



Mathematical models of biological invasions

A case study of gypsy moth in North America

Masha Jankovic

University of Leicester

Midlands MESS 2012- May 22, 2012- Birmingham

Contents

- Introduction to Biological invasions
- Gypsy moth- biology and formulation of mathematical model
- SI model results
- Predator prey model results
- Time delay models- introduction and results

A close-up photograph of a raccoon's head and upper body. The raccoon has dark brown fur with a prominent white patch around its black eyes and a white stripe running down its nose. Its ears are upright, and it has a ring of white whiskers. It is clinging to a rough, textured tree trunk with its front paws. The background is blurred green foliage.

Biological invasions

Biological invasions

- When do they occur? When non-native organisms are introduced to a new area beyond their original (native) range
- Biological invasions imply the arrival, establishment and spread of an organism beyond its native range
- Interesting and important to study both from a mathematical and biological viewpoint
- Even though a small percentage of introduced species become pests (**tens rule**), their cumulative effect is and will continue to remain large
- Consequences of biological invasions not only include economic costs but also impacts on ecosystem biodiversity

Biological invasions

- Records show that an outstanding \$137 billion is spent annually to control invasive species and their impact (*Defenders of wildlife*)
- One of the largest programs tackling bio-invasion problems is the SCOPE program
- Culprits behind bio-invasions are the increasing level of world trade and travel
- Human activity aids the overcoming of bio-geographical boundaries which would otherwise be a limiting factor to invasive species

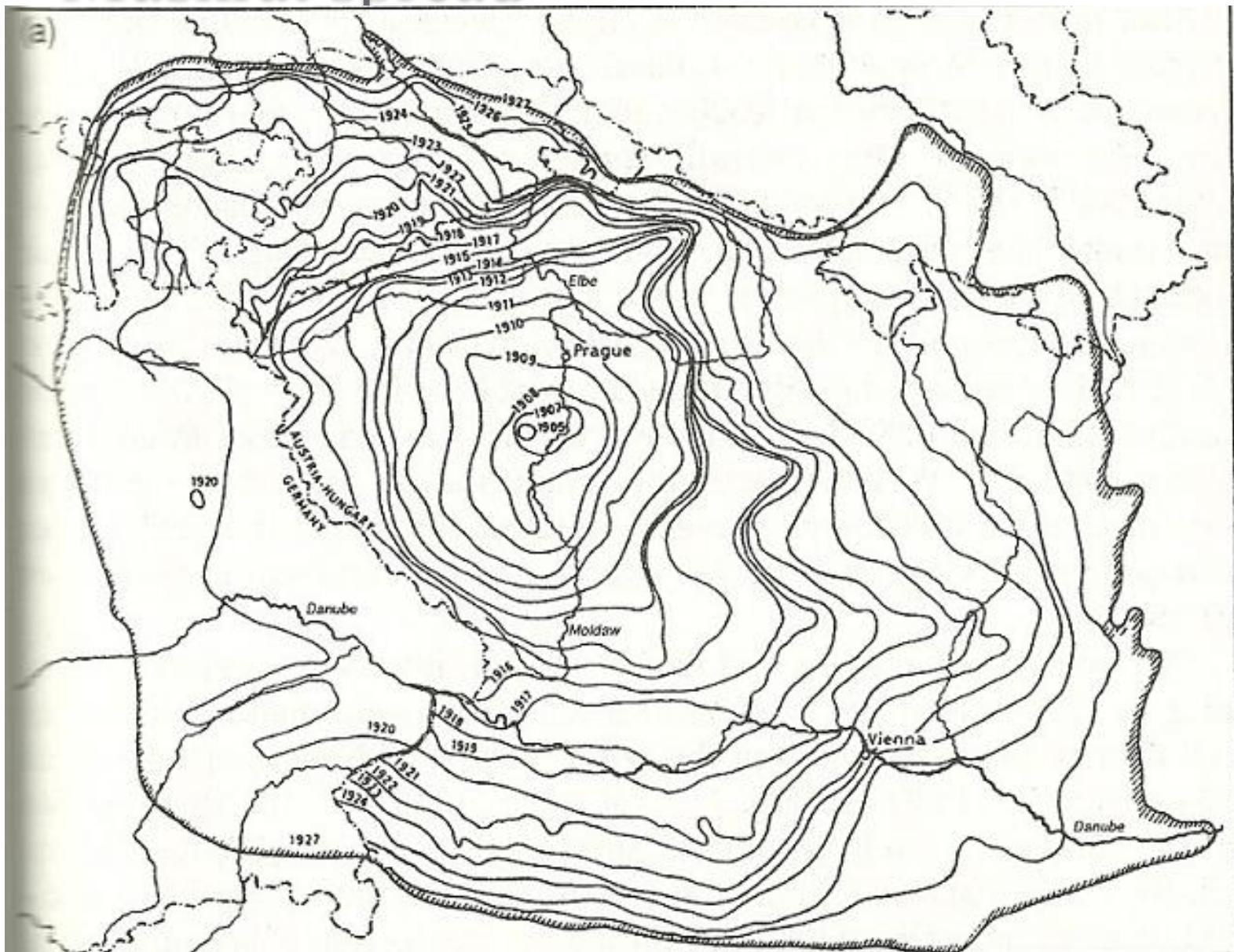
“Not every seed that falls to the ground becomes a tree” (A. Liebhold)

- Upon arrival, exotic species need to overcome certain obstacles to become established (coping with environmental stress, gaining access to resources, mate finding success)
- The role of Allee effect is particularly influential in early stages of establishment, and commonly influences successful invasion (“**Achilles’ heel of invasions**”)
- In the case of Allee dynamics the per capita growth rate is nonmonotonic and can even become negative at low population densities (“**strong**” Allee effect)
- Common causes: inbreeding depression, absence of cooperative feeding, failure to satiate natural enemies, failure in mate finding and temporal asynchrony in reproductive maturing between sexes

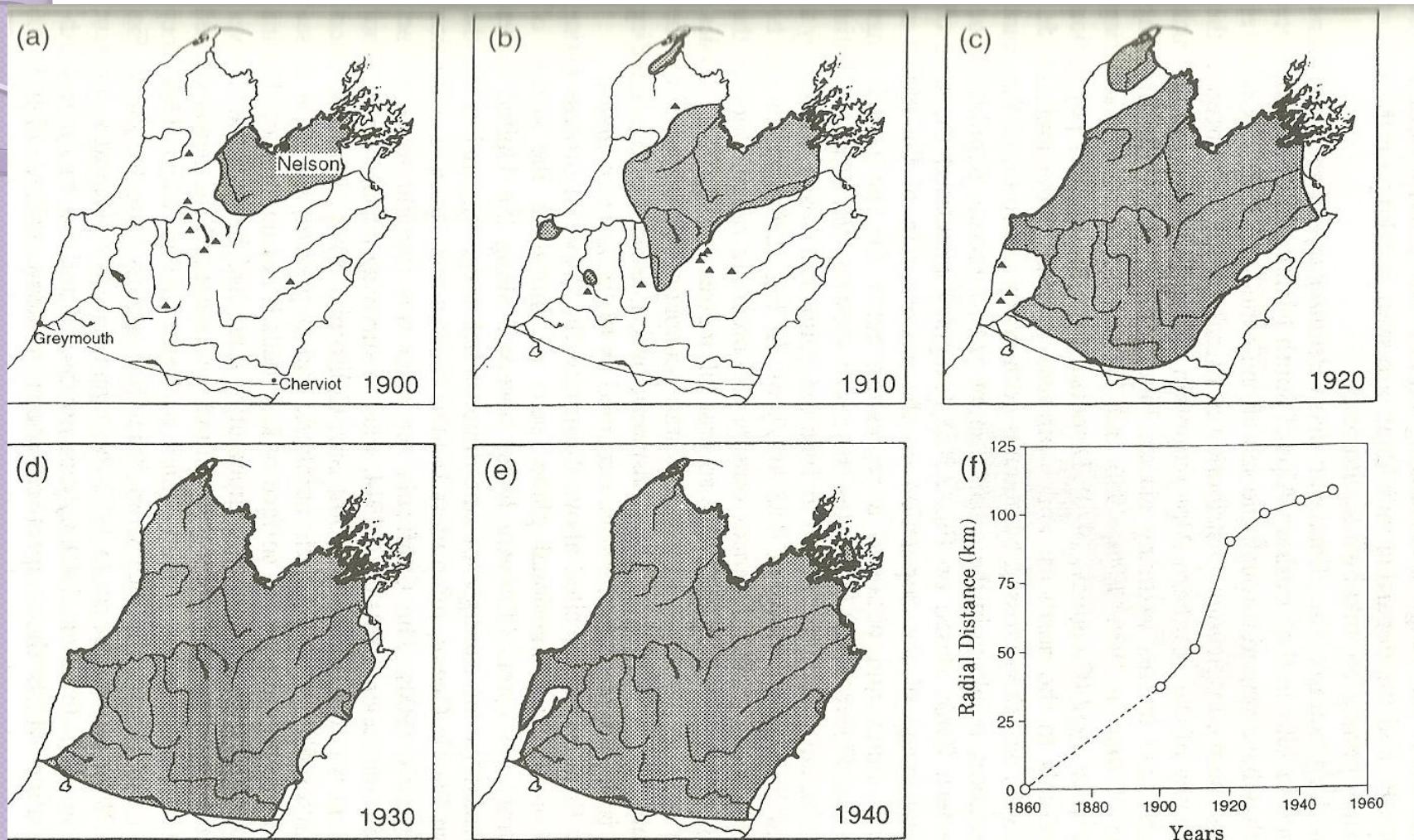
“Let it be remembered how powerful the influence of a single introduced tree or mammal has been shown to be”
(C. Darwin)

- Classic examples of invasion
- Muskrat invasion in central Europe (1909-1927)-11.3km/year average spread rate
- Red deer invasion in New Zealand- annual spread rate 1-4.3km/year
- House finch spread in eastern North America – spread rate 3.5-20.7km/year

Muskrat spread



Red deer invasion



2.2 Spread of red deer in South Island, New Zealand (after Clarke, 1971): (a)–(e) range expansion of red deer from 1900 to (▲, wandering males observed); (f) radial distance of breeding range versus time.

