

Biological invasion and biological control: A case study of the gypsy moth spread

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Abstract

Biological invasions are currently regarded as a major threat to biodiversity and agriculture all over the world, often resulting in huge economic losses. One of the worst cases in modern history has been the invasion of gypsy moth in the USA. The apparent importance of this issue has brought to life various strategies of invasive species management. However, a comprehensive understanding of the consequences of different strategies is still lacking. In this paper, we consider how the pattern of the gypsy moth spread can be affected by biological control when an infectious disease is introduced in the wake of the spreading species. We first revisit the available information on the gypsy moth biological traits and argue that the importance of the commonly accepted mechanism of its dispersal by means of “stratified diffusion” may be significantly overestimated. We then consider a diffusion-reaction model of the gypsy moth spread and show that it can produce pattern of spread very similar to what is seen in field observations. Having considered the system’s properties for different strength of the disease, we find that, rather counter-intuitively, the invasion success depends on the magnitude of the controlling effort in a non-monotonous way. An increase in control measures may reinstate the invasion that would fail otherwise. A message to pest control managers is therefore that a better result may sometimes be achieved by investing less money, contrary to what is usually done.

Key words: Gypsy moth, patchy spread, allee effect, viral infection

Introduction

Biological invasions make one of the most serious threats to biodiversity and agriculture across the globe, causing damage worth of billions pounds every year (Pimentel, 2002). Better understanding of the mechanisms of the ‘alien’ species invasion and their impact on the native ecosystems is therefore a problem of high practical importance.

Biological invasion typically has a few distinctly different stages such as (i) alien species introduction, (ii) their establishment in the new environment, and, eventually, (iii) their geographical spread (Hengeveld, 1989; Shigesada & Kawasaki, 1997). A more detailed classification of invasion stages can be made by taking into account different biological and environmental factors (Sakai *et al.*, 2001). Each of the stages has its own mechanisms and implications, which normally require application of specific research approaches. In this paper we focus on the challenges arising during the stage of the geographical spread.

A well-developed theory predicts a simple pattern of alien species spread consisting of a continuous traveling boundary or ‘population front’ separating the invaded and non-invaded

regions. An appropriate modeling framework is given by diffusion-reaction equations (Murray, 1989; Lewis & Kareiva, 1993; Petrovskii & Li, 2006). A propagating population front has been a paradigm of the invasive species spread for several decades (Fisher, 1937; Okubo *et al.*, 1989; Holmes *et al.*, 1994; Shigesada & Kawasaki, 1997). However, it also appears to be at odds with some observations. In some cases, the spread takes place through formation of a distinct patchy spatial structure without any continuous boundary. The most well known example of this ‘patchy invasion’ is the spread of the gypsy moth in the USA; e.g. see the US Forest Service website (www.fs.fed.us/ne/morgantown/4557/gmoth/atlas/#defoliation) for the maps and other details.

In this paper, we revisit the gypsy moth invasion with the purpose to identify the mechanisms and factors resulting in the patchy spread. By re-examining available evidence on gypsy moth biological traits, we argue that some of the commonly accepted explanations of this phenomenon may not be applicable. We then suggest an alternative mechanism of the patchy spread and show that it may result from the dynamical interaction between the spreading insect population and a certain infectious disease. We also show that, if this disease is used as a biological control tool, our results can be used as a guideline to develop a more effective control strategy.

The gypsy Moth, its Biology and Ecological Impact

The gypsy moth has one generation per year with four main life stages: egg, larva (caterpillar), pupa and adult. In spring (late April to early May) the eggs hatch into larvae, which crawl up to the tree tops then suspend themselves on silk threads and are passively dispersed by the wind (Liebhold *et al.*, 1992), it is at this stage that they feed. 4–6 weeks later in early summer (June to early July) they enter a pupal stage. 10 to 14 days later, adult gypsy moths emerge and are present in July and August. The females are unable to fly. Soon after emergence, they mate and lay their eggs, which overwinter. Egg masses can be found on the branches or trunks of trees, fences, buildings and vehicles and each mass contains around 100–1000 eggs.

