = 1 - \left(\frac{S(t_F)}{S(0)} \right) \quad \text{eqn 6}$$

where host density N at generation $T + 1$ is determined by three factors: (i) host fecundity λ ; (ii) the fraction of hosts not infected $1 - I_T$ during generation T ; and (iii) the fraction of hosts not depredated $1 - \frac{2abN_T}{b^2 + N_T^2}$ at generation T . The predation term consists of a type III functional response due to generalist predators such as general parasitoids, birds and small mammals (Dwyer, Dushoff & Yee 2004). b is the host density at which the highest percentage of the host population is consumed, and a is that maximum fraction at host density b . Pathogen density Z at generation $T + 1$ depends upon the overwinter survival (viability) rate of infectious cadavers produced during generation T and the fraction ξ of pathogen that survives from the previous generation. The fraction of larvae I_T infected during generation T can be calculated from eqn 3, which allows us to determine the number of susceptibles at the beginning $S(0)$ and the end $S(t_F)$ of the epizootic. To examine the effect of environmental stochasticity in the system, we employ a multiplicative log-normal random variable in the between-season host equation. The log of the random variable is normally distributed with zero mean and standard deviation σ .

ADDING BIOLOGICAL CONTROL

Gypchek and Bt have two different modes of action. The spraying of NPV injects pathogen in amount P_G into the system and is considered equivalent to a naturally occurring virus. By contrast, the spraying of Bt simply kills a fraction f_B of the larvae. Unlike NPV, Bt is not known to create epizootics and has no effect on pathogen reservoirs.

Independent of whether NPV or Bt is sprayed, a land manager needs to define a strategy for when to spray. The strategy would most likely be based on three different factors: the amount of the biocontrol agent to apply; the size of the population threshold required to trigger a spraying event; and the timing of the application within the season. For our models, spray application is implemented in a generation in which N_T exceeds a population threshold N_H of a continually rising population (i.e. $N_T > N_{T-1}$). This would be indicative of a population that is increasing in number towards potential outbreak levels. Thus, if Gypchek is selected as the biocontrol agent, the pathogen in the system is increased by P_G . If Bt is selected, the number of susceptibles S declines by the fraction f_B .

Using the rescaled equations for both within-season (eqns 1–3) and between-season (eqns 4–6) dynamics, we examined how Gypchek and Bt application affected the long-term dynamics of the system. Throughout the simulations, we used the field-derived parameter values from Dwyer, Dushoff & Yee (2004) ($\lambda = 74.6$, $a = 0.967$, $b = 0.14$, $\phi = 20$, $\xi = 0$ and $V = 1/1.06$). Note \bar{v} , μ and η drop out of the equations due to rescaling, and ϕ is added, see Rescaling in the Supporting Information). Each simulation was run for 100 years to control for transient dynamics due to initial conditions before allowing spray treatments to occur, and then for an additional 150 years. Our analysis considers only the final 150 years, during which biocontrol is acting on the system.

We also examined how changes in biocontrol addition may affect the stability of the equilibria associated with the base model (i.e. no biocontrol added). To this end, we conducted a classic stability analysis (May 1974). For the stability analysis, we assumed that either Gypchek or Bt was being constantly added to the system (see Stability Analysis in Supporting Information).

All stochastic iterations of the model are summarized by taking the mean value of the desired metric (e.g. cycle amplitude) of a 100 replicated runs. To determine how well the long-term dynamics of the system are replicated by the model, we compared model output when biocontrol was not in use to field data using standard statistical practices (Kendall *et al.* 1999; Dwyer, Dushoff & Yee 2004).

SPATIAL DYNAMICS

To explore the effects of biocontrol addition on spatial population dynamics, we constructed a two-patch spatial model where individuals can migrate between patches, similar in motivation to Bjørnstad, Robinet & Liebhold (2010). Two-patch models have a relatively long history in ecology for examining the effects of space on species interactions (Reviewed in Briggs & Hoopes 2004). Most of these efforts have focused on the impacts of spatial structure on host–parasitoid or predator–prey interactions. Few (e.g. Bjørnstad, Robinet & Liebhold 2010) have examined the effects of spatial structure on host–pathogen interactions.

In our spatial model, one patch was treated with the biocontrol agent and the other patch was left untreated. Migration between patches occurred after the epizootic. The two-patch equations took the following form:

$$N_{1,T+1} = \lambda N'_{1,T} - e_1 N'_{1,T} + e_2 N'_{2,T} \quad (7)$$

$$N_{2,T+1} = \lambda N'_{2,T} - e_2 N'_{2,T} + e_1 N'_{1,T} \quad (8)$$

where N' represents population 1 or 2 after the epizootic (eqns 4–6) and e_1 and e_2 are the migration rates of population 1 or 2, respectively, to the other patch. We varied e for both populations

using multiple biocontrol scenarios and examined the effects of migration rate between populations on the median and amplitude of each population as well as the correlation between host populations in each patch. We calculated the correlation coefficient using changes in log 10 abundance of population size, which has been used extensively in previous analyses of gypsy moth populations (Abbott & Dwyer 2008). For the start of each simulated run, the initial conditions for each population were the same.