House finch invasion

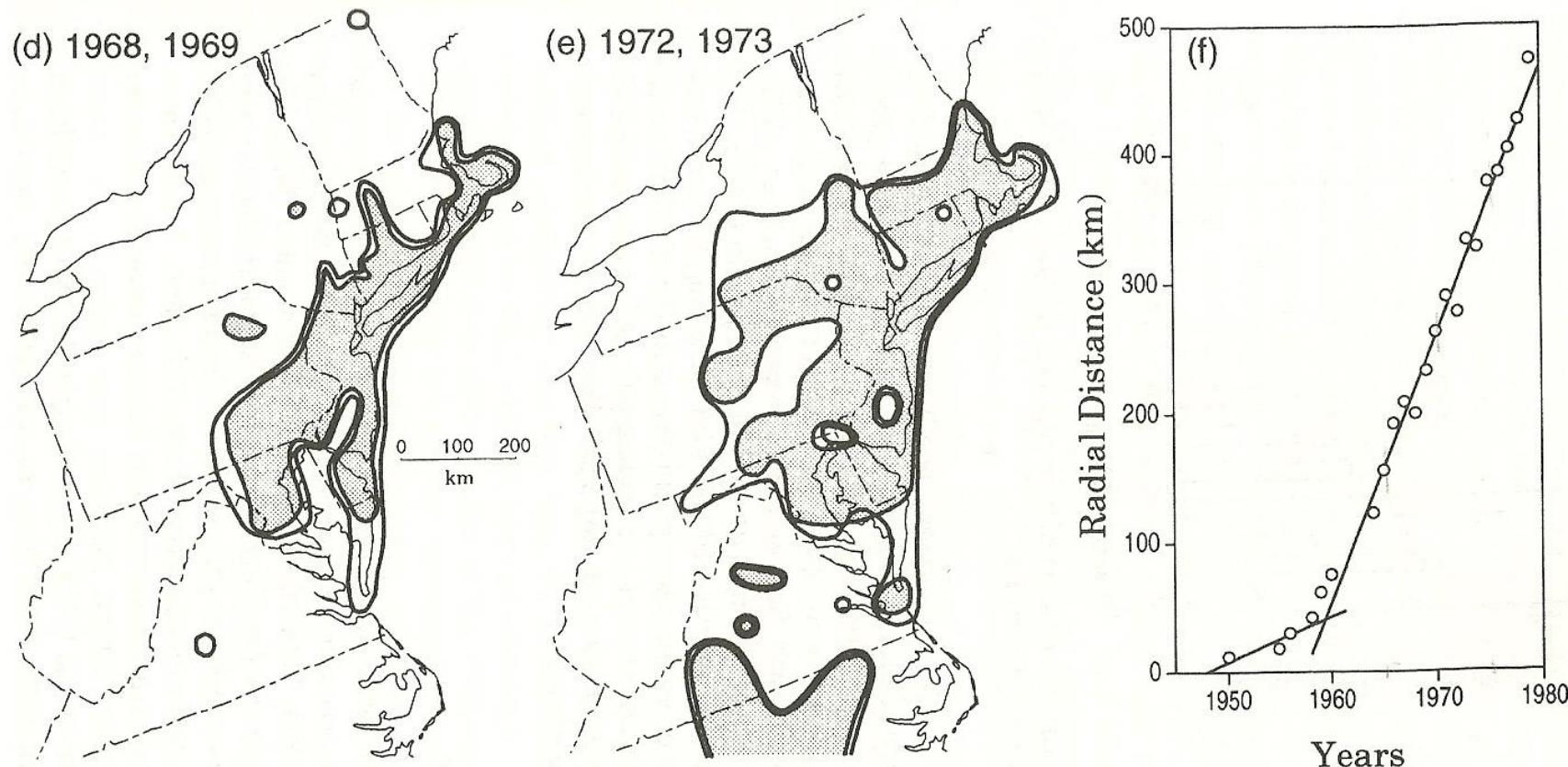


Fig. 2.6 Spread of house finch in eastern North America. (a)–(e) Expansion of winter range for several selected time intervals (after Mundinger and Hope, 1982); shaded and encircled areas represent the earlier and later years, respectively, on each map. (f) Radial distance of winter range versus time from 1950 to 1979. Speed of spread was initially 3.5 km/year, then shifted to a higher constant rate, 20.7 km/year. This calculation excludes another wave of spread that started from North Carolina around 1969 and continued to expand independently until merging with the main range originating from Long Island.



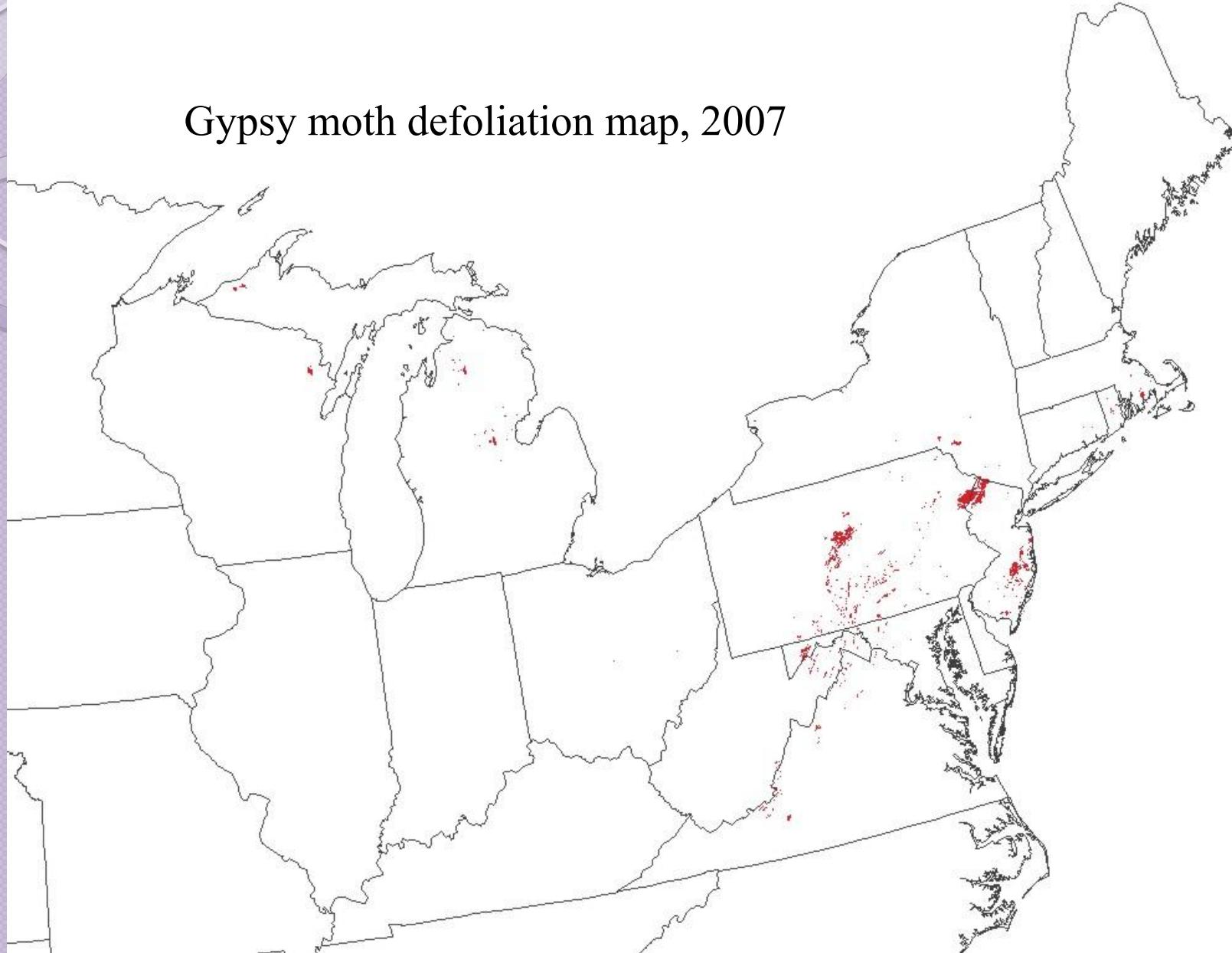
A close-up photograph of a Gypsy moth (Lymantria dispar) resting on a dark, textured surface, likely bark or a rock. The moth's wings are closed, revealing a mottled pattern of light cream, tan, and brownish-grey. Its body is a light cream color with darker, irregular markings. Two long, thin black antennae extend from its head. The background is a mottled grey and green, suggesting a natural outdoor setting.