The gypsy moth larva has a preference for the leaves of deciduous hardwood trees, particularly oak, but also species such as maple and elm. This preference for oak is particularly significant to the economy as oak is also favoured by the timber industry. In high densities, competition for food drives them to feed on almost any tree or shrub, including evergreens. Over 300 species of plants in the USA have already been identified as hosts (Liebhold *et al.*, 1995) and this figure will undoubtedly rise as the insect’s range expands. Two or three successive years of defoliation are usually needed to result in the death of a deciduous trees, but a single year of defoliation is generally enough to kill a conifer (Johnson & Lyon, 1991). Heavy defoliation also weakens trees defences to other causes of mortality, such as drought or pathogens (Davidson *et al.*, 1999).

The gypsy moth significantly impacts the American ecosystems it enters. Defoliation can alter the chemistry of water in nearby streams (Webb *et al.*, 1995). Woodland tree stands subjected to repeated infestations have lower tree densities and fewer oak trees (Herrick & Gansner, 1988). By defoliating and/or causing the the death of canopy trees, the insects alter the light, nutrients and moisture on the ground, and thereby increase the populations of both herb and shrub species (Witter *et al.*, 1992), changing the forest structure. This will then have an addition impact on the other animals present; for example canopy nesting birds may have fewer nesting spots available whilst shrub and ground nesting bird species populations increase (Thurber *et al.*, 1994), which further disturbs the forest ecosystem.

The Strong Allee effect

The Allee effect, i.e. a decrease in the *per capita* population growth rate at small values of the population density, is a common feature of ecological populations (*cf.* Courchamp *et al.*, 2008).

Its impact can modify the population dynamics significantly, in particular, resulting in more complicated patterns of invasive species spread (Malchow *et al.*, 2008). Four studies have indicated the presence of strong Allee effects in USA gypsy moth populations. Liebhold & Bascompte (2003) studied records of the total numbers of males caught in pheromone traps in Washington from 1974 to 1996 and detected a total of 194 isolated colonies. Of these, eradication treatments were applied to only 16%, whilst the rest died without intervention and 76% of which within a year of detection. They found that “the gypsy moth data analysed here indicate the existence of an Allee effect.” This is supported by a separate study by Whitemire & Tobin (2006) who concluded that the “inclusion of spatially explicit Allee effects into the colony-invasion models seems to be applicable for the gypsy moth.” Johnson *et al.* (2006) used parameters derived from long-term monitoring data to model an interaction between strong Allee effects and stratified diffusion to explain spatiotemporal variability in rates of spread. The main causes of an Allee effect in low-density gypsy moth populations appear to be the failure to find mates and to satiate predators. Especially the first cause has been shown to play an important role (Sharov *et al.*, 1995; Robinet *et al.*, 2007, 2008). The Allee effect has also been observed in attempts to control sparse populations when synthetic pheromones were used to prevent males from locating females (Thorpe *et al.*, 2006).

Possible Mechanisms for Patchy Spread

As we have mentioned it in the Introduction, the spatial spread of gypsy moth is distinctly patchy, without showing a continuous front at any time of observation. This clearly contradicts to the intuitively expected standard pattern of alien species spread by the population front propagation. Several theories have been proposed to explain the patchy spread such as “stratified dispersal” (Hengeveld, 1989; Shigesada & Kawasaki, 1997), stochasticity with long distance dispersal (Lewis & Pacala, 2000) and “fat-tailed” kernels (Clark *et al.*, 2001).