Results

The basic model eqns (4–6) using parameter values taken from Dwyer, Dushoff & Yee (2004) reasonably reproduce the long-term dynamics of gypsy moth populations (Fig. 1, Table 1). There are also relatively large regions of parameter space under which the mean period and amplitude correspond to data taken from natural population fluctuations (Figs S1 and S2, Supporting Information). Thus, the results presented are not due to the exact values of the model parameters chosen.

Adding biocontrol dramatically alters the long-term dynamics of the non-stochastic system (Fig. 2). However, the method of biocontrol, Gypchek or Bt, does not affect the overall appearance of the long-term dynamics. In general, each control application perturbs the system anew, preventing it from following the long-term trajectory it would take in the absence of control. Depending on the threshold population size and amount of biocontrol, the system may display large-amplitude cycles, steady states or a range of intermediate behaviours. Judicious use of the biocontrol agent can force the population into low-density stable equilibrium (Fig. 2a,b) with a few applications of the agent. This equilibrium corresponds to the region of state–space where population dynamics are determined by the generalist predator (Dwyer, Dushoff & Yee 2004) and would be favoured by most land managers. The use of a biocontrol agent can also drive the system to the unstable high-density equilibrium (Fig. 2c,d), which is governed by the pathogen (Dwyer, Dushoff & Yee 2004). From a management perspective, this would be a less than desirable outcome. Gypsy moth populations can also be driven to bounce between the stable and unstable equilibria (Fig. 2e,f). The stability analysis, where biocontrol is constantly added to the system, showed that the long-term dynamics are often determined by the domain of attraction the biocontrol agent forces the system towards. The domain could be associated with either the low-density stable or high-density unstable equilibrium (see Stability Analysis in Supporting Information). Thus, given various application amounts and thresholds, the system can display quite different dynamics, some of which are very far from a manager's goals.

Adding varying degrees of stochasticity alters long-term population dynamics (Fig. 3). With increasing levels of stochasticity, it becomes impossible to perturb the system into the low-level steady state with only a few spray treatments (i.e. the 'quick fix') and have it stay there

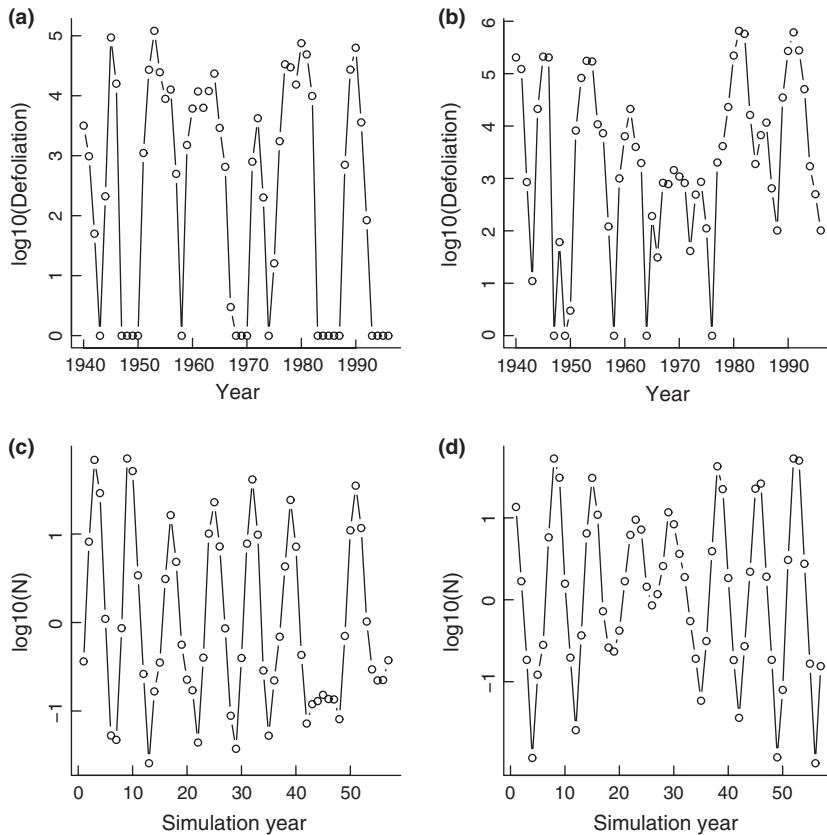


Fig. 1. Logarithm of acres defoliated in Vermont and Maine from 1940 to 1996, respectively (a and b). Sample output of two stochastic simulations showing simulated gypsy moth population dynamics (c and d). Parameters and stochasticity ($\sigma = 0.5$) are set to the values used in Dwyer, Dushoff & Yee (2004).