Gypsy moth

Gypsy moth: introduction

- Introduced in late 1860s and currently occupies all or parts of 19 north-eastern US states
- Since its introduction it has invaded over 1,000,000 km² of north-eastern US
- Eradication of gypsy moth to date has not been successful, and since it occupies roughly a third of its potential habitat, various management strategies are utilised to suppress gypsy moth populations
- Invasive Species Specialist Group (ISSG) has rightfully named it one of a hundred world's worst invasive species

Gypsy moth defoliation map, 2007



source:

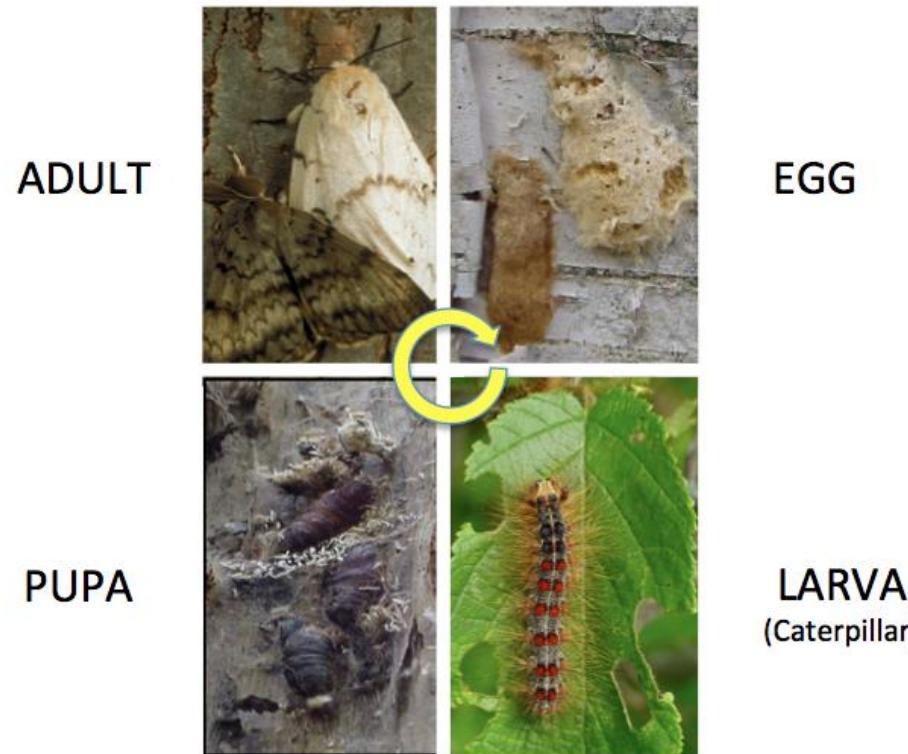
<http://www.fs.fed.us/ne/morgantown/4557/gmoth/atlas/#defoliation>

Gypsy moth: biology

- It is important to have a brief insight into basic biological traits to model gypsy moth invasion
- Well known invasive pest species, a polyphagous herbivore which currently feeds on over 300 tree species
- Like other forest defoliators gypsy moth populations exhibit sporadic outbreaks in which populations undergo fluctuations of several orders of magnitude - “**boom & bust**” dynamics
- Gypsy moth is univoltine (produces one generation per year)
- Females flightless whilst males are capable of flight

Gypsy moth: biology

- Stages of complete metamorphosis include: egg, larval, pupal (cocoon) and adult phase



Gypsy moth: means of spread

- As females are flightless, range distribution and expansion of the gypsy moth is largely reliant on spread mechanisms such as **larval crawling**, **male flight**, **windborne dispersal** of first instars, and increasingly dependent on **artificial dispersal** (human-assisted)
- Larvae crawl up to tree tops and suspend on silken threads awaiting passive wind dispersal (short range)
- Human assisted dispersal yields long range dispersal, and usually involves egg masses
- **Stratified dispersal/diffusion-** combination of different dispersal scales

Gypsy moth: spread rate

- Stratified dispersal leads to the formation of isolated colonies ahead of the initially infested area
- Colonies may grow, coalesce and enhance the spread rate
- Based on historical quarantine data throughout the past century gypsy moth spread rate varies from 2.82-20.78 km/year
- Various barriers and quarantines have been put in place since gypsy moth introduction, and are thought to have suppressed invasion rate
- Higher spread rates are attributed to increased human assisted long range dispersal

Gypsy moth: regulatory mechanisms

- Outbreak populations are regulated and diminished by naturally occurring viral infection Nuclear Polyhedrosis Virus (NPV)
- NPV induces a bi-modal pattern of mortality: early instars become infected with lethal doses of NPV on the surface of egg masses, and mortality occurs usually a week or two after hatch, thus cadavers of these larvae serve as inoculums of infection to older instars, feeding on contaminated foliage, causing a second wave of mortality
- Low density populations are controlled by small mammal predators, most noticeably by the white footed deer mouse

SI model: introduction

- General form of SI model

$$\frac{\partial S(r, T)}{\partial T} = D_1 \nabla^2 S(r, T) + P(S) - E(S, I)$$

$$\frac{\partial I(r, T)}{\partial T} = D_2 \nabla^2 I(r, T) + E(S, I) - MI$$

$S(r, T)$ and $I(r, T)$ - population densities of susceptible and infected populations

$r=(X, Y)$ position in space

$P(S)$ - local growth of susceptibles

$E(S, I)$ - disease transmission

M -mortality of infected

SI model: model assumptions

- Disease transmission occurs only through direct contact between infectious and susceptible individuals
- All susceptible individuals are equally prone to the disease, i.e. are equally at risk of infection
- All infected individuals are equally infectious
- There is no latent (incubation) period of the disease, hence susceptible individuals are instantaneously infected after contact with infected individuals
- Variables and model parameters are age independent

SI model: function choice

- As evidence suggests Allee dynamics is an integral part of gypsy moth populations, hence the local growth function of susceptible individuals has been chosen to be:

$$P(S) = \left(\frac{4\eta}{(K - S_0)^2} \right) S(S - S_0)(K - S)$$

η - maximum per capita growth rate

K- carrying capacity

S_0 -Allee threshold

- If $0 < S_0 < K$ Allee effect is strong, if $-K < S_0 < 0$ the Allee effect is weak, whilst in the case of $S_0 \leq -K$ the Allee effect is absent

SI model: function choice

- In epidemic modelling the form of the transmission function is always a sensitive and above all a key element in host pathogen interactions
- For our modelling purposes we have chosen the mass action assumption, yielding a constant transmission rate:

$$E(S, I) = ASI$$

A is the transmission parameter

- Studies utilising this form of transmission reproduced plausible results for high density gypsy moth populations, comparable with actual field studies

SI model

- For modelling purposes, simplifying numerical simulations we scale our SI model to dimensionless variables, thereby decreasing the number of parameters:

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

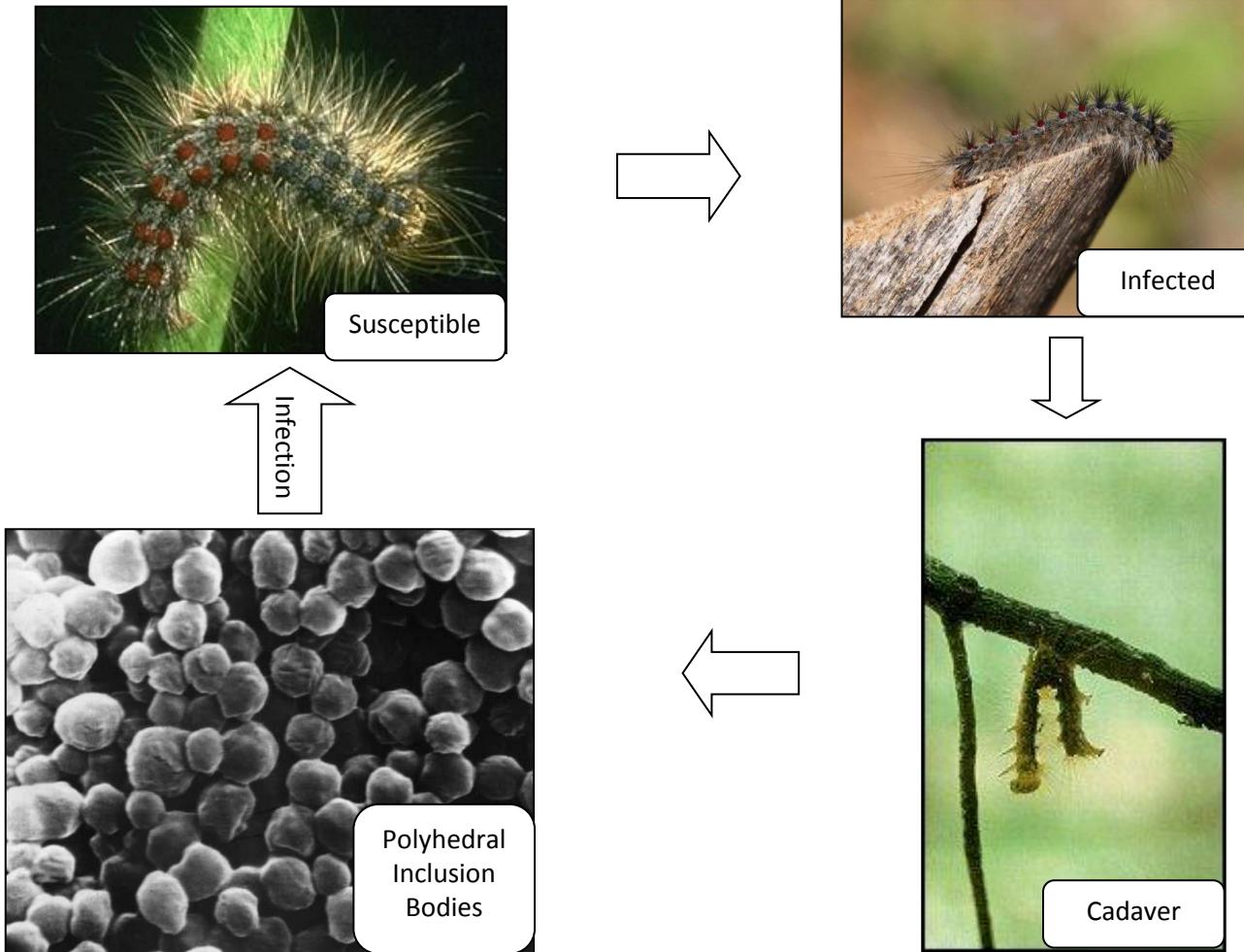
$$\frac{\partial i(x, y, t)}{\partial t} = \epsilon \left(\frac{\partial^2 i}{\partial x^2} + \frac{\partial^2 i}{\partial y^2} \right) + si - mi$$