One intuitive explanation is environmental heterogeneity. Indeed, in areas with more preferred tree species, higher numbers of gypsy moths are more likely (Liebhold *et al.*, 1994; Witter *et al.*, 1992). The availability and suitability of foliage has been found to influence larval survival, speed of development and pupal weight (Barbosa & Capinera, 1977; Hough & Pimental, 1978; Barbosa *et al.*, 1983; Stoyenoff *et al.*, 1994). Despite this, the evidence suggests spatial heterogeneity is not as significant a factor in distribution as one might expect. Sharov *et al.* (1997) looked at pheromone trap data from 1988–1994 in northern Virginia and southern West Virginia to find correlations between landscape characteristics (land use, slope, elevation, aspect and two forest classifications) and gypsy moth density that could be used to improve understanding of the spread. However, only elevation was found to be statistically significant, and only strongly significant in the transition zone. This may be due to lower human activity at higher elevation, which damps the intensity of vector-borne dispersal. Whitemire & Tobin (2006) looked at new outbreaks across the USA and found that the strength of the Allee effect varied geographically but could not determine the cause and concluded that “the abundance of preferred host tree species and land use category did not appear to influence persistence.” Liebhold *et al.* (2007) noted that the historical spread from the original site of introduction – examined in Liebhold *et al.* (1992) – was roughly at the same speed in all directions (except north, which was lower) despite marked spatial variation. Liebhold *et al.* (1992) attributed the slower northerly spread to the colder winter temperatures, which can cause significant mortality in the overwintering eggs (Madrid & Stewart, 1981). Sharov *et al.* (1999) looked at the historical spread in Michigan and also found slower spread to the north but concluded this was due to forest variation rather than winter temperature. Overall, spatial heterogeneity does not appear to be enough to explain patchy spread.

Stratified dispersal appears to be the most widely accepted theory (Liebhold *et al.*, 1992; Shigesada & Kawasaki, 1997; Sharov & Liebhold, 1997, 1998; Liebhold, 2003; Johnson *et al.*, 2006; Liebhold & Tobin, 2006, 2007, 2010; Liebhold *et al.*, 2007; Tobin & Blackburn, 2008;

Tobin *et al.*, 2009*a,b*), where local dispersal via the diffusion equation is combined with multiple long range “jumps”, resulting in small, isolated colonies establishing ahead of the population front. These colonies then also expand in range and may eventually coalesce with each other and the main expanding front, thus greatly hastening the spread compared to what is predicted by the standard single species reaction-diffusion model.

Whilst stratified dispersal is evidently a relevant mechanism to affect the gypsy moth dynamics, it may be unnecessarily complex if a simpler reaction-diffusion model can produce similar results¹. Moreover, we argue that the importance of stratified diffusion may be significantly overestimated. A generally accepted point of view on the mechanisms of gypsy moth dispersal (*cf.* Liebhold & Bascompte, 2003; Whitmire & Tobin, 2006; Tobin & Blackburn, 2008) is that accidental transportation “may be the principle movement mechanism” (Liebhold *et al.*, 1992). It is thought that the vector-borne dispersal may occur when people inadvertently transport gypsy moth eggs that have been laid on items such as vehicles. In particular, an attempt was made to relate new infestations to household moves from infested to uninfested regions (McFadden & McManus, 1991). However, here we argue that an occasional transport by a vehicle would unlikely bring away more than just a handful of gypsy moth eggs. Consequently, that would result in a new colony consisting from a small number of newly born insects. Then the impact of the Allee effect would normally bring a small colony to extinction. The hypothesis of the long-range vector-borne dispersal therefore appears to be not fully consistent with the evidence of the strong Allee effect.

We therefore leave aside the mechanisms of spread based on long-jump events and turn to the standard diffusion-reaction approach. The problem with diffusion-reaction equations seems to be that the vast majority of ecological studies that used them as the mathematical framework ended up with a conclusion that they cannot produce anything beyond spread with a continuous traveling population front. A closer look at the previous studies, however, reveals that most of them used the same few types of the diffusion-reaction models such as either a single-species model (e.g. Lewis & Kareiva, 1993) or a predator-prey model (Owen & Lewis, 2001), or two-species competition model (Shigesada & Kawasaki, 1997). Importantly, the latter two approaches usually assume that the spreading pest exhibits logistic population growth. In the above, however, we provided convincing evidence that the gypsy moth population dynamics is affected by the strong Allee effect. Remarkably, once the strong Allee effect is taken into account, e.g. in a predator-prey system, the model attains considerably different properties. It has been discovered by Petrovskii *et al.* (2002, 2005) and Morozov & Petrovskii (2006) that, in a predator-prey model with a strong Allee effect for the prey, in a certain parameter range, the standard continuous front scenario changes to the patchy spread. Similar results have been obtained in models of epidemics spread (*cf.* Petrovskii *et al.*, 2005). In the next section, we apply these results to the gypsy moth case.