Table 1. Comparison of model cycles without biocontrol to natural cycles. Mean (95% confidence intervals) across 1500 runs for cycle period and coefficient of variation of cycle period are presented for the stochastic models. Data on natural populations come from Dwyer, Dushoff & Yee (2004)

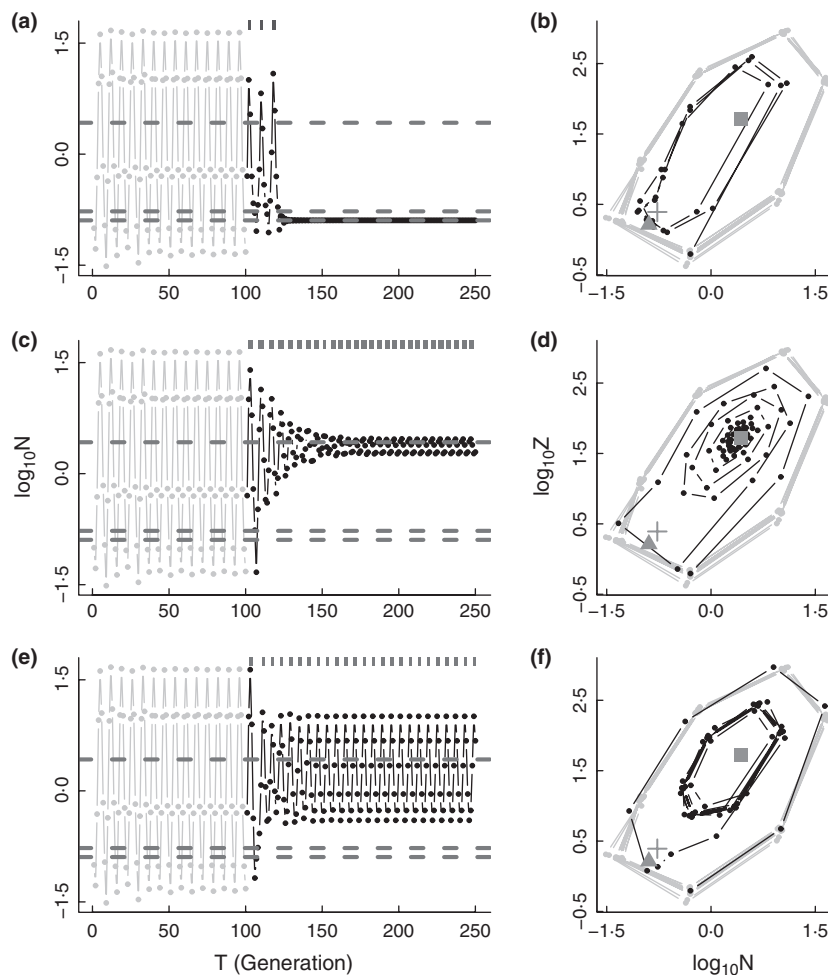
Data source	Cycle period	CV of cycle period
Natural populations	8.1–10.5	0.19–0.67
Low stochasticity model ($\sigma = 0.05$)	7.6 (7.0, 9.6)	0.10 (0.07, 0.72)
High stochasticity model ($\sigma = 0.15$)	7.5 (6.6, 8.4)	0.13 (0.07, 0.41)

permanently (Figs 2a,b vs. 3a,b). In the presence of stochasticity, effective control can only be achieved with frequent and continued spray applications year after year (Fig. 3a,b). Even then, the population does not settle down on the low-level equilibrium but instead displays cyclic behaviour around the equilibrium value. Stochastic trajectories can also still be held in the vicinity of the unstable equilibrium (Fig. 3c,d). The frequency of spraying the population must also increase to force the system to the high-level steady state. In general, accounting for environmental stochasticity still allows the system to settle into desirable and undesirable management scenarios.

To determine the threshold population sizes and the amount of agent that a manager needs to add to the system to achieve a desirable management goal, we

examined both median population size and amplitude while varying the threshold population size for spraying (N_H) and the amount of biocontrol added to the system, either Gypchek (P_G) or Bt (f_B). Varying both the amount of pathogen applied (P_G or f_B) and the population size threshold for spraying (N_H) had large effects on host–pathogen dynamics, measured either in cycle amplitude or in host median population size. For Gypchek, at relatively low threshold values and with a low addition of pathogen to the system, populations are forced towards the levels of low amplitude (Fig. 4 row a) and high median values (Fig. 4 row b). Interestingly, this region corresponds to trajectories converging on the high-density unstable equilibrium (Dwyer, Dushoff & Yee 2004). Even though this equilibrium is unstable when no biocontrol agents are added, the system can be forced to this point by periodic addition of either control agent. Since this high-density outcome occurs over a large area of the sample space, it represents a substantial risk and would likely constitute an unpleasant surprise from a management perspective. At moderate levels of addition, the populations can be held at the low-level steady state, characterized by low amplitude and low median values, provided that the threshold values for spraying are relatively low. It is also possible to drive the system to a wide variety of host cycles, generally displaying intermediate median population sizes, but amplitudes range from relatively large to small, depending on the effectiveness of the spray treatments.

Fig. 2. Time series, in the left column, and phase portraits, in the right column, of the deterministic model. Trajectories of the host population are plotted before (grey) and after (black) the beginning of the spray programme at year 100. Dark grey tick marks indicate years in which Gypchek was applied. The dashed lines in the time series indicate the three analytical equilibria for the gypsy moth model without biocontrol addition. In the phase portraits, these equilibria are marked by the dark grey symbols that represent the source (square), sink (triangle) and saddle-point (cross) equilibria. For (a) and (b) where $P_G = 150$, $N_H = 0.30$, the host population is quickly sent to low-level steady state without need for continued spray treatments. For (c) and (d) where $P_G = 10$, $N_H = 0.15$, Gypchek application holds the host at a high-level steady state which would be unstable without continued application. For (e) and (f) where $P_G = 72$, $N_H = 1.00$, the host displays a long-period cycle that cycles around the source. Similar patterns are seen when using Bt as a control agent (see Supporting Information).