$$s = S/K, i = I/K, a = AK, x = X(a/D_1)^{1/2}, y = Y(a/D_1)^{1/2}, t = aT, \beta = S_0/K, \gamma = 4\eta K/(A(K - S_0)^2), m = M/a \text{ and } \epsilon = D_2/D_1.$$

- The sum $s+i$ represents the total population density, whereas the product si now depicts the disease transmission rate from infected to susceptible individuals.

SI model: infection occurrence cycle

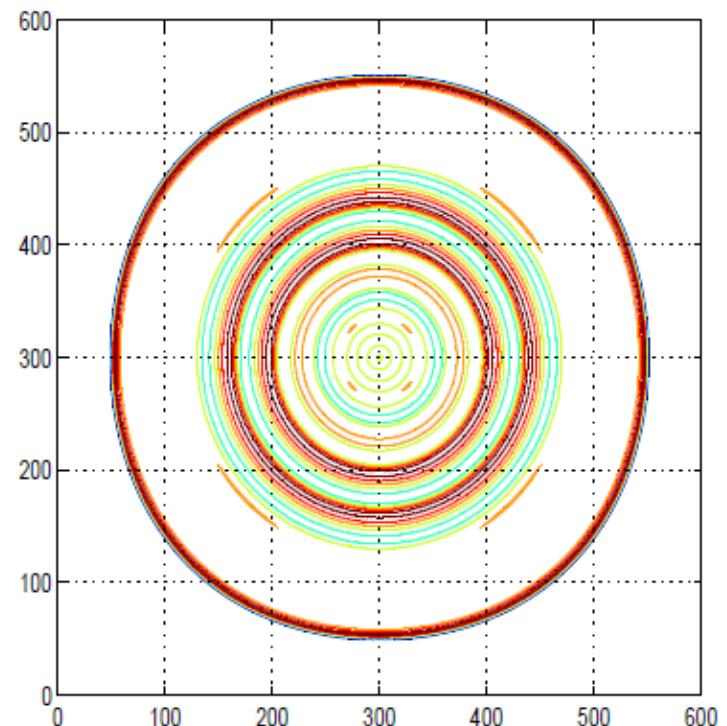
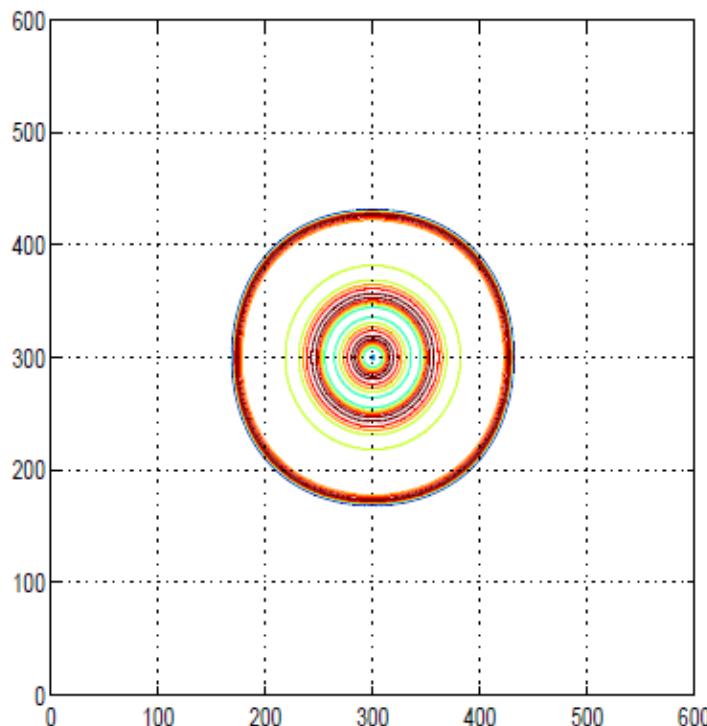
Infection occurrence cycle



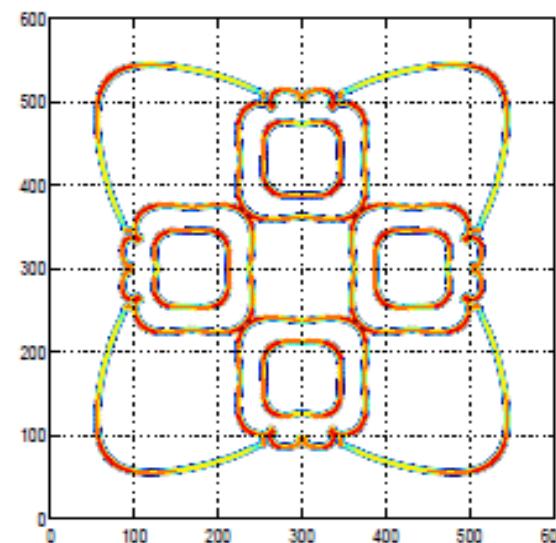
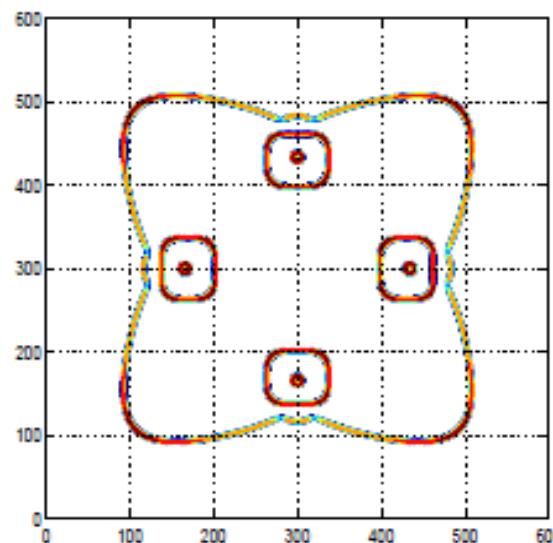
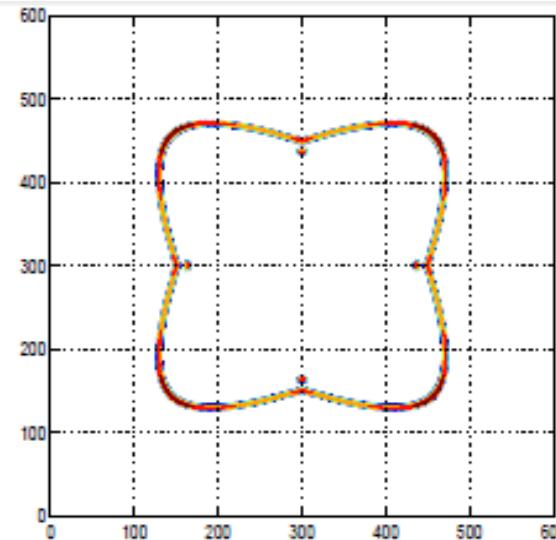
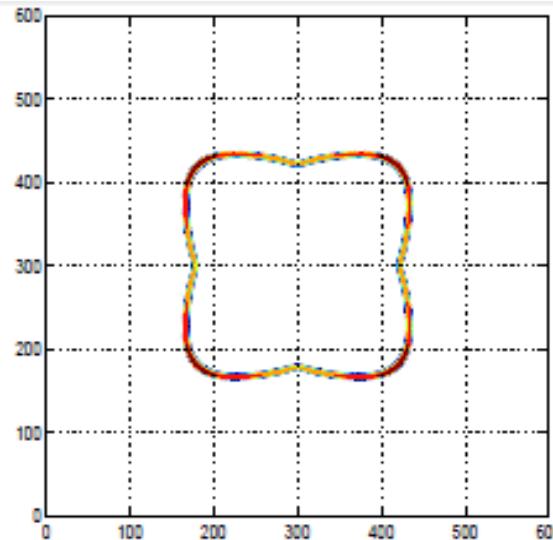
SI model: model properties and behaviour

- SI model was solved by implementing the explicit forward Euler scheme
- Mesh steps used: $\Delta t = 0.1$, $\Delta x = \Delta y = 1$
- Numerical domain is square-shaped with length L , so that $0 < x < L$ and $0 < y < L$, with Neumann “no flux” conditions set at the boundaries
- Initially the populations are assumed to be homogeneously distributed with $s + i = 1$, within a square domain such that $|x| < \Psi$ and $|y| < \Psi$.
- Centred inside this domain, another sub-domain is placed ($|x| < \Omega$, $|y| < \Omega$) with a portion, K , of infected individuals ($0 < K < 1$).