Justification for a Reaction-Diffusion Model

Before attempting to apply a reaction-diffusion model to the gypsy moth spread, we need to first establish the following facts:

- (i) Spatial spread can be adequately described by the diffusion equation.
- (ii) Population dynamics is subject to predation or infection.

The Diffusion Equation

Gypsy moths are dispersed by two different mechanisms: wind-borne and vector-borne. Wind-borne dispersal occurs via the young larvae dangling on silken threads from the tree tops to be

¹To quote Isaac Newton, “We are to admit no more causes of natural things than such as are both true and sufficient to explain their appearances. Therefore, to the same natural effects we must, so far as possible, assign the same causes.”

carried away by wind currents. Wind dispersal is known to be described by the diffusion equation (Okubo, 1980; Okubo & Levin, 1989), subject to appropriate choice of the diffusion coefficient. Vector-borne dispersal, as we mentioned it above, is mainly linked to occasion transport with humans and vehicles. While its long-range impact is controversial, the contribution of the vector-borne mechanism to the short-range dispersal is not necessarily damped by the Allee effect and hence should be taken into account. Human movement was shown to be fat tailed (Brockmann *et al.*, 2006). However, since we disregard the contribution of the tail, it can be approximated as a diffusion process and described by the diffusion equation (Petrovskii & Li, 2006).

Note that gypsy moth females are flightless, so the two mechanisms mentioned above are the only means of spreading. Thus, using the diffusion equation in order to model the population spatial movement seems feasible.

Predators and Infections

Many species prey on the gypsy moth, including small mammals, birds and insects. There are also a wide range of bacterium, viruses and fungi that the gypsy moth is susceptible to.

Predators

Predation can have a significant impact on gypsy moth populations, particularly at low densities. Most birds and small mammals will consume the gypsy moth in one or more of its life stages (Smith, 1985). Generalist native rodents, such as the deer mouse (*Peromyscus* spp.) and the white-footed mouse (*Peromyscus leucopus*), which prey on the caterpillars are generally considered the most significant predators (Bess *et al.*, 1947; Elkinton *et al.*, 1996; Jones *et al.*, 1998; Liebhold *et al.*, 2000). However, predator populations appear to be affected by the gypsy moth densities (Elkinton *et al.*, 1996; Bjørnstad *et al.*, 2010) as the moths do not represent a significant enough part of their diets (Elkinton *et al.*, 1996; Jones *et al.*, 1998). Gypsy moth larvae are only available for a few weeks of each year and are apparently not a favoured food source (Elkinton *et al.*, 2004; Smith, 1985). There have been some attempts to introduce exotic predators and parasitoids to the USA, but with limited success so far (Kenis & Vaamonde, 1998). Thus, predation does not appear to be a significant factor in the patchy spread.

Infection

The most common pathogen is wilt disease, the *Lymantria dispar* multicapsid nuclear polyhedrosis virus (LdMNPV, or NPV), which is present in almost every gypsy moth population. Combined with stress from high densities, NPV can lead to population collapse (Elkinton & Liebhold, 1990). It is also a widely used biological pesticide, “Gypchek,” as it targets only the gypsy moth. Another significant infection is the bacterium *Bacillus thuringiensis* ‘Kurstaki’ (BtK), which is also often used as a biological pesticide but – unlike NPV – outbreaks tend not to spontaneously occur in populations. So, infection appears to be a more useful avenue of investigation, in particular NPV.

Gypsy Moths and the Nuclear Polyhedrosis Virus

The Nuclear Polyhedrosis Virus (NPV) is a naturally occurring viral infection of the gypsy moth. It is also commonly known as “wilt disease” due to the limp appearance of the infected larvae. There are varying figures for gypsy moth mortality – from around 70–95% – depending on various factors including the specific strain of NPV present and the general health of the gypsy moth population, but most papers place the figure at around 90% (Reardon *et al.*, 2009). Transmission occurs both within and across generations. Infected young larvae typically die hanging on leaves.