The addition of Bt to the system allows for similar dynamics but over different regions of parameter space. However, unlike Gypchek, the spray threshold has little impact on the population's amplitude or median (Fig. 4). For Bt, low to medium levels of Bt addition result in populations being maintained at the high-level equilibrium (Fig. 4 rows c and d). At high levels of Bt addition, populations are maintained at the low-level equilibrium state. Since the low-level equilibrium is stable, it is possible to drive the system there with only a few initial treatments, as is true with Gypchek addition, and have it remain there indefinitely, but only in the absence of stochasticity.

Adding stochasticity to the system does not dramatically alter the results. However, it does increase the frequency at which the biocontrol agent is applied to the system (see Fig. S5, Supporting Information). In general, the danger of forcing the system into a high-level steady state appears much greater under Bt than under Gypchek. Additionally, using Bt as a biocontrol agent requires that a large portion of the pest population is killed in order to force it to the desired low-level equilibrium.

For the two-patch model, relatively small rates of migration between the populations synchronize the dynamics between the Gypchek sprayed and unsprayed patch (Fig. 5). For the unsprayed patch, there is considerable

danger in populations being maintained at the high-level equilibrium solely due to migration from the sprayed patch (Fig. 6). When the sprayed population is being maintained at the high-level equilibrium, a large area of parameter space results in the unsprayed patch being pushed to a steady state at relatively high population densities. There also appears to be a threshold of immigration from the sprayed patch into the unsprayed patch at which this occurs (Fig. 6). This can result in a high level of correlation between patches. Adding stochasticity to the system does not dramatically change the results (see Fig. S6, Supporting Information). The same results hold true when spraying Bt with and without environmental stochasticity (see Figs S7 and S8, Supporting Information). However, much higher levels of migration have to occur between these patches. Regardless of the agent being sprayed, there appears to be considerable risk in driving nearby populations to a high-level steady state.

Discussion

While biological control may be effective in controlling short-term outbreaks of forest pests (Podgwaite *et al.* 1984, 1992; Moreau *et al.* 2005; Maclauchlan *et al.* 2009) and other insects (Moscardi, Allen & Greene 1981;

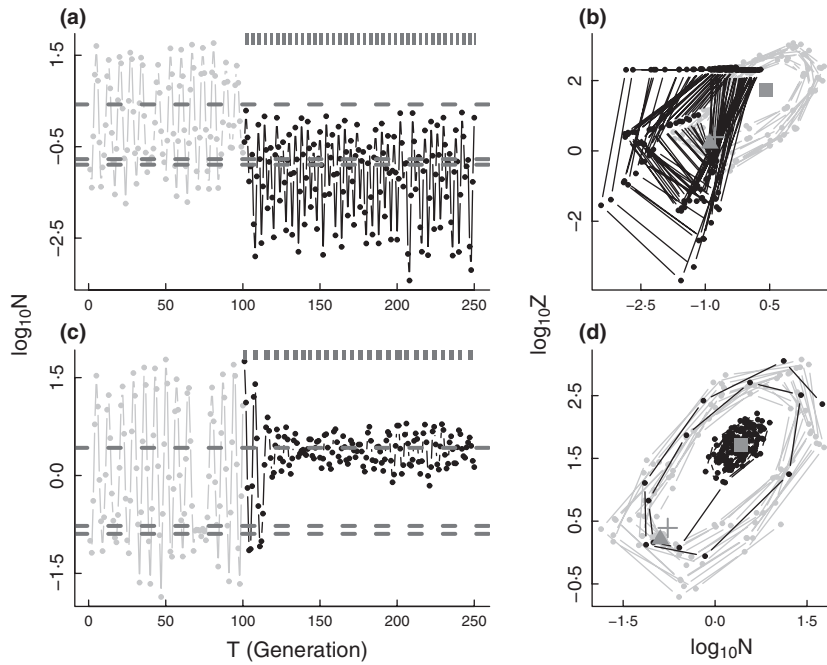


Fig. 3. Time series, in the left column, and phase portraits, in the right column, for stochastic model. The graphs demonstrate that spraying can result in the system exhibiting cycle dynamics near the high- and low-level equilibrium even with the addition of stochasticity. Trajectories of the host population are plotted before (grey) and after (black) the beginning of the spray programme at year 100. Dark grey tick marks indicate years in which Gypchek was applied. For (a) and (b) where $\sigma = 0.15$, $P_G = 200$ and $N_H = 0.001$, the addition of stochasticity requires continued spray applications to display cycles around the low-level equilibrium. For (c) and (d) where $\sigma = 0.15$, $P_G = 10$ and $N_H = 0.15$, the addition of stochasticity can also result in cyclic dynamics around the high-level equilibrium.