SI model: simulation results

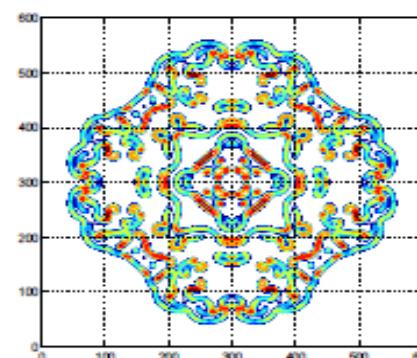
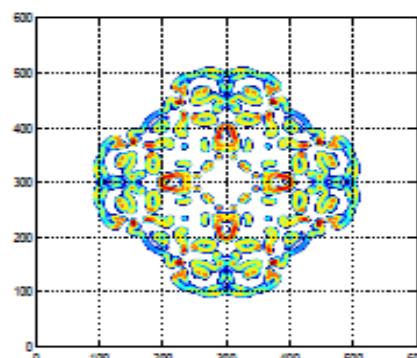
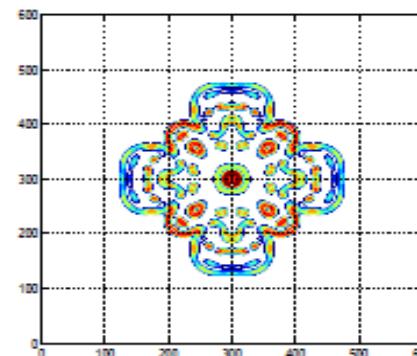
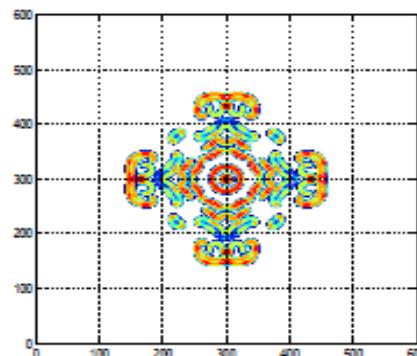
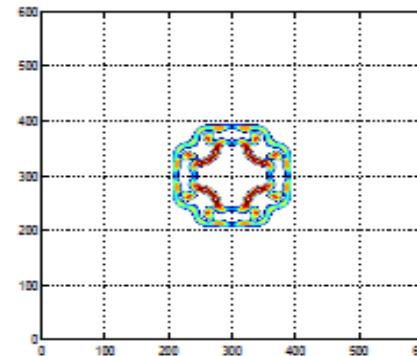
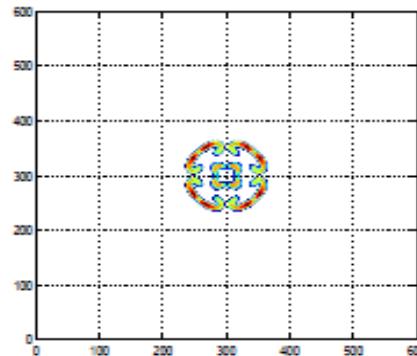


Snapshots of the susceptible population density at times $t = 200$ and $t = 400$, respectively. Propagation occurs through circular expanding fronts, with the parameter set used in simulations: $\gamma = 3$ and $m = 0.57$.

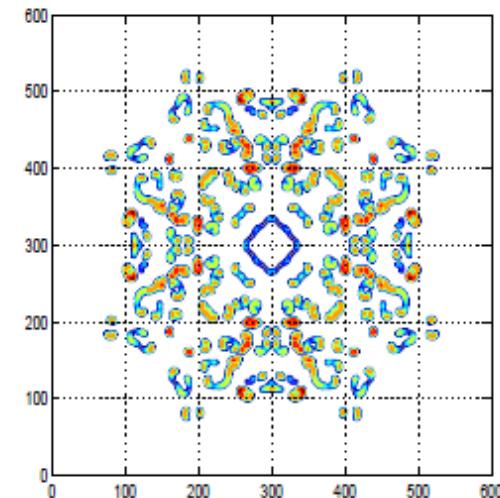
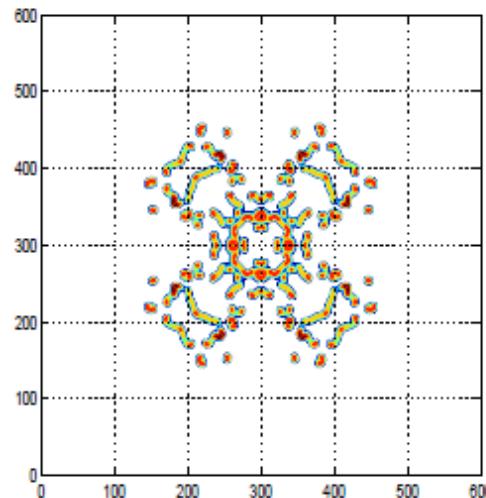
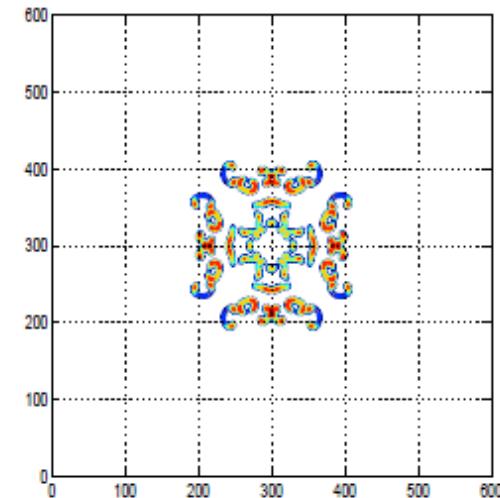
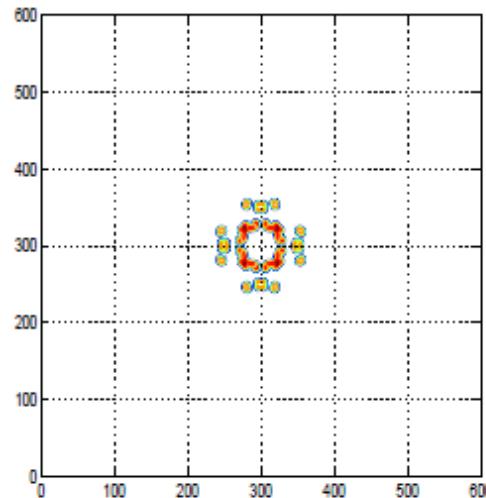


Snapshots of susceptible population show slightly distorted continuous fronts, with slight “butterfly” appearance, at $t=150$, $t=200$, $t=250$ and $t=300$. Parameter set used in simulations: $\gamma = 9.5$ and $m = 0.31$

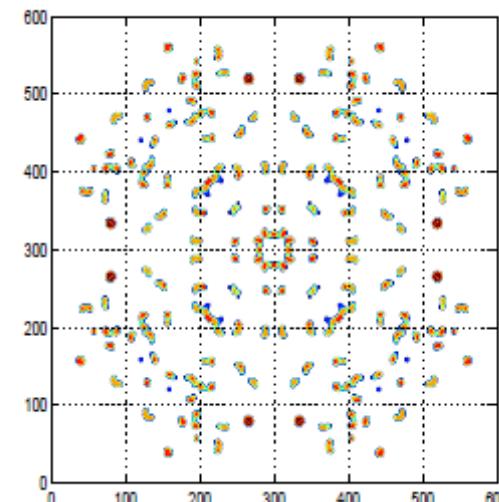
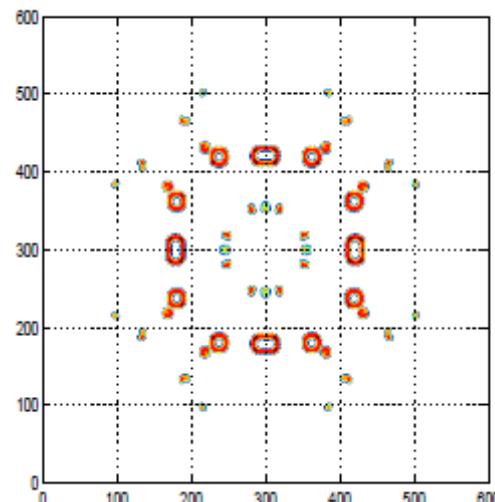
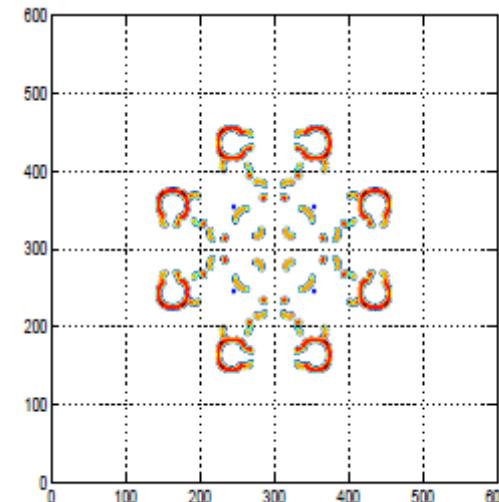
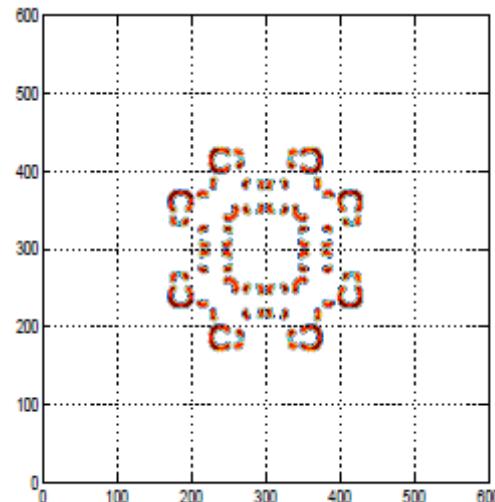
SI model: transitional dynamics



