PATRES
PATTERN RESILIENCE
EU FRAMEWORK 6 NEST PROJECT

Bridging the gap between structurally realistic models and viability theory in savanna ecosystems

Justin M. Calabrese & Volker Grimm

HELMHOLTZ
CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

PATRES: Savanna case study

Overview:

1) Start with a detailed, site-specific savanna model

2) Identify essential pattern dynamics of the model

3) Build a low dimensional, mathematically tractable approx. capturing key pattern dynamics

4) Apply viability theory to approximate model

HELMHOLTZ
CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Savannas

Defined by:

1) Continuous grass layer
2) Discontinuous tree layer

Cover ~20% of Earth’s terrestrial surface area

Harbor considerable biodiversity

Economically significant as grazing lands

HELMHOLTZ
CENTRE FOR
ENVIRONMENTAL
RESEARCH – UFZ

Current threats to savannas

Human population growth

Global climate change

Changing land use patterns

Overexploitation by humans
-Specifically overgrazing

Bush encroachment

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Savanna management

Must balance system integrity against economic goals

Price of failure is high. Bush encroached savannas effectively useless for grazing

Manage by manipulating fire and/or grazing regimes

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

“Structurally realistic” savanna models

Relatively complex models used to integrate knowledge on particular savannas

Typically stochastic. Include many parameters and variables

Often reproduce key features of focal site

Seldom used for management purposes

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

The Jeltsch model

Developed by Jeltsch and colleagues in 1990’s

Focuses on a South African savanna

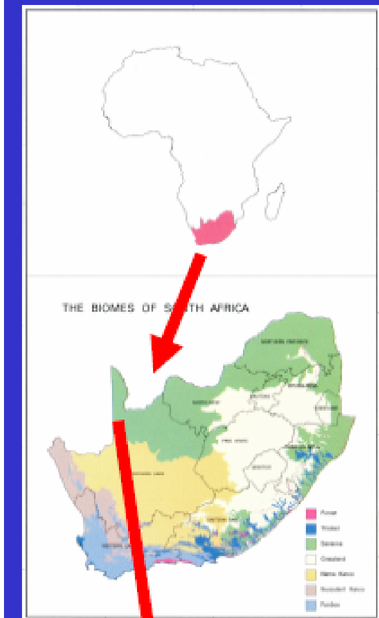
Integrates 30+ years of detailed empirical data from this site

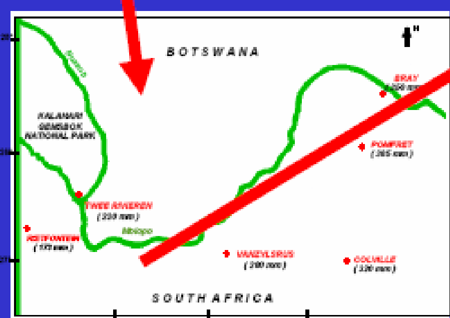
Widely cited and still widely used

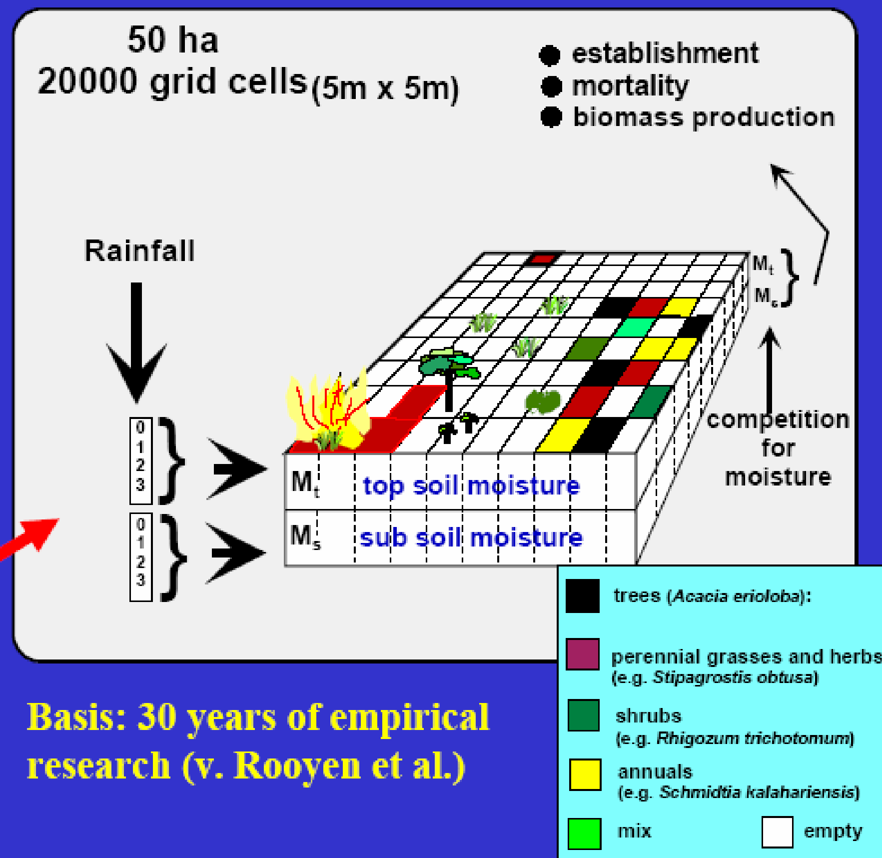
Jeltsch et al. 1996; 1997a, b; 1998;1999

HELMHOLTZ
CENTRE FOR
ENVIRONMENTAL
RESEARCH – UFZ

Grid-based savanna model







Basis: 30 years of empirical research (v. Rooyen et al.)