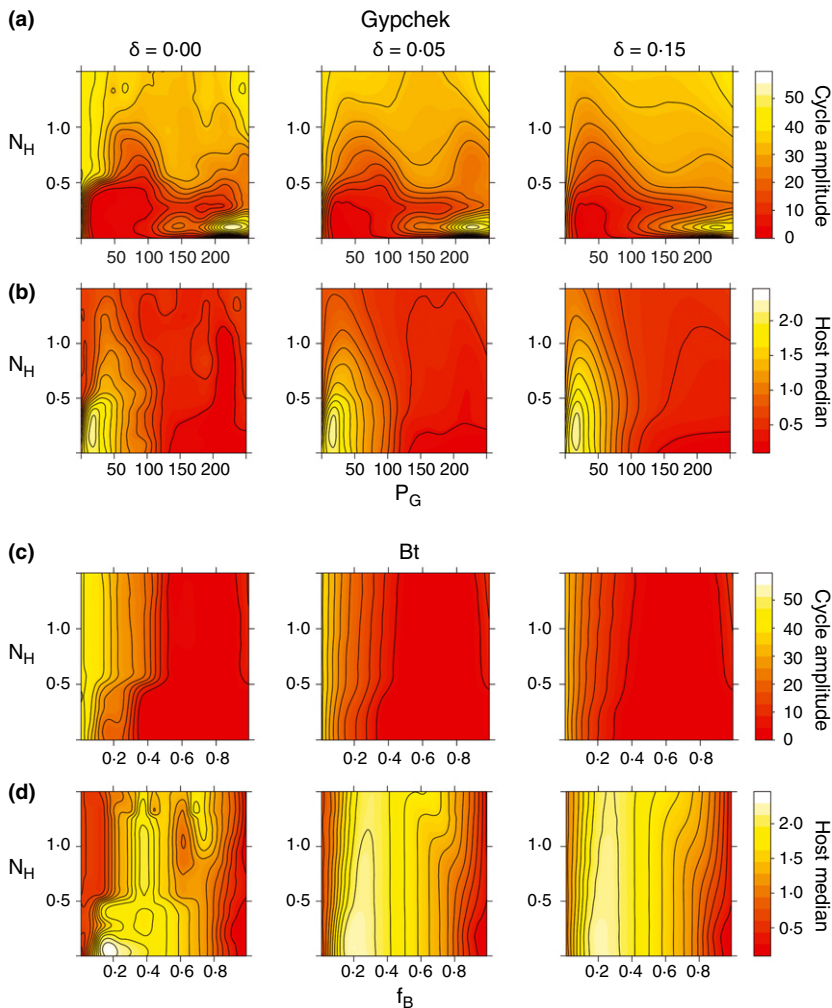


Fig. 4. Summary plots of the stochastic model for a range of Gypchek, P_G (rows a, b) and Bt, f_B (rows c, d) addition vs. threshold spray values, N_H . Stochasticity increases from $\sigma = 0$ in the left column to $\sigma = 0.15$ in the right column. Contour lines and shading correspond to levels of cycle amplitude (rows a, c) and cycle median (rows b, d). All plots include only the 150 years following the start of the spray programme. Note for rows (a) and (c), darker/redder colours indicate small amplitude cycles or steady states, and yellow/white corresponds to large amplitude cycles. For rows (b) and (d), yellow/white shading indicates areas where the population's median values are the largest.