Their cadavers are fragile and easily ruptured, releasing millions of occlusion bodies. Healthy larvae then consume the viral occlusion bodies along with the foliage and become infected. The time between infection and death is about 10 to 14 days, depending upon the size of the larva, virus dose, and ambient temperature (Reardon *et al.*, 2009). Transmission can also occur when egg masses are laid upon NPV contaminated surfaces as NPV can remain at high levels in soil, litter, and on bark for at least one year (Podgwaite *et al.*, 1979). The larvae hatching from the contaminated eggs the following spring then have a high risk of infection. Birds and mammals can also disperse NPV (Lautenschlager & Podgwaite, 1979), and parasitoids and invertebrate predators may play a role in transmit NPV within gypsy moth populations (Reardon *et al.*, 2009).

Mathematical Modelling

Having now revealed the main features of the gypsy moth dynamics in space and time, we can endeavor to address the phenomenon of the patchy spread by applying mathematical modeling. In agreement with the above evidence, we assume that the main factor regulating gypsy moth spread is NPV. Taking also into account the impact of the strong Allee effect, we consider the following spatially explicit SI model of the viral infection spread:

$$\frac{\partial s}{\partial t} = \left(\frac{\partial^2 s}{\partial x^2} + \frac{\partial^2 s}{\partial y^2} \right) + \gamma s(s - \beta)(1 - s) - si, \quad (1)$$

$$\frac{\partial i}{\partial t} = \left(\frac{\partial^2 i}{\partial x^2} + \frac{\partial^2 i}{\partial y^2} \right) + si - mi, \quad (2)$$

where $s(x,y,t)$ and $i(x,y,t)$ are, respectively, the densities of susceptible and infected insects at time t and position (x,y) . The terms in the brackets describe diffusion; other terms in the right-hand side of the equations describe the population growth and the impact of the disease, where β , γ and m are parameters with obvious meaning. Note that, for convenience, all variables and parameters in Eqns (1–2) are scaled to dimensionless values (for details, see Petrovskii *et al.*, 2002, 2005; Morozov & Petrovskii, 2006; Malchow *et al.*, 2008).

Model (1–2) is known to exhibit a rich and complicated dynamical behaviour (e.g. see Malchow *et al.*, 2008) and its detailed study is beyond the scope of this paper. Instead, here our goal is to demonstrate that, when applied to the problem of biological invasion, it can produce patterns in population density that are very similar to the ones observed in the gypsy moth spread.

Equations (1–2) are solved numerically by finite differences using the standard 5-points explicit scheme. We consider a square-shaped domain of size L so that $0 < x < L$ and $0 < y < L$. At the boundaries of the domain, we use the Neumann type zero-flux conditions. For the initial conditions, we consider that at $t=0$ the whole population is distributed homogeneously with the density $s+i=1$ (i.e. at the carrying capacity) inside a square of size ε , i.e. for $|x| < \varepsilon$ and $|y| < \varepsilon$. In a smaller sub-domain inside this area, i.e. for $|x| < \eta$ and $|y| < \eta$ where $\eta < \varepsilon$, a certain fraction κ of the population is infected with NPV, $0 < \kappa < 1$.

Fig. 1 shows the simulation results obtained for parameters $\gamma=10$, $\beta=0.2$ and $m=0.26$ and the initial conditions with $\varepsilon=10$, $\eta=5$ and $\kappa=0.5$. For the sake of brevity, only the density of susceptible insects is shown, the density of infected exhibits the same properties. It is readily seen that, apart from an early stage of the system's dynamics (not shown here), the spread of the population follows a distinct patchy pattern. At any moment, the infested area consists of an ensemble of small patches qualitatively similar to what is observed in field observations, without any continuous population front or boundary.

