Recall

no heterogeneity

$$N_{t+1}(x) = \int_{-\infty}^{\infty} K(x-y) F(N_t(y), y)\, dy$$

Landscape heterogeneity and the spread of forest insects

heterogeneity

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University of Ottawa

University of Ottawa

March 2017

Forest Insects can do massive damage Aukema et al 2011

OPEN ACCESS Freely available online PLoS one

Economic Impacts of Non-Native Forest Insects in the Continental United States

Juliann E. Aukema[1*], Brian Leung[2,3], Kent Kovacs[4], Corey Chivers[2], Kerry O. Britton[5], Jeffrey Englin[6], Susan J. Frankel[7], Robert G. Haight[8], Thomas P. Holmes[9], Andrew M. Liebhold[10], Deborah G. McCullough[11], Betsy Von Holle[12]

Gypsy Moth

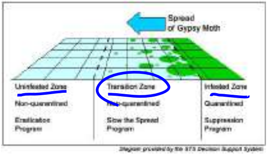
Emerald Ash borer

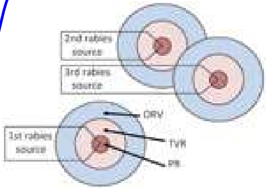
Asian Longhorn beetle

Beech scale

Ways to control?

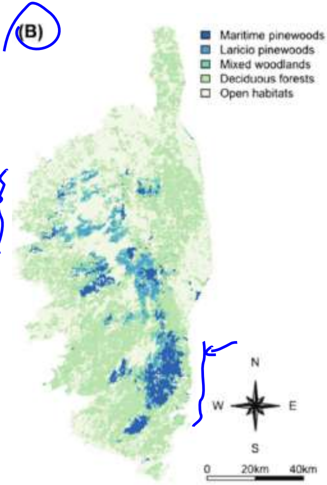
- large-scale chemicals: kill the pest
  expensive, harmful, limited success Liebhold and Tobin 2008
- biological control agent
- local detection and control Sharov et al 2002
  - barrier zones (‘detect early and act locally’)
  - manipulation of landscape structure
  - ‘fire breaks’ and ‘ring vaccination’ With 2002





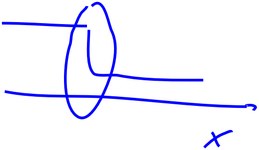
Silvicultural measures Liebhold 2012

- reduce or remove resources
  - if organism is host specific
    Brockerhoff et al 2010
  - Ontario ash-free zone failed
    10×30 km
  - theoretical and empirical support
    With 2004, Rigot et al 2014
  - buffer zones around wind throw
    Nikolov et al 2014
- thinning: increase tree vigor
  Liebhold 2012
- increase diversity
  Brockerhoff et al 2006, Jactel et al 2005, Rigot et al 2014
  - resource concentration hypothesis
  - enemy release hypothesis



Organisms adjust movement behaviour

behaviour ?



Edge effects

- Insects: increase residence time in host patch

  Ries and Debinski, Schultz and Crone, Reeve and Cronin ...

- Birds: gap crossing probability

  Creegan and Osborne, Robertson and Redford...

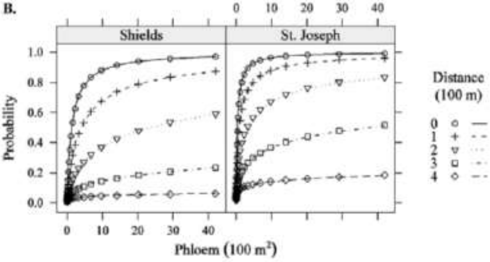
- Mammals: carnivores and linear features

  Whittington et al, McKenzie et al...

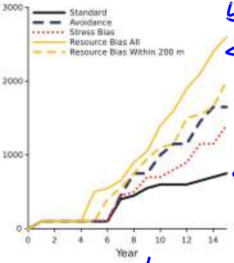
Organisms adjust movement behaviour

Invasion-dynamic consequences

- observation of increased dispersal distances Siegert et al 2010
- simulation shows faster spread at equal total phloem Mercader et al 2011 a,b



front



bias

K(x-y)

time

Make a model!