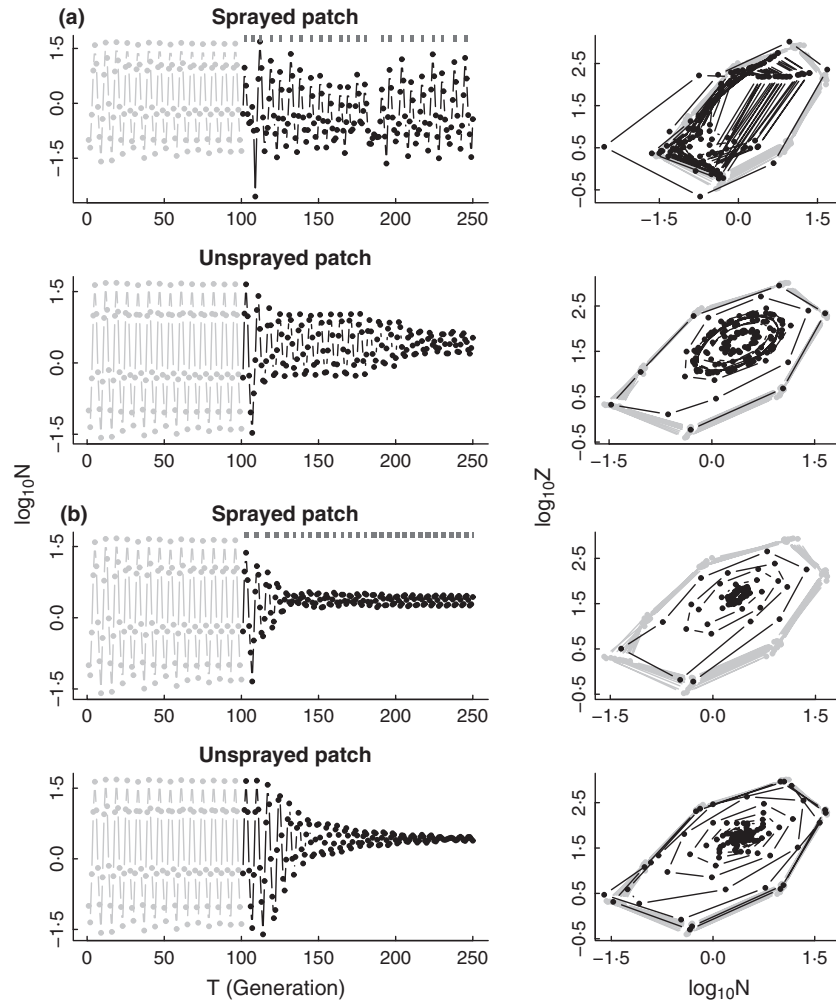


Fig. 5. Time series, in the left column, and phase portraits, in the right column, of the deterministic model two-patch models. Trajectories of the host population are plotted before (grey) and after (black) the beginning of the spray programme at year 100. Dark grey tick marks indicate years in which Gypchek was applied. For (a) where $P_G = 150$, $N_H = 0.30$, $e_1 = 0.075$ and $e_2 = 0.01$, the sprayed population fluctuates around the equilibria and the unsprayed population fluctuates around the unstable high-level equilibrium. For (b) where $P_G = 10$, $N_H = 0.15$, $e_1 = 0.075$ and $e_2 = 0.01$, Gypchek application holds the host at a high-level steady state in both patches, which would be unstable without continued application. Similar patterns are seen when stochasticity is added to the system and when using Bt as a control agent.

Asser-Kaiser *et al.* 2007), the long-term effects of its use on population dynamics are little known. Useful data are even less common for systems exhibiting long-period cycles, especially when biocontrol has been recently adopted or monitoring has been inconsistent. Our results suggest that prudent use of biocontrol can result in a truly desirable outcome – low-density pest populations over the long term (Fig. 2). With the right spray regime, a so-called quick fix may even be achievable. However, ill-advised use of a biocontrol agent, while dampening the boom and bust cycles, can lead to unexpected failures (Paine, Tegner & Johnson 1998; Doak *et al.* 2008) by maintaining the population at a high density over the long term (Fig. 2). In fact, sustained high-density populations, which occur over a large region of parameter space (Fig. 4), may be a serious risk for managers.

If the population is forced near the higher equilibrium level through biocontrol, there is a decrease in overall amplitude of the outbreak cycles when compared to natural outbreaks. This suggests that the system could be characterized by continuous partial defoliation rather than by the nearly total defoliation, which is typically observed only in the years near the peak of a natural outbreak (Leonard 1981). For gypsy moth populations driven solely

by natural dynamics, this equilibrium is not reachable because it is unstable (Dwyer, Dushoff & Yee 2004). By implementing the wrong biocontrol programme due to a focus on a short-term reduction in population size, the population can be held near this level indefinitely. Thus, while mitigation of the peak outbreak years could be desirable in the near term, the increase in the median pest population might place the forest under constant stress. If herbivory levels are sufficient to prevent trees from building up the nutrient reserves necessary for compensation, tree growth declines (Muzika & Liebhold 1999) and eventually mortality could occur. Further, the inefficient use of the biocontrol agent maintains the population at a density too high for generalist predators to play a major role in host density reduction.

Stochasticity also plays an important role and, if sufficiently large, can create movement between equilibria or prevent stable equilibria from being reached. Under high levels of stochasticity, the danger of settling on the higher-level equilibrium maintained by the pathogen (Dwyer, Dushoff & Yee 2004) declines as it becomes more difficult to hold the system to an unstable equilibrium in the face of random fluctuations. Yet, there still is a likelihood of ultimately having higher than expected number