HELMHOLTZ
CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Complex model, but complex dynamics?

Dynamics of macroscopic state variables might not be complicated

This appears to be the case for the Jeltsch model

Idea: Use the relatively simple dynamics of a few key patterns to reduce model dimensionality

Targets of analysis

Focus on trees (and grasses):

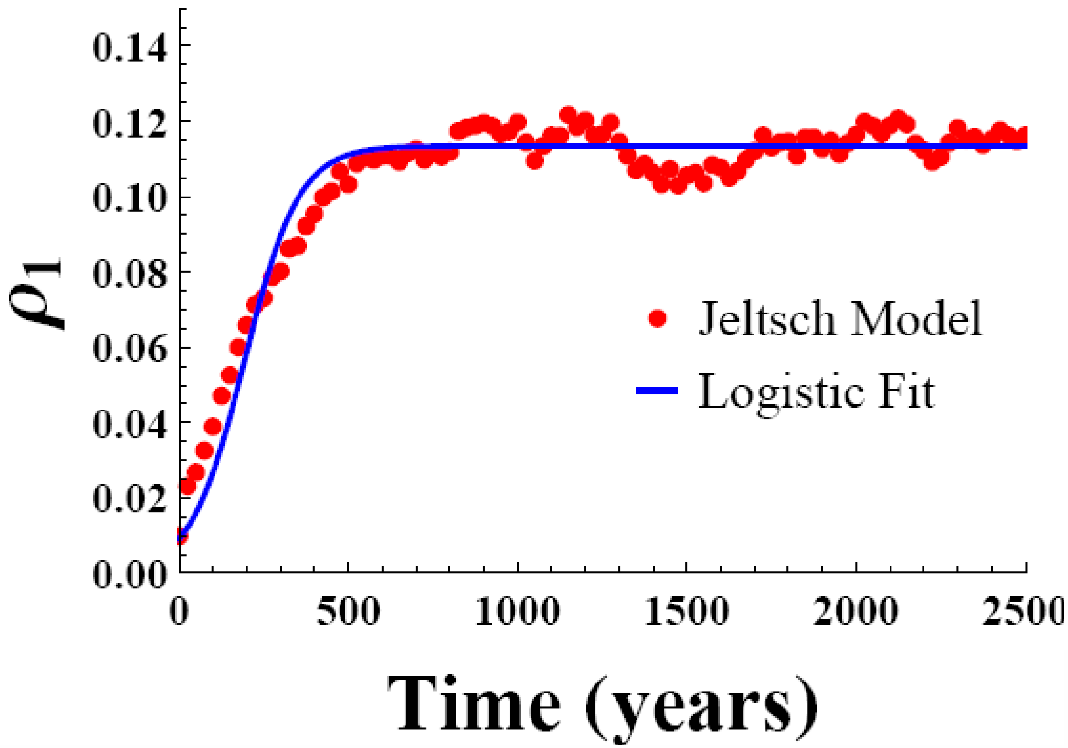
1) Population density time series $\left(\rho_1 = \frac{\# trees}{\# sites} \right)$

2) Distance-dependent spatial pattern (*g* statistic)

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Logistic-like population growth

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$



HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Point-pattern analysis

Normalized pair correlation statistic

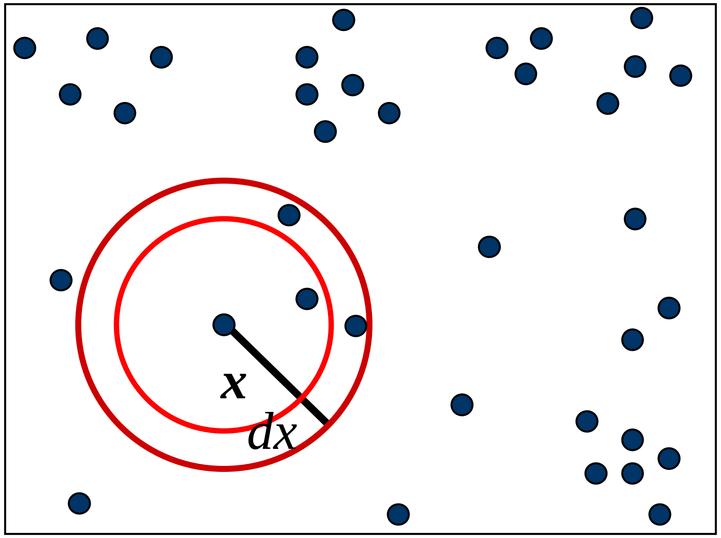
Stoyan & Stoyan 1994; Condit et al. 2000