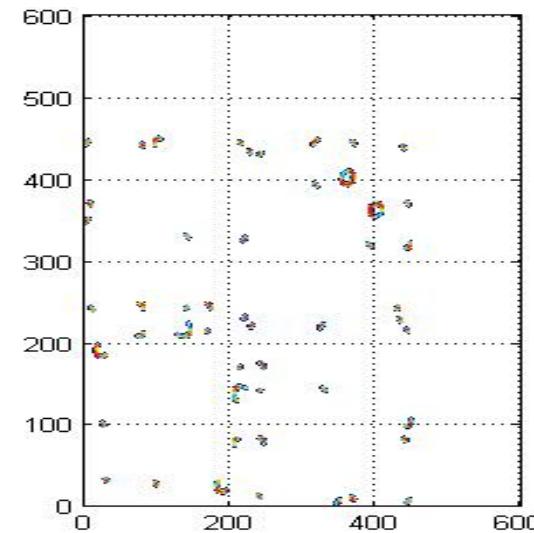
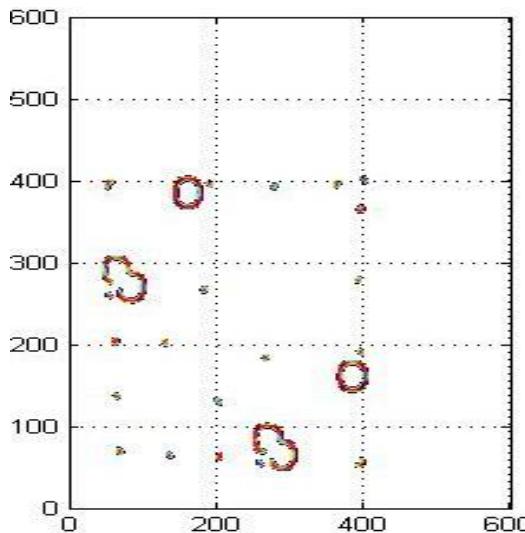
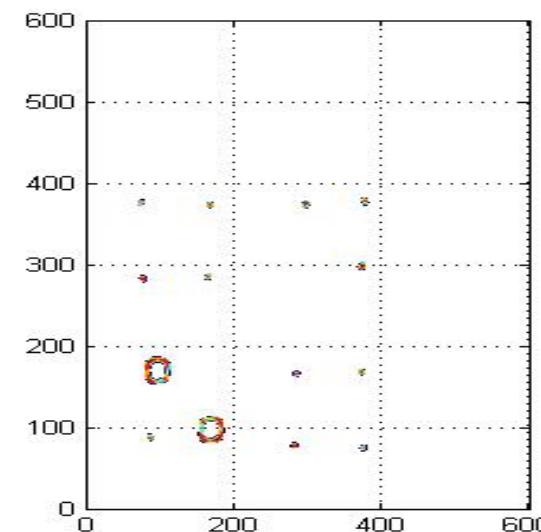
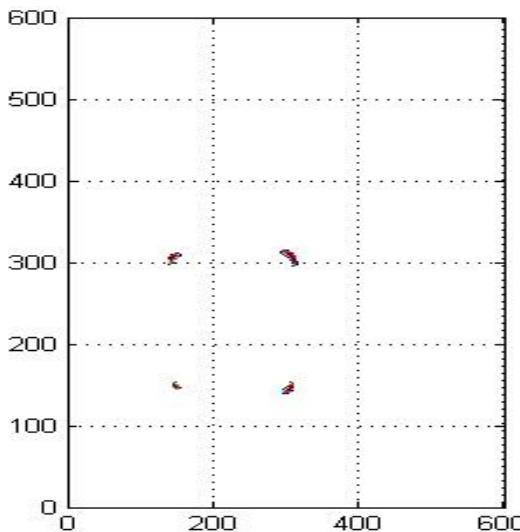
SI model: patchy dynamics



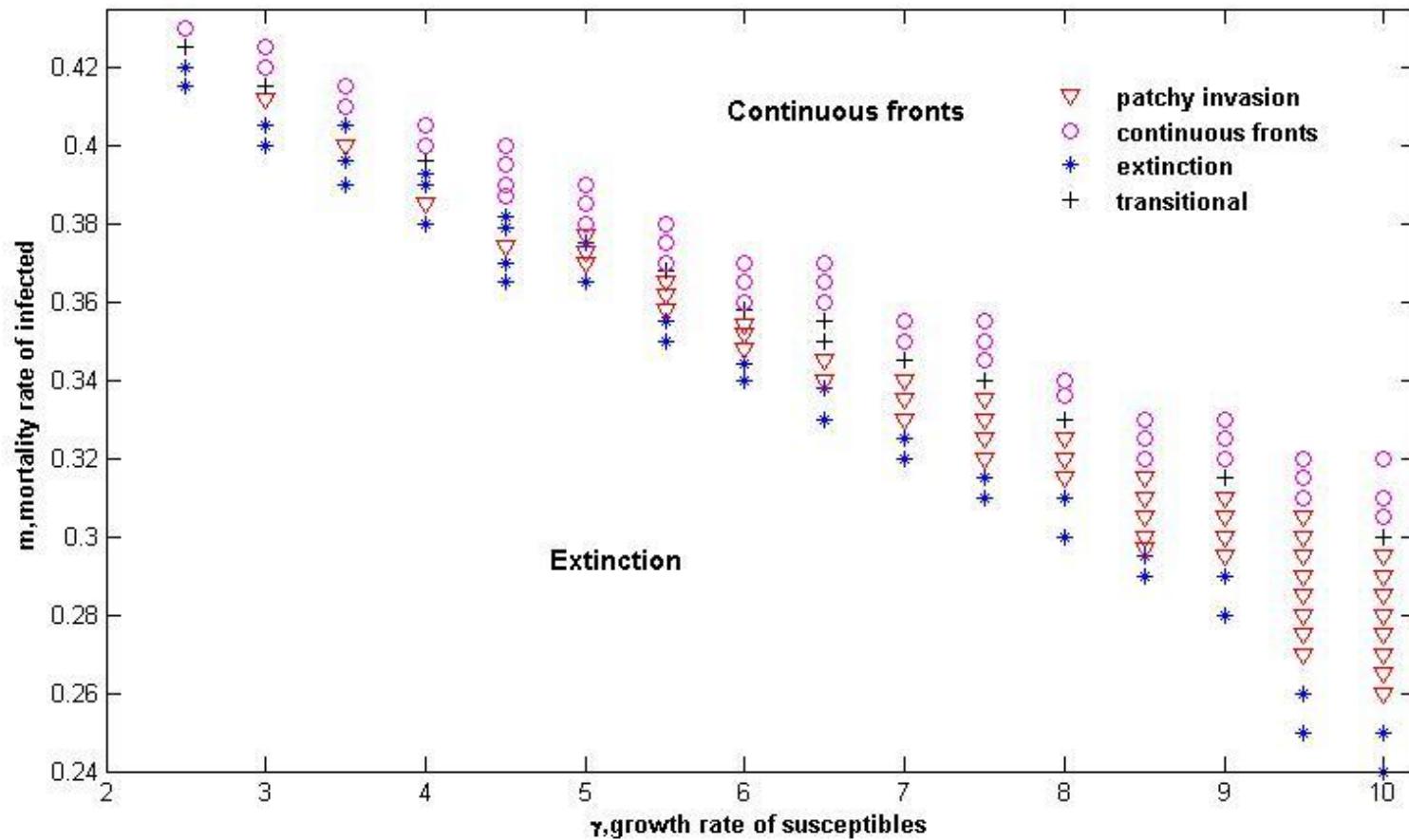
SI model: patchy dynamics



SI model: asymmetric initial conditions



SI model: simulation results



All simulation results were obtained for the following set of parameters: $\beta = 0.2$, $\Psi = 10$, $\Omega = 5$ and $K = 0.5$.

SI model: parameter estimation

- The main objective of modelling gypsy moth population dynamics with the SI model, was to estimate the rate of spread:

$$\frac{\Delta X}{\Delta T} = \frac{\Delta x}{\Delta t} \sqrt{a D_1} \quad [\text{km/year}]$$

$\Delta x/\Delta t$ presents the dimensionless rate of spread, and $\sqrt{a D_1}$ is the scaling factor

- The results are going to be as good as the weakest link, which is parameter estimation

Table 1: Summary of parameter estimates. Estimates for the transmission coefficient are given in $m^2/\text{PIB day}$ units.