Overview

1. The model
   - Population dynamics
   - Movement
2. Analysis
   - Persistence
   - Spread
3. Results
   - Movement and persistence
   - Movement and spread rate
4. Discussion

Population dynamics

egg deposition $\xrightarrow{\textit{survival}}$ larval development $\xrightarrow{\textit{consumption}}$ reproductive adults $\xrightarrow{\textit{oviposition}}$

egg survival: s
phloem requirement: $\bar{P}$
egg production: r
phloem reduction: w

$$\text{eggs} \quad E_{t+1} = \frac{r}{2}\left(1 - e^{-P_t/\bar{P}}\right) sE_t,$$

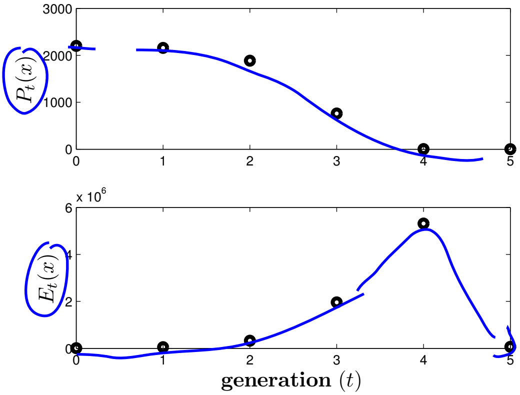
$$\text{phloem} \quad P_{t+1} = P_t e^{-wsE_t}.$$

No re-growth of phloem

Dynamics of the population model

$$E_{t+1} = \frac{r}{2}\left(1 - e^{-P_t/\bar{P}}\right) sE_t$$

$$P_{t+1} = P_t e^{-wsE_t}$$



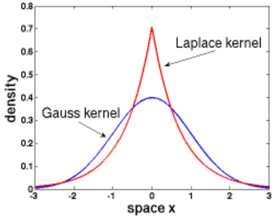
Musgrave 2013

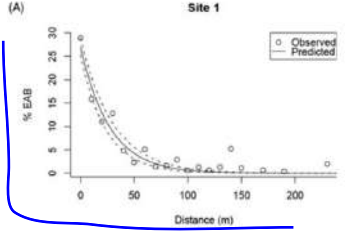
The growth-dispersal model Musgrave and L (2017) Ecology

$$E_{t+1}(x) = \int K(x,y)\frac{r}{2}\left(1 - e^{-P_t(y)/\bar{P}}\right) sE_t(y)dy,$$

$$P_{t+1}(x) = P_t(x)e^{-wsE_t(x)}.$$

Dispersal kernel $K(x,y)$: probability of moving from y to x



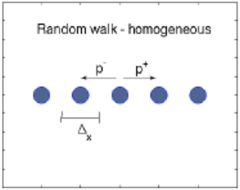


Mercader et al 2009

Heterogeneity?

Movement behaviour – the random walk Turchin (1998)

$p^{\pm}$: right/left probability
ξ: space step
τ: time step



Master equation:

$$u(t+\tau,x) = [1-(p^{+}+p^{-})]u(t,x) + p^{+}u(t,x-\xi) + p^{-}u(t,x+\xi)$$

Diffusion limit ($p^{+} = p^{-}$):

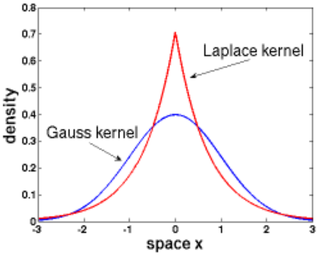
$$\frac{\partial}{\partial t}u(t,x) = D\frac{\partial^2}{\partial x^2}u(t,x) \qquad D = \lim_{\tau,\xi\to 0}\frac{(p^{+}+p^{-})\xi^2}{2\tau}$$

Kernels in homogeneous landscape

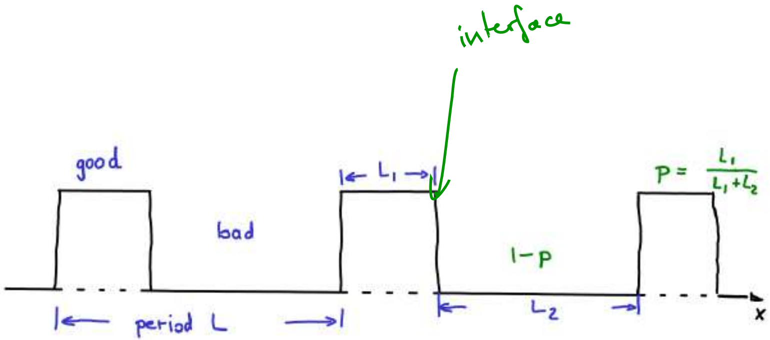
$$\frac{\partial}{\partial t}u(t,x) = \underbrace{D\frac{\partial^2}{\partial x^2}u(t,x)}_{movement} - \underbrace{m(t)u(t,x)}_{oviposition}, \qquad u(0,x) = \delta(x)$$

$$K(x,0) = \int_0^\infty m(t)u(t,x)dt$$

1. $m(t) = \delta(t - t_0)$
   $\Rightarrow$ Gaussian
2. $m(t) = m$
   $\Rightarrow$ Laplace