$$g_x = \frac{\sum N_x}{\lambda \sum A_x}$$

g=1 ⟶ Random

g>1 ⟶ Clustered

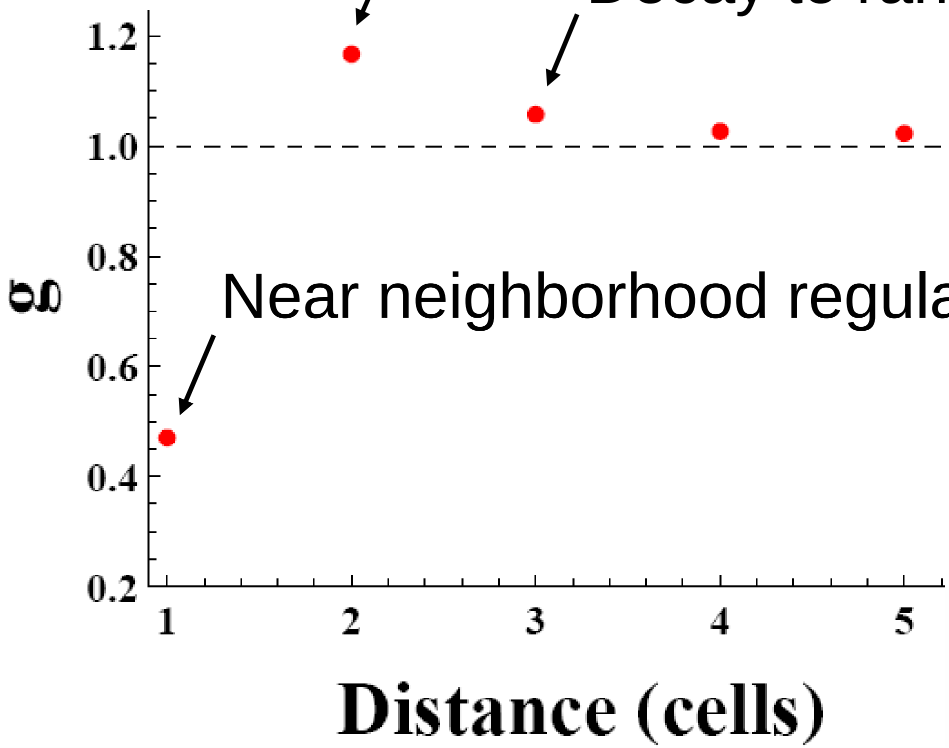
g<1 ⟶ Regular



Where λ is the density of the point pattern, and N_x A_x are the # of neighbors and area of the annulus, respectively, at dist. *x*.

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Strong signatures of competition and short dispersal



Key patterns

Logistic-like population growth

Spatial pattern:

1) Near neighborhood regularity
2) Far neigh. clustering
3) Decays to randomness thereafter

Suggests a ***spatial logistic model*** with 2 interaction scales

Model overview

Square lattice, periodic boundary conds., two states:
tree (1) or grass (0)

Prop. of sites in state 1 is ρ_1 and in state 0 is $\rho_0 = 1 - \rho_1$

Model is an extension of the contact process

Tree dispersal & competition occur within defined (Moore) neighborhoods

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Interaction neighborhoods

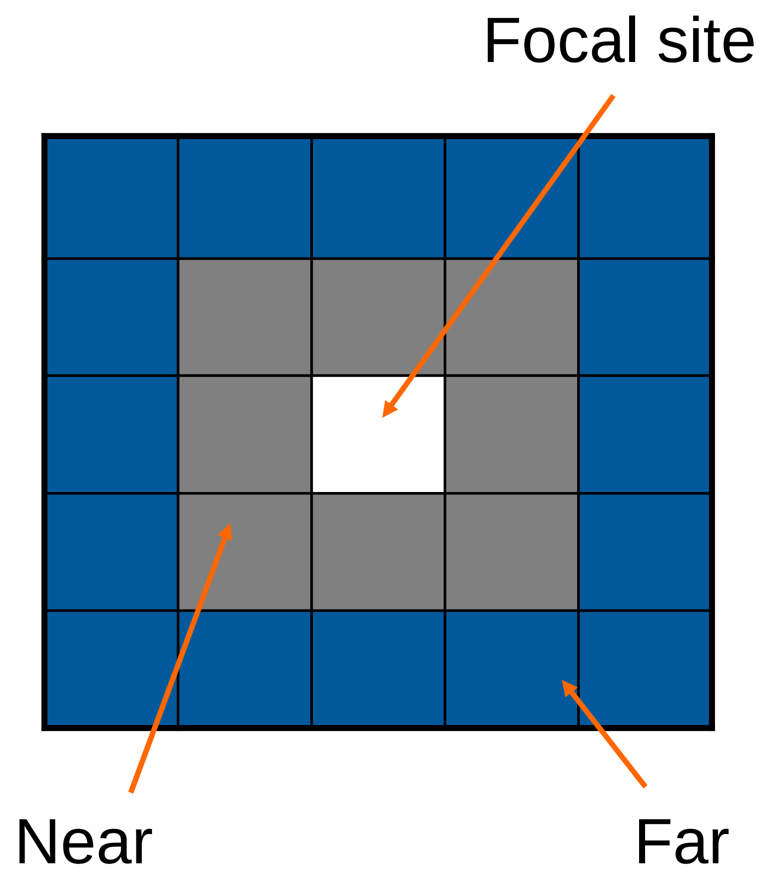
Define two neighborhoods—
"near" and "far"

Assume:

1) establishment comp. occurs only over near neigh.