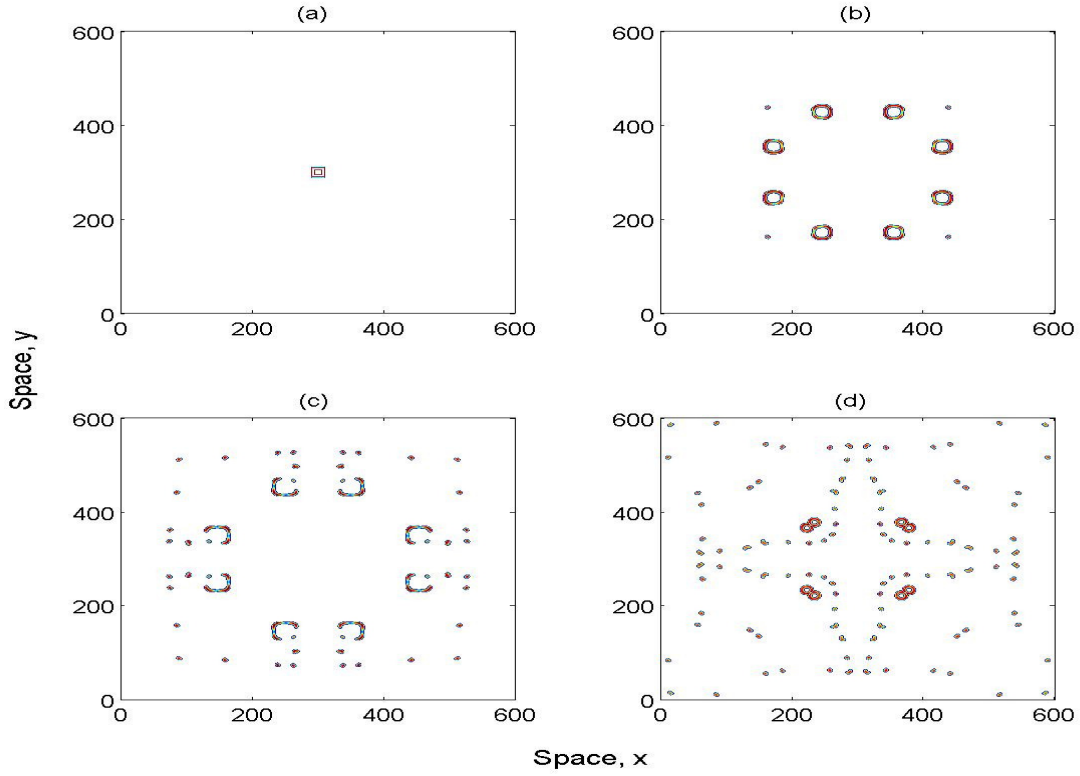


Fig. 1. Spatial distribution of the density of susceptibles, as described by the model (1–2), obtained at (a) $t=0$, (b) $t=250$, (c) $t=450$ and (d) $t=650$ for parameters $\gamma=10$, $\beta=0.2$ and $m=0.26$.

Simulations have been made for other parameter values as well. The pattern shown in Fig. 1 appears to be robust to variation of parameter values inside a certain range; however, a larger variation may result either in a different pattern of spread or in the population extinction. For instance, for the values of β and γ as in Fig. 1, the values of m higher than 0.3 results in a spread though the propagation of a continuous front while the values of m lower than 0.2 results in population extinction. These simulation results are summarized in Fig. 2. The situation stays qualitatively the same for other values of γ , although the position of the curves in the (β, m) parameter plane will be somewhat different.