Two types of patches



Shigesada et al (1986) TPB

$$\frac{\partial}{\partial t} u = \cancel{D} \frac{\partial^2}{\partial x^2}\left(D(x) u\right) - m(x) u$$

$$D = \begin{cases} D_1 & \text{if } x \in \text{good} \\ D & \text{if } x \in \text{bad} \end{cases}$$

Equations and matching conditions

Good patches

$$\frac{\partial u}{\partial t} = D_1 \frac{\partial^2 u}{\partial x^2} \cancel{+ r_1 u}$$

Bad patches

$$\frac{\partial u}{\partial t} = D_2 \frac{\partial^2 u}{\partial x^2} \cancel{- r_2 u}$$

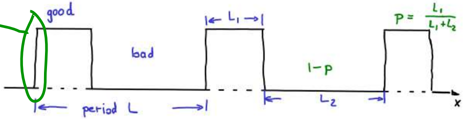
Remember the smoothing property?

Continuous flux

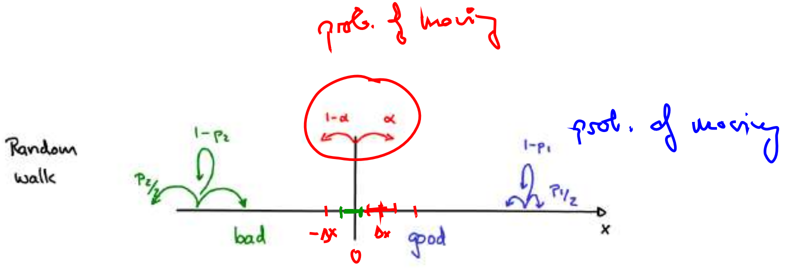
$$\lim_{x \to 0^-} u(t,x) = \lim_{x \to 0^+} u(t,x),$$

$$\lim_{x \to 0^-} D_1 \frac{\partial}{\partial x} u(t,x) = \lim_{x \to 0^+} D_2 \frac{\partial}{\partial x} u(t,x)$$

?



Heterogeneity II: Movement at interfaces



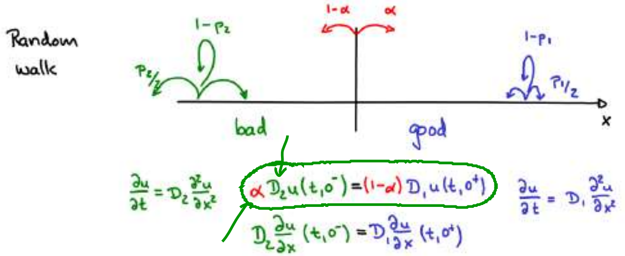
$$u(\Delta x, t+\Delta t)\Delta x = (1-p_1)\, u(\Delta x, t)\Delta x + \frac{p_1}{2} u(2\Delta x, t)\Delta x + u(0,t)\Delta x_0 \cdot \alpha$$

$$u(0, t+\Delta t)\Delta x_0 = \frac{p_1}{2} u(\Delta x, t)\Delta x + \frac{p_2}{2} u(-\Delta x, t)\Delta x$$

$\vdots$

Ovaskainen and Cornell (2003), Maciel and Lutscher (2013)

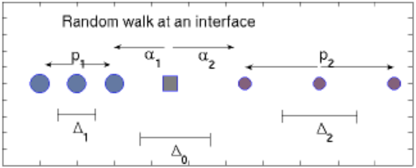
Heterogeneity II: Movement at interfaces