2) birth occurs in both near & far neighborhoods

3) Neighborhood status is symmetric



Disp. scale > Comp. scale

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Birth

Trees reproduce at constant rate *b*

Each site within birth (*n* + *f*) neighborhood of a tree receives offspring at rate:

$$\beta = \frac{b}{z_n + z_f}$$

If an seed lands on a tree occupied site, nothing happens

If it lands on a grass occupied site, it has a chance to establish

HELMHOLTZ
CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Establishment

Given birth, the seed establishes with probability

$$P_E = P_C^{Surv} P_F^{Surv}$$

where:

$$P_C^{Surv} = e^{-\delta C} \quad \text{and} \quad P_F^{Surv} = 1 \quad \text{(for now)}$$

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Moment equations

An open hierarchy of equations of the form

$$\frac{d\rho_1}{dt} = f(\rho_1, \rho_{11})$$

Mean Density

$$\frac{d\rho_{11}}{dt} = f(\rho_1, \rho_{11}, \rho_{111})$$

Most Spatial Structure

Spatial Structure

$$\frac{d\rho_{111}}{dt} = f(\rho_1, \rho_{11}, \rho_{111}, \rho_{1111})$$

$$\vdots$$

Increasingly Minute Spatial Detail

By itself, this is useless, but mean-field and pair approximations make this approach tractable

Multi-scale pair approximation, Ellner 2001

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Moment approximations: Mean dynamics

Eqn. for mean is a simple balance equation

per neigh. contribution | # near neighs | # far neighs | prop. unocc. sites | prob. survive fire | prob. survive comp.

$$\frac{d\rho_1}{dt} = \beta\left(z_n q_{1/0} + z_f \tilde{q}_{1/0}\right)\left(1-\rho_1\right) P_F^{Surv} e^{-\delta z_n q_{1/0}} - \alpha \rho_1$$

Birth | Establishment | Death

Local density terms carry spatial information

HELMHOLTZ
CENTRE FOR
ENVIRONMENTAL
RESEARCH – UFZ

Moment approximations: Density

$q_{1/0}$ and $\tilde{q}_{1/0}$ are the near & far neighborhood local densities

Pair:

$$\frac{d\rho_1}{dt} = \beta\left(z_n\, q_{1/0} + z_f\, \tilde{q}_{1/0}\right)\left(1-\rho_1\right)P_F^{Surv}\, e^{-\delta\, z_n\, q_{1/0}} - \alpha\,\rho_1$$

Mean field:

$$\frac{d\rho_1}{dt} = \beta\left(z_n\, \rho_1 + z_f\, \rho_1\right)\left(1-\rho_1\right)P_F^{Surv}\, e^{-\delta\, z_n\, \rho_1} - \alpha\,\rho_1$$

Multiscale pair approximation: Ellner 2001

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Pair Approx.: Pair correlations

Local dens. can be written in terms of pair and singlet probs.

$$q_{1/0} = \frac{\rho_1 - \rho_{11}}{1-\rho_1} \quad \& \quad \tilde{q}_{1/0} = \frac{\rho_1 - \tilde{\rho}_{11}}{1-\rho_1}$$

Each int. neighborhood requires a pair dens. eqn.

Near:

$$\frac{1}{2}\frac{d\rho_{11}}{dt} = \beta\left(1+(z_n-1)q_{1/0}+z_f\,\tilde{q}_{1/0}\right)\left(\rho_1-\rho_{11}\right)P_F^{Surv}\,e^{-\delta\left[1+(z_n-1)q_{1/0}\right]} - \alpha\,\rho_{11}$$

Far:

$$\frac{1}{2}\frac{d\tilde{\rho}_{11}}{dt} = \beta\left(z_n\,q_{1/0}+1+(z_f-1)\tilde{q}_{1/0}\right)\left(\rho_1-\tilde{\rho}_{11}\right)P_F^{Surv}e^{-\delta\,z_n\,q_{1/0}} - \alpha\,\tilde{\rho}_{11}$$

Full analysis of PA savanna model in Calabrese *et al.* (*In press, American Naturalist*)

Back to the Jeltsch model

We have an equation for ρ_1

g statistics can be derived from PA: $g_n = \frac{\rho_{11}}{\rho_1^2}$ $g_f = \frac{\tilde{\rho}_{11}}{\rho_1^2}$

PA has two free parameters: *b* and δ (plus α)

They can be estimated by fitting the PA to the Jeltsch model

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Calculating the death rate

Only “background” mortality important for adult trees

Jeltsch et al. 1996 describe the (background) mortality process:

1) Established adults survive to age 120

2) Linear increase in the mortality rate from 120 to a max. age of 250.