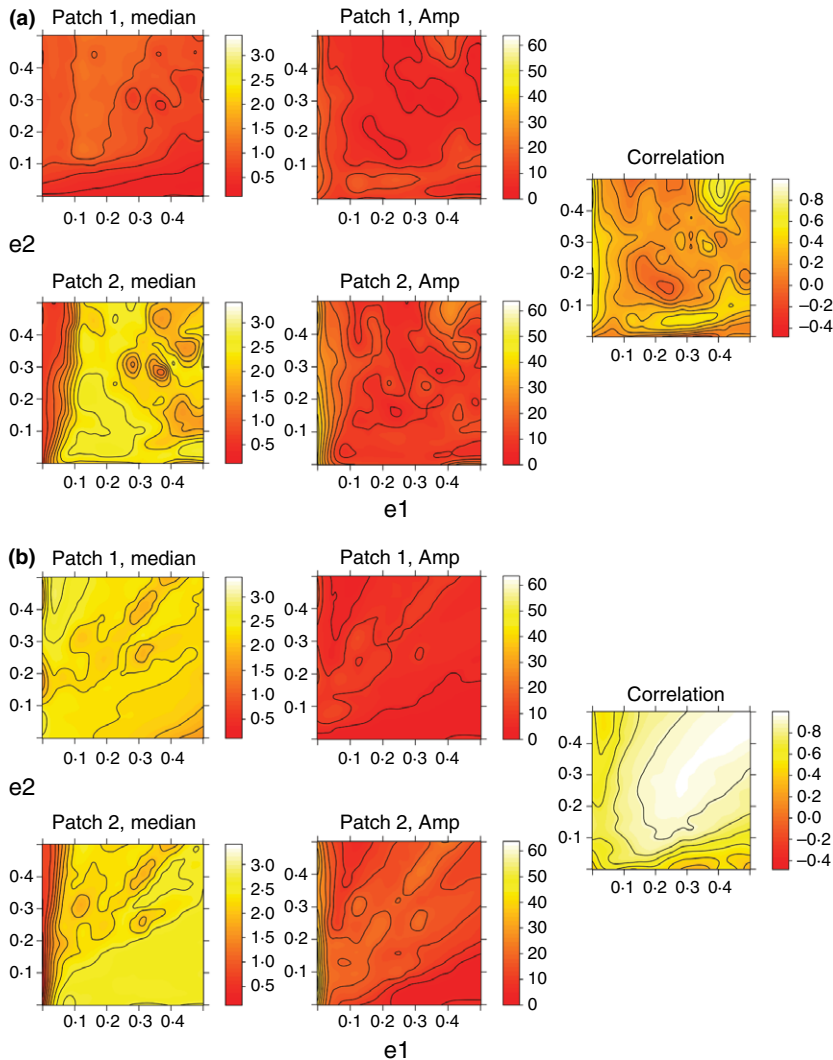


Fig. 6. Effects of emigration rate between a sprayed and unsprayed patch on median population size for each patch, amplitude of population swings for each patch and the correlation between patches. Correlation between patches was measured by examining the correlation in log 10 differences in population size from one time period to the next. (a) $P_G = 150$ and $N_H = 0.30$ as in Fig. 2a. (b) $P_G = 10$ and $N_H = 0.15$ as in Fig. 2c. All model runs were deterministic. Note that the lower left corner of the figure shows the population dynamics when each patch is isolated. Similar results occur when stochasticity is added to the system and when Bt, instead of Gypchek, is sprayed (see Supporting Information).

of gypsy moths in the system. It is also still possible to send the system to the low-density equilibrium, which is maintained by the generalist predator (Dwyer, Dushoff & Yee 2004). However, holding it at this level will require frequent biocontrol applications. From a biocontrol perspective, too much stochasticity hampers the ability of any management effort to quickly control the system.

For the two-patch spatial model, the danger of the unsprayed patch being maintained at the high-density equilibrium as the populations synchronize exists over a large area of parameter space. For host–parasitoid and predator–prey spatial models, constant immigration can stabilize the system as a whole (Briggs & Hoopes 2004). This also holds for host–pathogen systems. When a single patch is at an equilibrium level due to biocontrol addition, it provides a constant number of immigrants into the non-sprayed patch, which results in both patches exhibiting a stable equilibrium (Fig. 5). Adler (1993) found that for the classic unstable Nicholson–Bailey model, if the initial conditions differ between the two patches, the system exhibits bounded oscillations. In essence, adding biocontrol changes the initial conditions

in the sprayed patch such that the two patches no longer exhibit similar dynamics as compared to before the application of the biocontrol. As migration between patches increased, the patches became more synchronous as would be expected (Ranta, Lundberg & Kaitala 2006).

While the two-patch model provides a spatial extension of the long-term dynamic model, the model from a spatial perspective is simple. Additionally, the likelihood of maintaining the unsprayed patch at abnormally high levels increases as emigration increases to levels that may not be realistic. A logical extension of the two-patch model would be to explore dynamics at a large spatial scale to determine the extent of synchronization across the landscape due to biocontrol efforts in a single forest patch. At a larger scale, one would expect that the potential effects of spraying would decrease as distance from the sprayed patch increased due to potential limits of gypsy moth dispersal.

Previous work has shown that similar models of gypsy moth dynamics do reasonably well when describing the natural long-term population cycles (Dwyer, Dushoff & Yee 2004; Elderd, Dushoff & Dwyer 2008; Bjørnstad,

Robinet & Liebhold 2010). However, as is true of all models, there are limitations based on the data available and the level of model complexity. For instance, the number of times that a biocontrol agent needs to be applied to the system changes based on the level of environmental stochasticity in the system (see Fig. S5, Supporting Information). Thus, proper quantification of stochasticity would allow us to more accurately pinpoint how often certain management outcomes could be met. Additionally, while the model does reasonably well at reproducing time series associated with natural population dynamics (Fig. 1 and Table 1), what about populations that have been sprayed with biocontrol? Currently, there is some evidence that spraying Gypchek has resulted in altering the cyclic dynamics of gypsy moth populations in central Michigan (G. Dwyer, *pers. comm.*). Comprehensive data sets collected from these and other populations would allow for a direct test of the biocontrol version of the model.

Lastly, we have chosen a relatively simple non-spatial and spatial version of a long-term dynamic model that does not directly take into account other factors that may be important for determining gypsy moth cycles such as forest composition (Bjørnstad, Robinet & Liebhold 2010; Elderd *et al.* 2013), dispersal (Abbott & Dwyer 2008) and host evolution (Elder, Dushoff & Dwyer 2008). The model also does not include the effects of the recently established fungal pathogen *Entomophaga maimaiga*. However, *E. maimaiga* does not affect the gypsy moth's cycles since mortality attributed to the fungus is density independent (Liebhold *et al.* 2013) and including *E. maimaiga* should not affect our conclusions. In general, the above represent future research avenues that could improve our analysis. However, to paraphrase the statistician George Box (Box & Draper 1987), all models are wrong, but some are useful. The usefulness of the current model is that it shows the real possibility that managers could help maintain gypsy moth populations at much higher levels than desired.