Remember? Matching condition $u(t,0^-) = u(t,0^+)$

Movement behaviour – the interfaces MACIEL AND L (2013) AM NAT

α_i: probability to move into patch (type) i



within-patch equations

$$\frac{\partial}{\partial t} u_1 = D_1 \frac{\partial^2}{\partial x^2} u_1$$

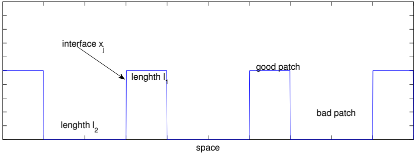
$$\frac{\partial}{\partial t} u_2 = D_2 \frac{\partial^2}{\partial x^2} u_2$$

interface conditions

$$D_1 \frac{\partial}{\partial x} u_1(t, 0^-) = D_2 \frac{\partial}{\partial x} u_2(t, 0^+)$$

$$u_1(t, 0^-) = \frac{\alpha_1}{\alpha_2} \frac{D_2}{D_1} u_2(t, 0^+)$$

Movement behaviour – dispersal kernel Musgrave and L (2014a,b) JMB



Continuous movement, egg deposition, and mortality

$$\frac{\partial}{\partial t}u = D_i \frac{\partial^2}{\partial x^2}u - m_i u - \mu_i u, \quad x \neq x_j$$

Interface conditions $u(x_j^-) = k_j u(x_j^+)$

Dispersal kernel

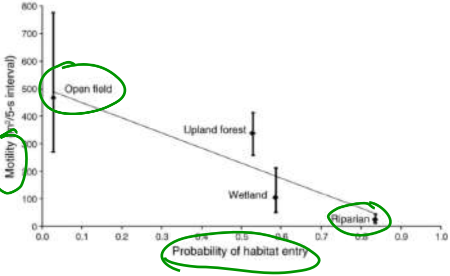
$$\boxed{K(x,y) = \int_0^\infty m(x)u(t,x)dt}$$

Ragged kernels Musgrave and L (2014a,b) JMB

Butterfly

Satyrodes appalachia

D



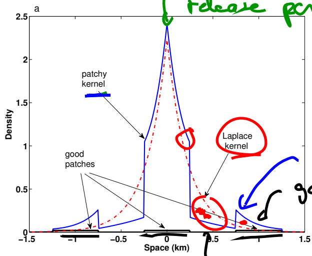
Kuefler et al 2010

α

bad : $D_2 > D_1$ good

$\alpha > \frac{1}{2}$, $1-\alpha < \frac{1}{2}$

{ release point



good

bad

$$\text{oviposit: } m(x) = \begin{cases} m_1 & \text{in good} \\ m_2 < m_1 & \text{in bad} \end{cases}$$

The growth-dispersal model Musgrave and L (2017) Ecology

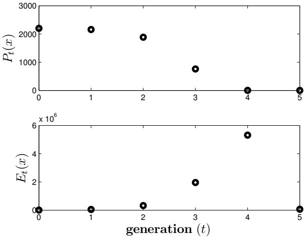
- E_t in # eggs/km
- P_t in m^2/km of phloem

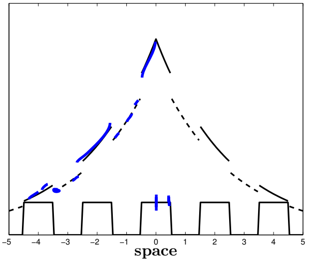
pred-prey relationship

$$E_{t+1}(x) = \int K(x,y)\frac{r}{2}\left(1 - e^{-P_t(y)/\bar{P}}\right) sE_t(y)dy,$$

$$\boxed{P_{t+1}(x) = P_t(x)e^{-wsE_t(x)}.}$$

no dispersal





Parameter estimation for EAB

Parameters for population dynamics

- $r = 70$ (eggs per female)
- $s = 0.55$ (probability of winter survival)
- $P_0 = 2200$ m^2/km (initial phloem density)
- $\bar{P} = 5000$m^2/km (phloem requirement)
- $w = 0.000005$km/larvae (impact on phloem)

Dispersal parameter in homogeneous landscape

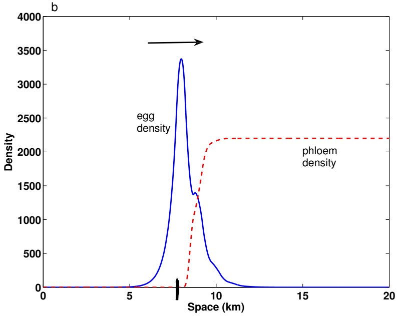
- mean dispersal distance of 0.22km
- $m = 2$ per day (ovipositioning rate)
- $D \approx 0.1$km^2/day

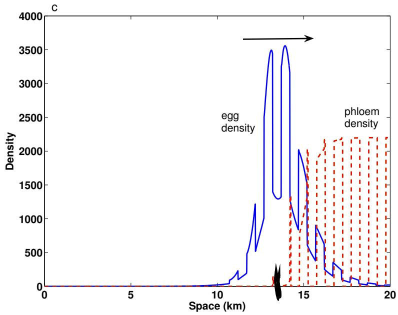
Anunlewicz et al 2008; Rutledge and Keena 2012; Crosthwaite et al 2011; McCullough and Siegert 2007; Mercader et al 2009, 2011, Siegert et al 2010

First numerical observation Musgrave and L (2017) Ecology

Initial condition: 70 eggs near $x = 0$

$\boxed{L_1 = L_2}$





$c_h = 0.82\text{km/year}$

$\underbrace{D_2 = 3D_1}, \underbrace{m_2 = 0.5m_1}, \underbrace{\alpha = 0.5}$

Mercader et al (2016): 0.4-0.7 (small) 1.2-1.7 (large)

Analysis?