Can use this info to calculate the mean lifespan $\bar{a}$, and then calculate the death rate in the PA as:

$$\alpha = 1/\bar{a}$$

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Average life span

$$m_1 = d_1 \qquad m_2 = (1-d_1)d_2 \qquad m_3 = (1-d_1)(1-d_2)d_3$$

$$d_1 = \frac{1}{k} \qquad d_2 = \frac{2}{k} \qquad d_n = \frac{n}{k} \quad for\, n \le k$$

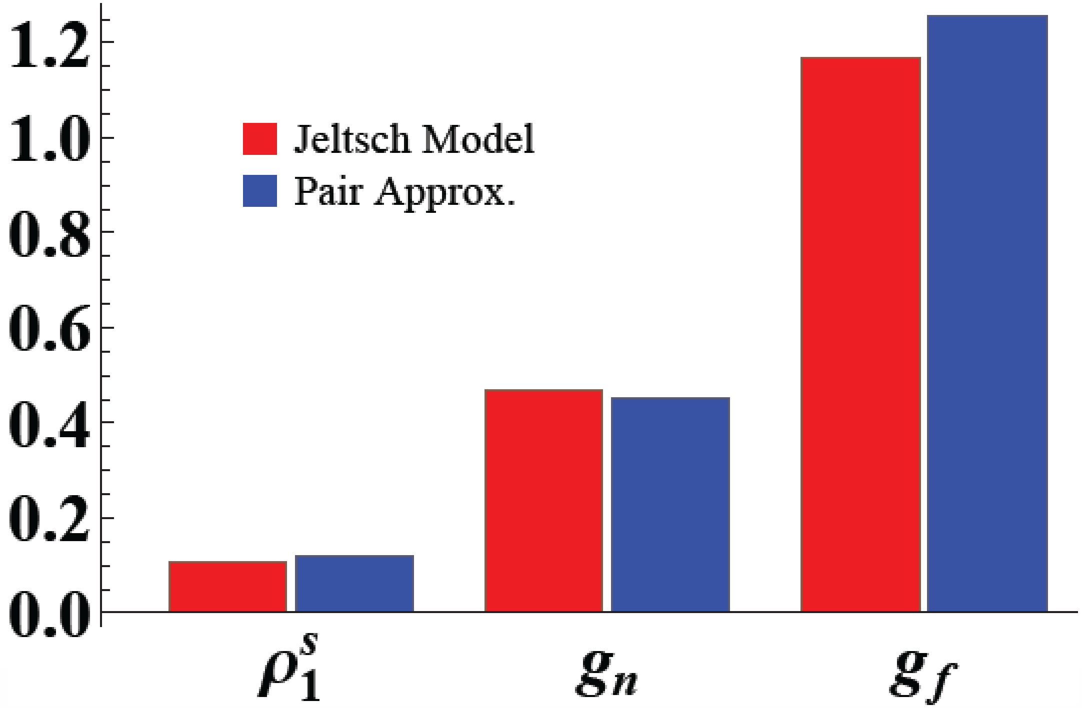
$$m_n = \frac{n}{k}\prod_{i=1}^{n-1} 1 - \frac{i}{k} \qquad \bar{a} = \sum_{i=1}^{k} m_i i$$

$$k = 130 \qquad \bar{a} = 120 + \sum_{i=1}^{130} m_n i \qquad \bar{a} = 133.9656$$