From a management perspective, a key for implementing an effective control strategy is to determine the threshold population at which to spray along with the amount to spray. For the gypsy moth, egg mass counts (a common and fairly low-effort method of surveying gypsy moth populations) roughly correspond to population size (Talerico 1981). When egg mass count data are collected on a yearly basis, land managers can infer whether populations are rising or falling. The same logic can be applied when using other metrics of population size. For instance, data from pheromone traps could be used in place of egg mass counts. By monitoring populations and shrewdly using biocontrol agents, a desirable management outcome can be achieved – low pest population levels with relatively low input of biocontrol. Paired with any control programme should be an effort to monitor future population levels as far forward as possible. Combining this information with spray frequencies and amounts will produce valuable insight into the potential for various system

behaviours and would help specify key missing parameter values such as environmental stochasticity levels.

In general, efforts to control natural systems can be limited in their success (Paine, Tegner & Johnson 1998; Doak *et al.* 2008). This is due, in part, to not having enough data following short-term management efforts to establish long-term trends. However, using field-tested mathematical models, we can forecast long-term dynamics under a variety of management strategies. Using these forecasts, we can hopefully reveal any unexpected management consequences before they come true. At the very least, exploration of the system using models can help alert us to potential outcomes that can be watched for in field data. As we demonstrate for the gypsy moth, the addition of an anthropogenic input into the system can have far-ranging and unintuitive consequences on the long-term dynamics of this pest. The model results also suggest the potential for an intriguing set of experiments whereby with proper inputs a cyclic system could be driven to stability. Using such experiments, a clearer understanding of the mechanisms behind long-term population cycles could be gained. The experiments can then be used to better inform management practices and ensure that the most useful data are being collected.

Our results are likely to be applicable to many systems that undergo population cycles or outbreaks regulated by density-dependent processes and in which disease or pesticide application is used in control. It is often assumed that killing any number of pests can only help, but our work explores a new mechanism through which the outcomes may be otherwise. Due to the density-dependent dynamics of host and pathogen, preventing the extreme highs may also have the consequence of preventing the extreme lows. Depending on the system, this could be an issue especially when populations typically remain low for multiple years between outbreaks. The loss of extreme population lows is also of concern because it could deny the role of important natural controls such as allee effects or generalist predators that are effective only at low density (Dwyer, Dushoff & Yee 2004; Johnson *et al.* 2006). On the other hand, preventing the highest peaks of the outbreak may be the desired management outcome, even at the cost of increased pest numbers overall. With the knowledge that such a trade-off may be occurring, continued monitoring of post-treatment populations may allow the control strategy to be modified to best meet the management goals.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Data S1. Model formulation, sensitivity analysis, stability analysis, and an examination of chaotic dynamics.

Table S1. Parameter values used in the simulations for the rescaled delay-differential eqns S9–S19.

Fig. S1. Effects of changes in fecundity λ , coefficient of variation $V^{1/2}$, overwintering viability of cadavers produced in the current generation ϕ and the viability of pathogen produced in previous generations ξ on the mean period between cycles.

Fig. S2. Effects of changes in fecundity λ , coefficient of variation $V^{1/2}$, overwintering viability of cadavers produced in the current generation ϕ and the viability of pathogen produced in previous generations ξ on the magnitude of the changes in population size from the trough to the peak of single cycle.

Fig. S3. Effects of constant addition of either Gypchek (A) or Bt (B) on the greatest eigenvalue, α_1 , as the amount of pathogen, P_G , or fraction of individuals killed, f_B , increases.

Fig. S4. Time series, in the left column, and phase portraits, in the right column, of the deterministic model where Bt is sprayed.

Fig. S5. Summary plots of the stochastic model for a range of Gypchek, P_G , (row A) and Bt, f_B , (row B) addition vs. threshold spray values, N_H , for biocontrol spray frequency.

Fig. S6. Effects of emigration rate between a Gypchek sprayed (Patch 1) and unsprayed (Patch 2) patch on median population size for each patch, amplitude of population swings for each patch, and the correlation between patches for a stochastic version of the spatial model.

Fig. S7. Effects of emigration rate between a Bt sprayed (Patch 1) and unsprayed (Patch 2) patch on median population size for each patch, amplitude of population swings for each patch, and the correlation between patches for a deterministic version of the spatial model.

Fig. S8. Effects of emigration rate between a Bt sprayed (Patch 1) and unsprayed (Patch 2) patch on median population size for each patch, amplitude of population swings for each patch, and the correlation between patches for a stochastic version of the spatial model.

Fig. S9. Effects of biocontrol input (P_G or f_B), threshold population size at which the biocontrol agent is administered (N_H), and stochasticity (σ) on the Global Lyapunov Exponents (GLEs) using the burnout approximation (eqn 3).

Fig. S10. Plot of long-term dynamics of the basic model using the delay-differential equations.

Fig. S11. Plots of cycle amplitude values from the deterministic model for a range of within-season spray times and (A) P_G or (B) f_B values.