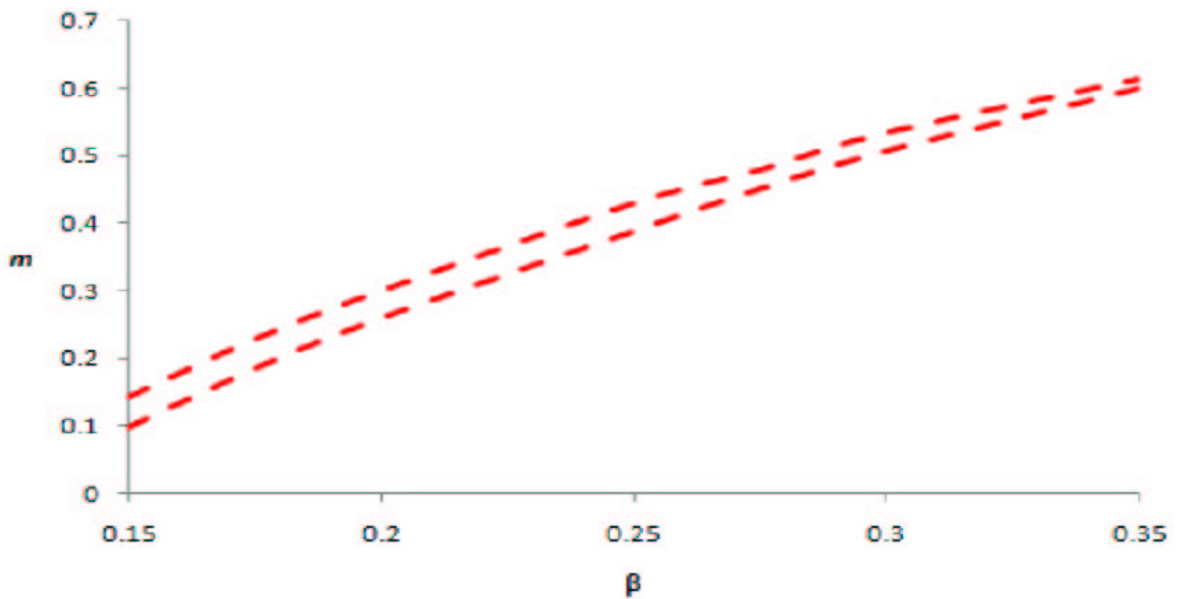


Fig. 2. A map in the (β, m) parameter plane (obtained for $\gamma=10$). The patchy spread is observed for the parameters between the two dashed curves.

Interestingly, the population spread through the propagation of continuous fronts does not result in successful invasion. A generic example of the system's dynamics in this case is shown in Fig. 3. We assume that the invasive species has been spreading successfully during the early stage of spread until, at a certain moment, the mortality m increases to a new value. Correspondingly, we use the snapshot shown in Fig. 1b as the initial condition for a new simulation run with $m=0.3$, keeping other parameters the same as in Fig. 1. It is readily seen that the patches grow into travelling population bands, which eventually merge to produce bands of larger radius, *cf.* Figs 3b and 3c. Remarkably, the invasive species is absent both in front of the travelling band and in its wake. Consequently, after the bands leave the domain (see Fig. 3d) there will be no alien species left behind; therefore, the invasion fails.

Concluding Remarks

Understanding the main features of alien species spread and identification of the factors that affects the pattern of geographical spread is the problem of high practical importance. Propagation of a population front separating invaded and non-invaded areas has been a paradigm of invasive species spread as it is indeed often seen in field data (e.g. see Shigesada & Kawasaki, 1997) and supported by a well-developed theory (Skellam, 1951; Volpert & Petrovskii, 2009). During the last two decades, however, there has been increasing evidence that, at least in some cases, geographical invasion follows a completely different scenario when no continuous front is formed and the spread occurs through formation and movement of patches of high population density. Probably the most well known and well studied example of this patchy invasion is the spread of gypsy moth in the USA; see the long list of references in the reference section.