$$\alpha = 1/133.9656 = 0.00746$$

HELMHOLTZ
CENTRE FOR
ENVIRONMENTAL
RESEARCH – UFZ

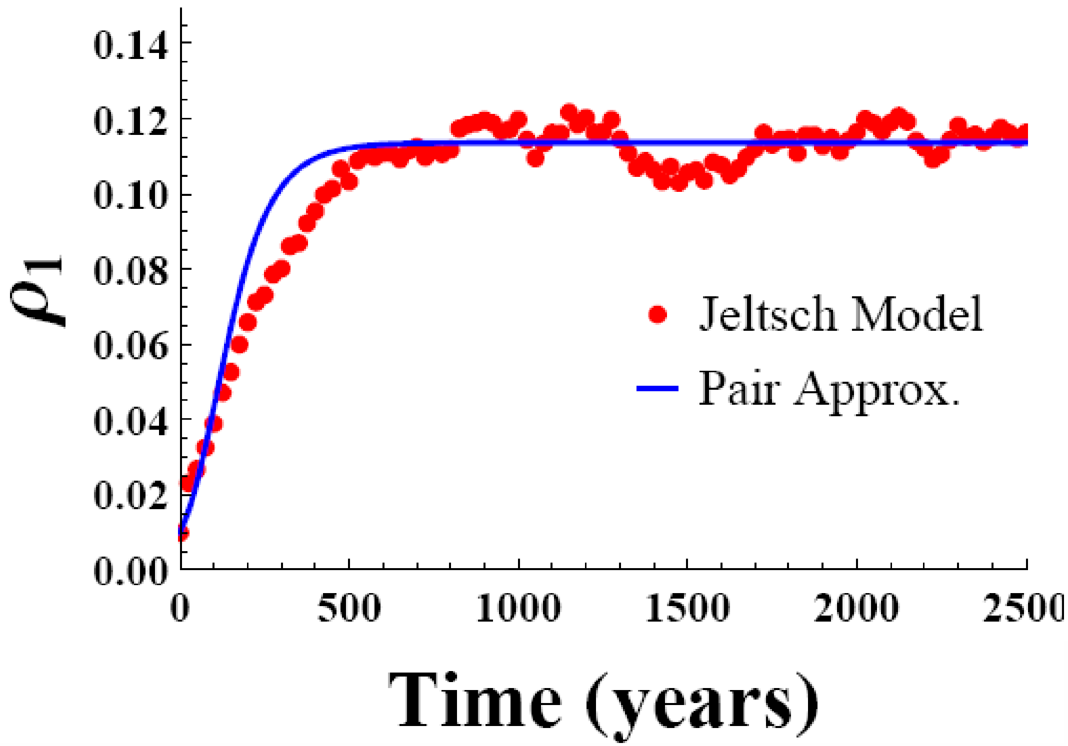
Fit PA to 3 patterns



$$b = 4.4 \qquad \delta = 1.3$$

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Transient dynamics



HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Adding fire

Negatively affects trees by killing primarily juveniles

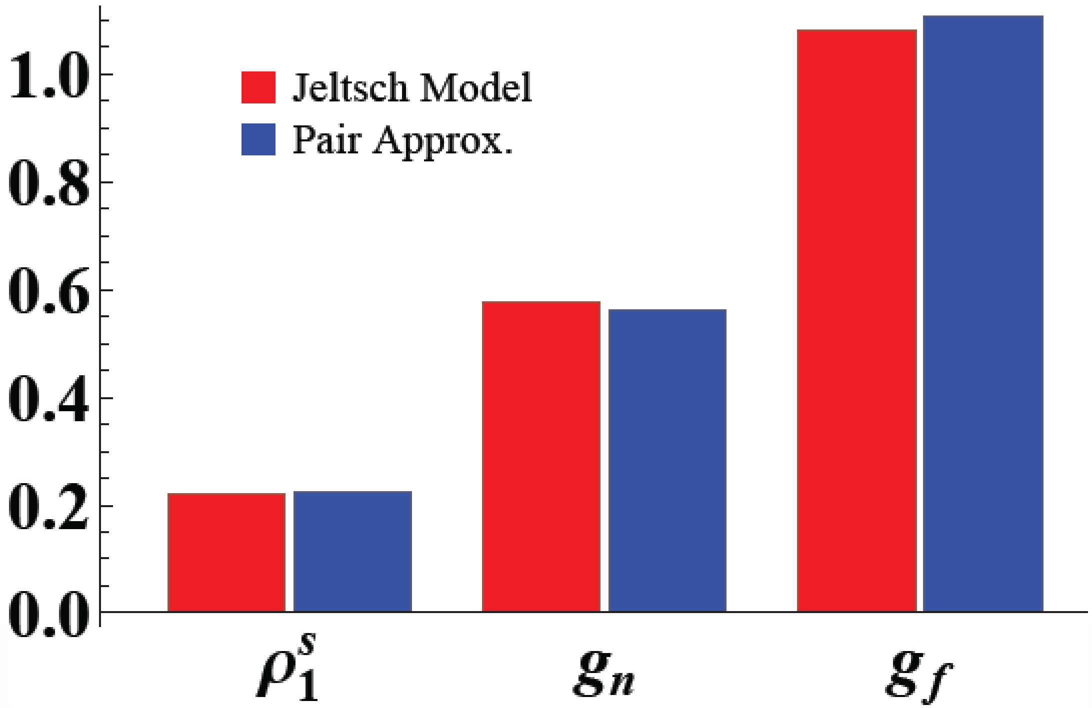
Fire regimes can be manipulated to control trees