Parameter	Species	Parameter Estimate	Reference
Transmission coefficient, A	<i>Lymantria dispar</i>	1.7×10^{-12}	<i>Barlow et al. (2000)</i>
	<i>Orygia pseudotsugata</i>	$0.01 - 6.82 \times 10^{-9}$	<i>Dwyer (1991)</i>
	<i>Lymantria dispar</i>	$2.12 - 13.1 \times 10^{-12}$	<i>D'Amico et al. (1996)</i>
	<i>Lymantria dispar</i>	1.45×10^{-12}	<i>Dwyer and Elkinton (1993)</i>
	<i>Lymantria dispar</i>	1.45×10^{-10}	<i>Elkinton et al. (1995)</i>
	<i>Orygia pseudotsugata</i>	1×10^{-9}	<i>Vesina and Peterman (1985)</i>
	<i>Spodoptera exempta</i>	$3.38 - 6.65 \times 10^{-12}$	<i>Reeson et al. (2000)</i>
Diffusion coefficient, D_1	<i>Mamestra brassicae</i>	2.16×10^{-12}	<i>Goulson et al. (1995)</i>
	<i>Lymantria dispar</i>	$0.003 \text{ km}^2/\text{generation}$	<i>Liebhold and Tobin (2006), Robinet et al. (2008)</i>
	<i>Battus philenor</i>	$239 \text{ m}^2/\text{day}$	<i>Kareiva (1983)</i>
	<i>Lymantria dispar</i>	0.1 ha/year	<i>Wilder et al. (1995)</i>
	<i>Orygia pseudotsugata</i>	$0.0274 \text{ m}^2/\text{day}$	<i>Dwyer (1992)</i>
	<i>Lymantria dispar</i>	332 m/generation	<i>Liebhold et al. (1992)</i>
	NPV	0.003 day^{-1}	<i>Barlow et al. (2000), Dwyer and Elkinton (1993)</i>
Disease decay rate, M	NPV	0.002 day^{-1}	<i>Dwyer (1992)</i>
	NPV	4.8 year^{-1}	<i>Vesina and Peterman (1985)</i>
	<i>Lymantria dispar</i>	283 moth/trap	<i>Tobin et al. (2007)</i>
	<i>Lymantria dispar</i>	673 moth/trap	<i>Tobin et al. (2007)</i>
	<i>Lymantria dispar</i>	687 moth/trap	<i>Johnson et al. (2006)</i>
	<i>Lymantria dispar</i>	$200\,000 \text{ egg masses/km}^2$	<i>Sharov and Liebhold (1998)</i>
	<i>Lymantria dispar</i>	500 larva/m^2	<i>Dwyer and Elkinton (1993)</i>
Carrying capacity, K	<i>Lymantria dispar</i>	2.2 moth/trap	<i>Tobin et al. (2007b)</i>
	<i>Lymantria dispar</i>	20.7 moth/trap	<i>Tobin et al. (2007b)</i>
	<i>Lymantria dispar</i>	17 moth/trap	<i>Johnson et al. (2006)</i>
	<i>Lymantria dispar</i>	$106.7 \text{ male moth/colony}$	<i>Liebhold and Bascompte (2003)</i>
	<i>Lymantria dispar</i>	2×10^9	<i>Barlow et al. (2000)</i>
	<i>Orygia pseudotsugata</i>	10^7	<i>Dwyer (1991)</i>
	<i>Lymantria dispar</i>	2×10^9	<i>Dwyer and Elkinton (1993)</i>
Allee threshold, S_0	<i>Lymantria dispar</i>	4×10^8	<i>Elkinton et al. (1995)</i>
	<i>Orygia pseudotsugata</i>	$1 \times 10^7 - 4 \times 10^8$	<i>Vesina and Peterman (1985)</i>
Number of virus particles produced per larval cadaver			

SI model: parameter estimation

- Dimensionless spread rate $\Delta x / \Delta t$ is estimated to be ≈ 0.8 , corresponding to simulations based on parameter set $\gamma = 10$ and $m = 0.26$ (patchy invasion), and was kept constant throughout spread rate estimation attempts.
- Scaling factor $\sqrt{aD_1}$ determined the upper and lower bounds of spread rate estimate range
- Diffusion coefficient was chosen to be $D = 3 \times 10^3 \text{ m}^2/\text{year}$
- Carrying capacity was kept at 500 larvae/m^2
- Transmission parameter varied, but was scaled to a constant number of PIBs released by larval cadavers (2×10^9)
- Allee threshold in simulations was taken to be 0.2

SI model: parameter estimation

- Upper and lower bound of our estimated spread rate:

$$\begin{aligned} \text{Rate of spread} = \frac{\Delta X}{\Delta T} &= 0.8 \times (1.7 \times 10^{-12} \times 70 \text{ m}^2/\text{PIByear} \times 2 \times 10^9 \text{ PIB/larva} \\ &\quad \times 500 \text{ larva/m}^2 \times 3 \times 10^3 \text{ m}^2/\text{year})^{1/2} \\ &\approx 478 \text{ m/year} \approx 0.48 \text{ km/year}. \end{aligned}$$

$$\begin{aligned} \text{Rate of spread} = \frac{\Delta X}{\Delta T} &= 0.8 \times (1.45 \times 10^{-10} \times 70 \text{ m}^2/\text{PIByear} \times 2 \times 10^9 \text{ PIB/larva} \\ &\quad \times 500 \text{ larva/m}^2 \times 3 \times 10^3 \text{ m}^2/\text{year})^{1/2} \\ &\approx 4414 \text{ m/year} \approx 4.4 \text{ km/year}. \end{aligned}$$

Predator prey model: introduction

- General form of model:

$$\frac{\partial U(r,T)}{\partial T} = D_1 \nabla^2 U(r,T) + F(U) - f(U,V)$$

$$\frac{\partial V(r,T)}{\partial T} = D_2 \nabla^2 V(r,T) + \kappa f(U,V) - MV$$

$U(r,T)$ and $V(r,T)$ - population densities of prey and predator populations

$r=(X,Y)$ position in space

$F(U)$ - local prey growth

$f(U,V)$ - predation term

κ - food utilisation coefficient

M -mortality of predator

Predator prey model: function choice

- In our case $f(U,V)$ involves a Holling type II trophical response:

$$f(U,V) = \frac{AV}{U + B}$$

- Whilst the local prey growth function is chosen to be damped by the Allee effect:

$$F(U) = \left(\frac{4\nu}{(K - U_0)^2} \right) U(U - U_0)(K - U)$$

Predator prey model

- For convenience we introduce dimensionless variables, so our model is of following form:

$$\frac{\partial u(x, y, t)}{\partial t} = \left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + \gamma u(u - b)(1 - u) - \frac{uv}{1 + \lambda u}$$
$$\frac{\partial v(x, y, t)}{\partial t} = \epsilon \left(\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + \frac{uv}{1 + \lambda u} - \mu v$$

with $u = U/K$, $v = V/K$, $a = A\mathbf{K}/B$, $x = X(a/D_1)^{1/2}$, $y = Y(a/D_1)^{1/2}$,
 $t = aT$, $\lambda = K/B$, $b = U_0/K$, $\gamma = 4VBK/(A\mathbf{K}(K - U_0)^2)$, $\mu = M/a$
and $\epsilon = D_2/D_1$

Predator prey model

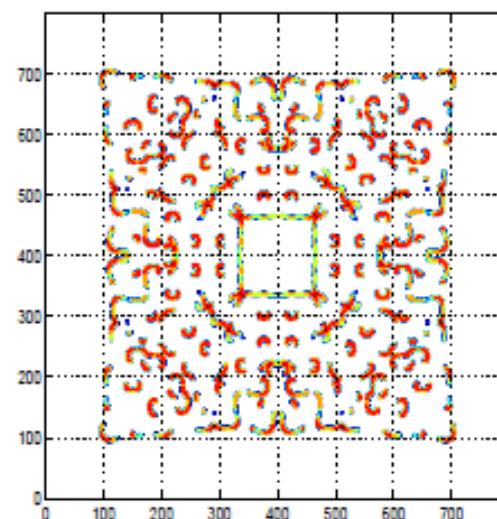
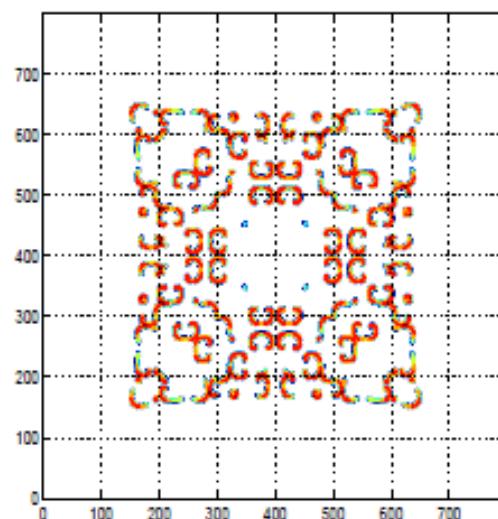
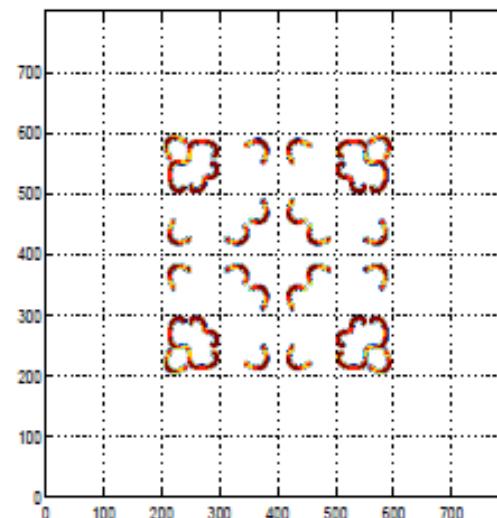
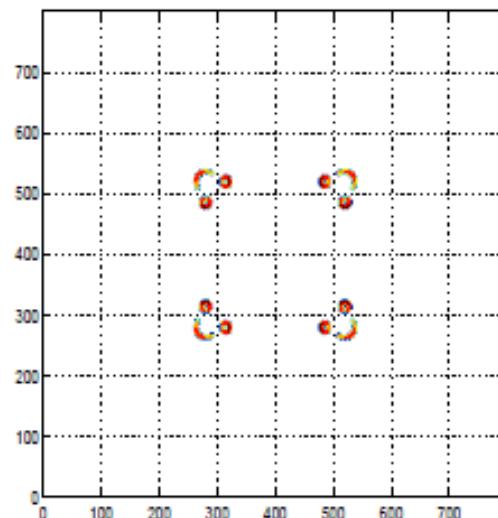
- Initial conditions of predator prey model are functions of compact support:

$$u(x, y, 0) = u_0 \text{ if } x_{11} < x < x_{12} \text{ and } y_{11} < y < y_{12} \text{ otherwise } u(x, y, 0) = 0$$