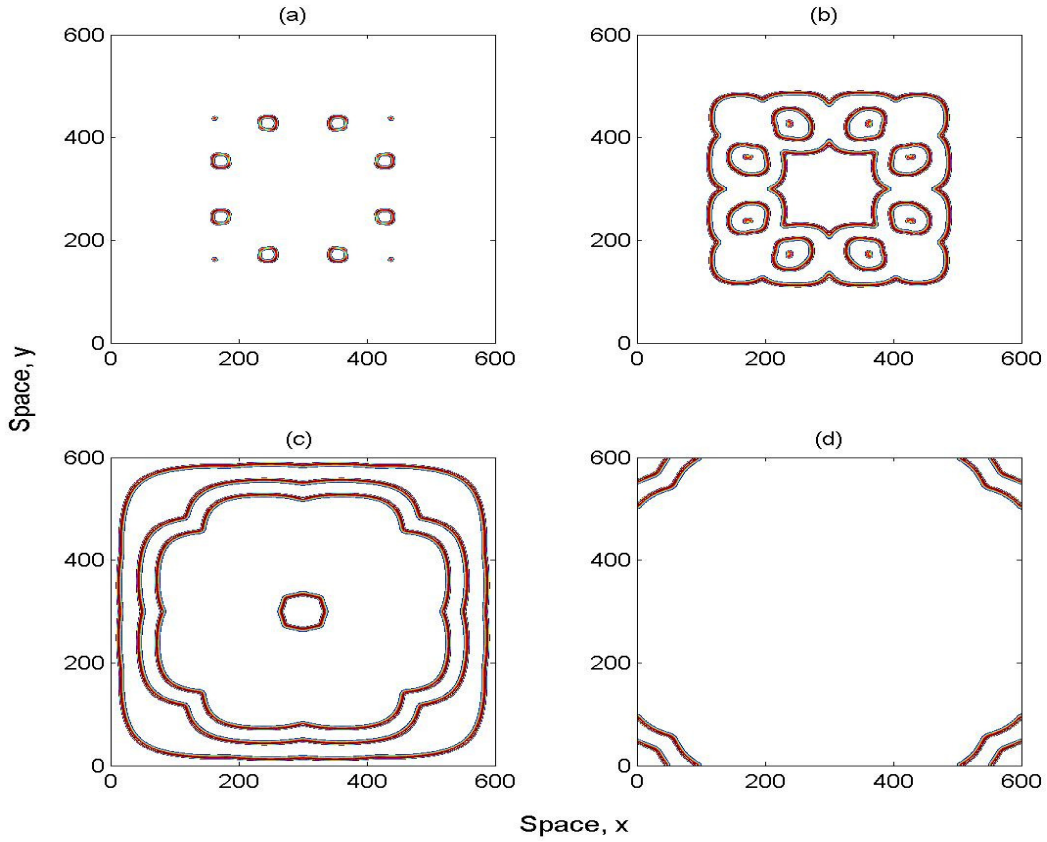


Fig. 3. Spatial distribution of the density of susceptibles, as described by the model (1–2), obtained at (a) $t=0$, (b) $t=50$, (c) $t=150$ and (d) $t=250$ using the distribution shown in Fig. 2a as the initial condition. Parameters are $\gamma=10$, $\beta=0.2$ and $m=0.3$.

A number of attempts have been made to develop a new theoretical framework capable of taking the patchy spread into account (Hengeveld, 1989; Shigesada & Kawasaki, 1997; Lewis & Pacala, 2000; Clark *et al.*, 2001). All of them are based on long jump events when a small group of individuals is carried away (usually, by a vector species or humans) out of the infested area over the distances much longer than the usual short-range dispersal. In this paper, however, we argue that contribution from the long-range dispersal to the gypsy moth spread may be significantly overestimated as the new small colonies would normally be wiped out by the strong Allee effect. Instead, basing on our previous theoretical findings (Petrovskii *et al.*, 2002, 2005; Morozov & Petrovskii, 2006; Malchow *et al.*, 2008), we have shown that the patchy spread of gypsy moth can be a consequence of viral infection by Nuclear Polyhedrosis Virus (NPV). A spatially explicit model of epidemics spread predicts a pattern qualitatively similar to what is observed in field data.

We want to mention it here that the high degree of symmetry of the patterns shown in Fig. 1 is an artifact of over-simplistic properties of the model (1–2). In a more realistic model of epidemics spread taking into account relevant factors such as environmental heterogeneity and/or spatially dependent noise or less symmetric initial conditions, the emerging patchy pattern would not be symmetric (*cf.* Malchow *et al.*, 2008). (A similar comment applies to Fig. 3 as well.) Addressing these issues in detail lies beyond the scope of this paper. Our goal here is to demonstrate that the principal features of the gypsy moth patchy spread can be taken into account in a simple conceptual model, thus highlighting the importance of NPV as an agent of biological control.

Note that the patchy spread predicted by the diffusion-reaction model (1–2) appears to be the mechanism of invasion “at the edge of extinction” (Petrovskii *et al.*, 2005; Morozov & Petrovskii, 2006): a relatively small change in parameter values leads to invasion failure; see Fig. 3 and the last paragraph of the previous section. This conclusion can have important implications for the control and management of the gypsy moth spread. Since NPV is widely used as a component of the biological control strategy (e.g. see Strazanac & Butler, 2005), we assume that the virus-related mortality m can be regarded as a measure of the controlling effort. Correspondingly, our approach predicts that a better result in stopping gypsy moth spread, and possibly even the pest eradication, can be achieved by decreasing the magnitude of the controlling effort rather than increasing it.

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