Direct: Prescribed burns
Indirect: Varying grazing pressure

Fire and grazing represent key control actions

HELMHOLTZ
CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

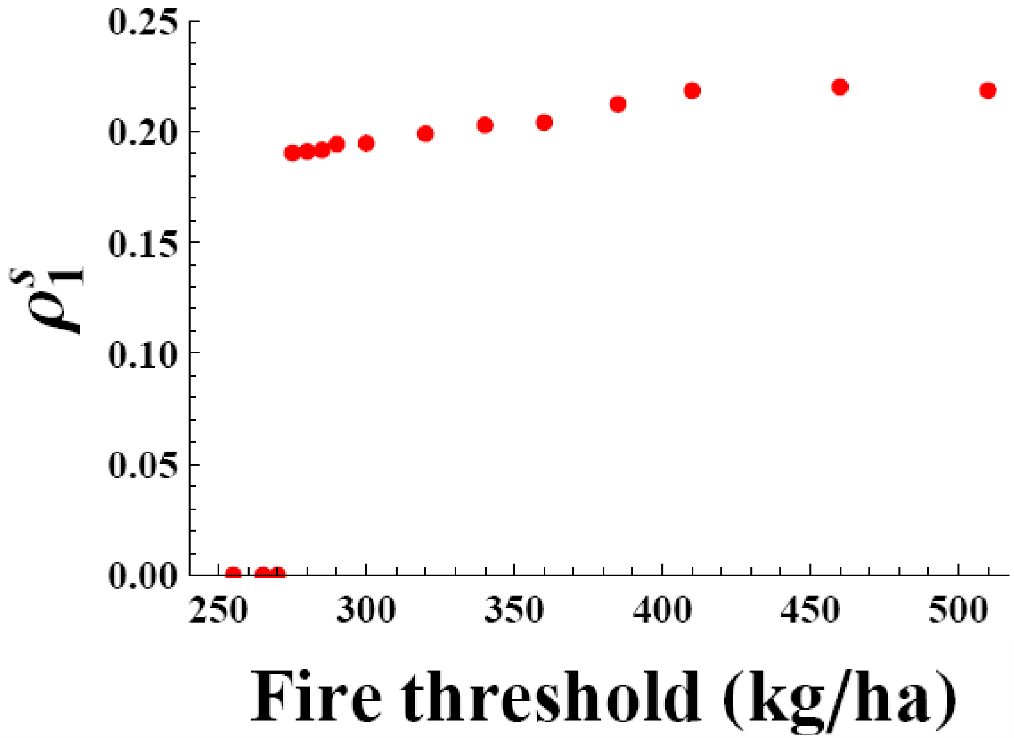
First fit competition model w/o fire



$$b = 11.7 \qquad \delta = 1.1$$

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

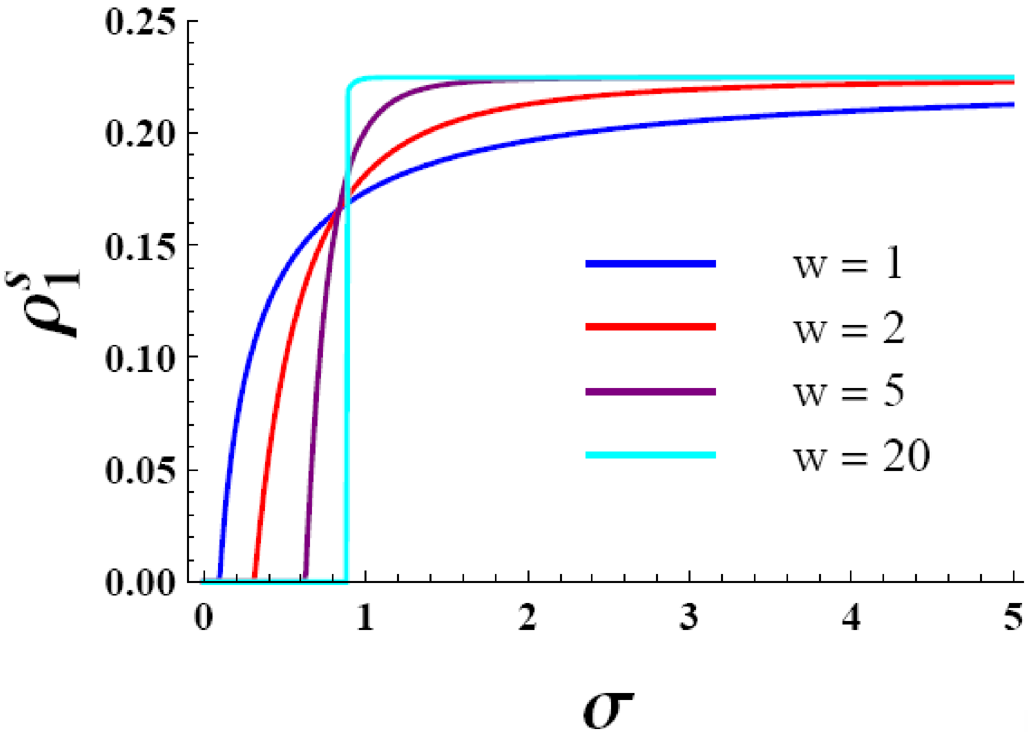
Fire in the Jeltsch model



HELMHOLTZ
CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Fire in pair approx.

$$P_F^{Surv} = 1 - \frac{\left(c(1-\rho_1)\right)^w}{\left(c\sigma\right)^w + \left(c(1-\rho_1)\right)^w}$$