Challenges

- Numerics
- Discontinuous functions
- Non-cooperative system, equivalent to

$$E_{t+1}(x) = \int k(x,y)\frac{rs}{2}\underbrace{\left(1 - \exp\left(-\frac{P_0}{\bar{P}}e^{-sw\sum_0^{t-1}E_k(y)}\right)\right)}_{\text{Ricker}} E_t(y)dy$$

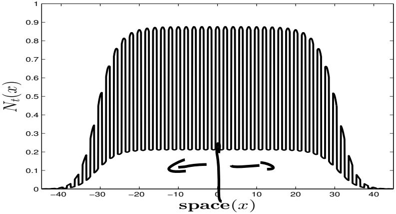
$$1 - e^{-E}$$

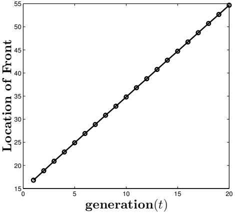
Opportunities

- Linearize
- Stability conditions
- Travelling periodic waves
- Homogenization

Travelling periodic waves

Pattern of spread





Musgrave and L (2014)

Travelling periodic waves Shigesada et al (1986)

The TPW ansatz for speed c and shape s

$$E_t(x) = e^{-s(x-ct)}\theta(x), \qquad \theta(x) = \theta(x+L)$$

in the linear equation

$$E_{t+1}(x) = \int_{\mathbb{R}} K(x,y)r(y)E_t(y)\,dy$$

gives

$$e^{sc}\theta(x) = \int_{\mathbb{R}} K(\overset{(x-y)}{x,y})r(y)e^{s(x-y)}\theta(y)dy$$

$\Longrightarrow$ Dispersion relation $c = c(s)$

$K(x+L, y+L) = K(x,y)$

$\Rightarrow \quad \theta''$

Dispersion relation Musgrave and L (2014)

$$\frac{q_1^2 + q_2^2}{2q_1q_2}$$

Relationship between speed c and steepness s of a TPW

$$\frac{q_1^2 + (q_2\bar{z})^2}{2\bar{z}q_1q_2}\sinh(q_1l_1)\sinh(q_2l_2) + \cosh(q_1l_1)\cosh(q_2l_2) = \cosh(sL)$$

with

$$q_i = \sqrt{\sqrt{D_i/m_i}[1-\exp(-sc)r_i]}$$

$$\frac{D_i}{m_i}$$

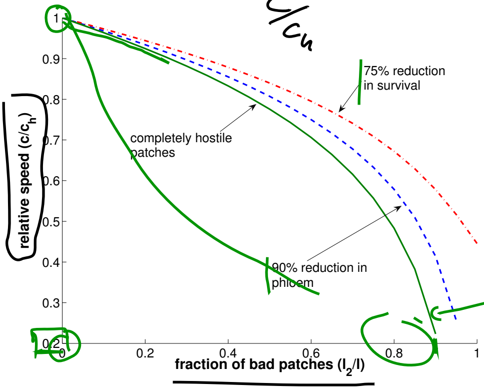
and

$$\bar{z} = (1-\alpha)/(1+\alpha), \qquad l_1 + l_2 = L$$

Results: Landscape-independent movement

c_h : speed in homog. landscape

Scenario: inoculation, spraying

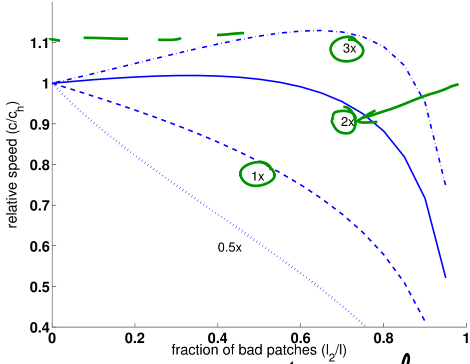


Laplace kernel

Results: Landscape-dependent diffusion

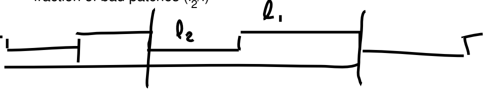
Scenario: detectable landscape alteration, no patch preference