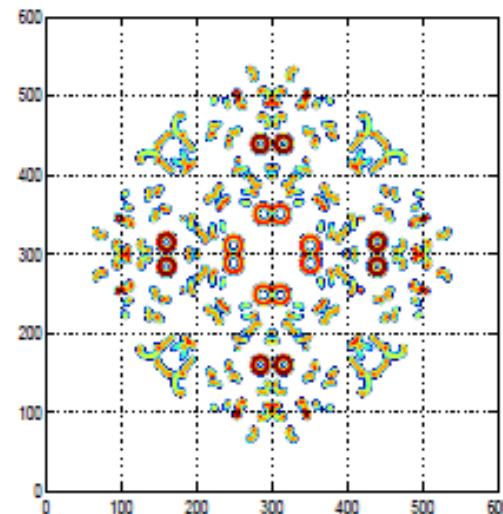
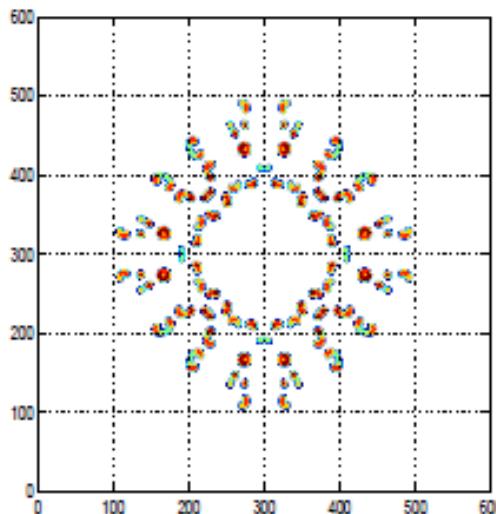
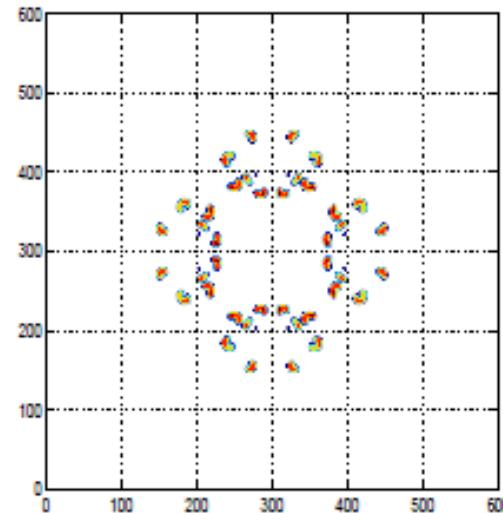
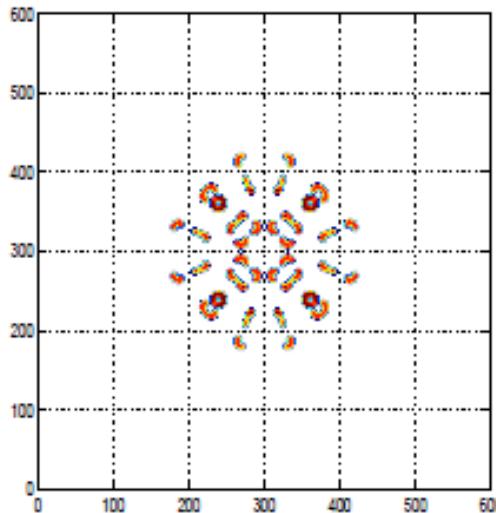
$$v(x, y, 0) = v_0 \text{ if } x_{21} < x < x_{22} \text{ and } y_{21} < y < y_{22} \text{ otherwise } v(x, y, 0) = 0$$

- Model was solved using the explicit Euler scheme with mesh steps $\Delta x = \Delta y = 1$, $\Delta t = 0.1$
- Neumann “no flux” conditions are implemented at boundaries
- Throughout simulations $\varepsilon = 1$

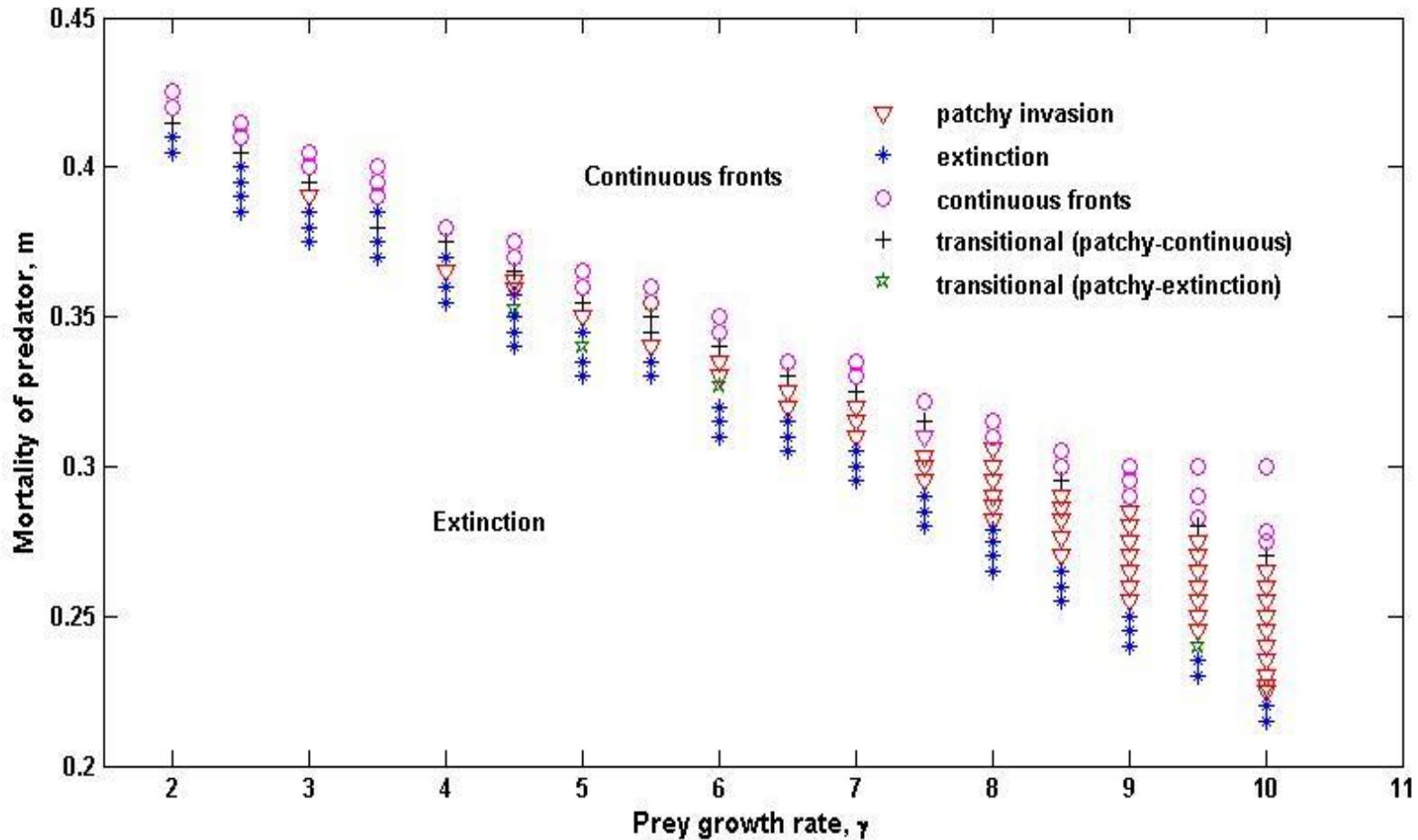
Predator prey model: simulation results



Predator prey model: simulation results



Predator prey model: simulation results



Parameter set used in simulations: $\lambda = 0.1$ and $b = 0.2$

Brief summary of results

- As can been seen, using the SI model we were able to reproduce not only the pattern but also the rate of spread of gypsy moth as indicated by field and historical data
- Using the predator prey model we have been able to reproduce the pattern of spread of gypsy moth populations
- Ideas for future work include formulating both epidemics and predation as regulatory mechanisms controlling gypsy moth populations and incorporating artificial dispersal in model as well

Picture references

- <http://www.sciencedaily.com/releases/2010/12/101220150804.htm>
- Shigesada N, Kawasaki K (1997) Biological invasions: theory and practice. Oxford University Press
- <http://www.butterfly-conservation.org/Moth/440/Moth.html?MothId=182>
- <http://www.fs.fed.us/ne/morgantown/4557/gmoth/atlas/#defoliation>

Thank you for listening