$D_2 = n \times D_1$
bad patches
hostile



$m_2 \to \frac{1}{2} m_1$

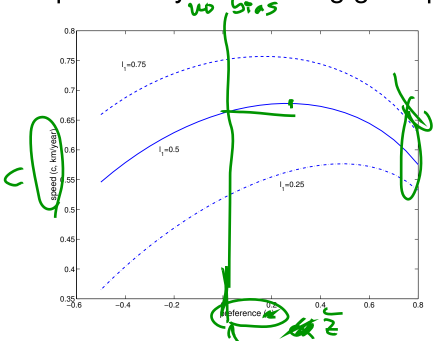
For ovipositioning: $D_i/m_i =$ const.

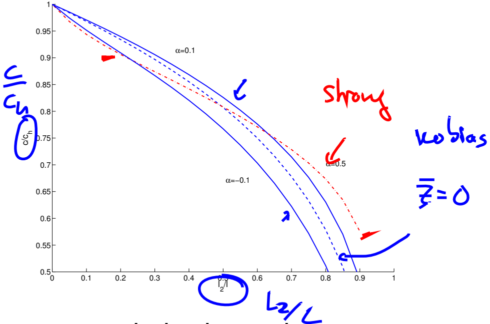


Results: Patch preference

Scenario: Edge behaviour

α: probability of choosing good patch





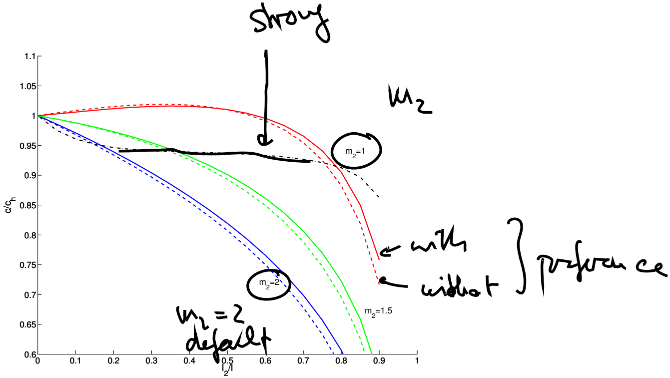
equal movement and oviposition parameters in both patch types

bad patches hostile

$\alpha = \frac{1}{2} \longleftrightarrow \bar{z} = 0$

Results: Combined effects

oviposition and patch preference



no preference (dashed)
weak preference (solid)
strong preference (dash-dot)

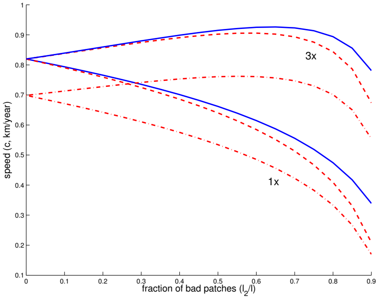
Results: Dispersal-related mortality

Scenario: hazard or energy requirements for dispersal

no mortality (solid)

low, equal mortality (dash-dot)

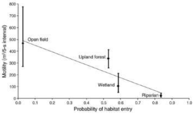
high bad-patch mortality (dashed)

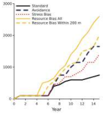


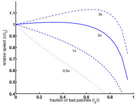
- persistent effect
- mortality in good patches counts

Summary and Discussion

- Invasives and control measures
  - Explore indirect measures Brockerhoff et al 2010
  - thinning, removal, diversity Muzika and Liebhold 2000, Jactel et al 2006, Liebhold 2012
  - fragmentation With 2002, 2004
- Individual movement response to control measures
  - Empirically observed Ruefler et al 2010
  - heuristically simulated Mercader et al 2011a,b
  - analytically investigated
- Exploitation versus exploration
  - higher diffusion, lower oviposition in bad patches







Summary and Discussion

- Edge behaviour
  - Emerald Ash borer
  - Asian longhorned beetle (strong flight, slow spread)
  - beech scale (wind dispersed, fast spread)
- Integrate optimal foraging with spatial spread models

wind

Summary and Discussion

- Analytical challenges
  - width and total mass of the pulse
  - linear determinacy
  - existence theory for discontinuous waves
- Allee effect
- Stepping stones