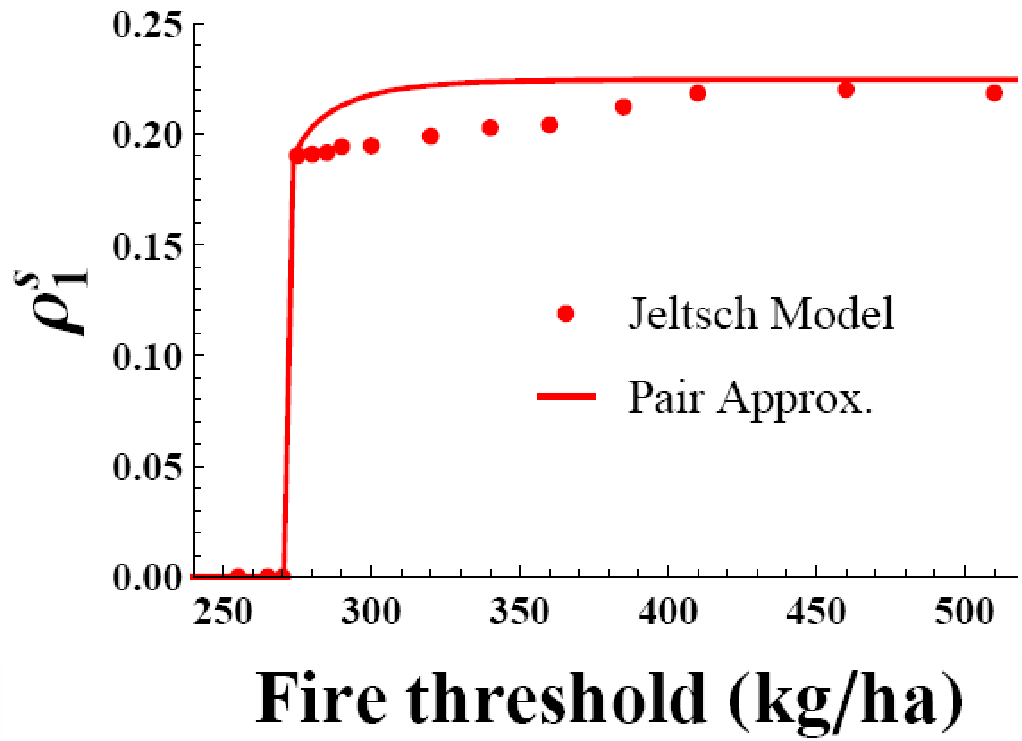
σ affects fire freq.

w determines abruptness and location of trans.

c rescales x-axis

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Comparing the transitions

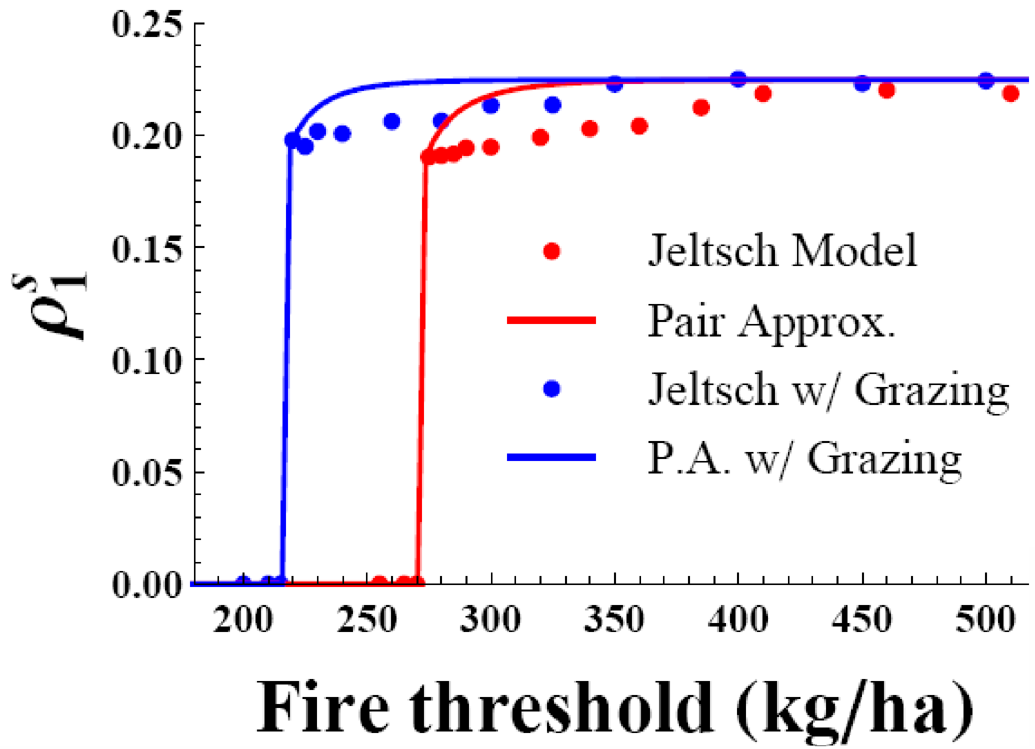


$$c = 322 \qquad w = 14$$

HELMHOLTZ
CENTRE FOR
ENVIRONMENTAL
RESEARCH – UFZ

Grazing

$$P_F^{Surv} = 1 - \frac{\left((1-h)c(1-\rho_1)\right)^w}{(c\sigma)^w + \left((1-h)c(1-\rho_1)\right)^w}$$



$h = 0.205$

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Summary of Approximation

$$\frac{d\rho_1}{dt} = \frac{b}{3}\left(q_{1/0} + 2\tilde{q}_{1/0}\right)(1-\rho_1)P_F^{Surv}\, e^{-8\delta q_{1/0}} - \alpha\rho_1$$

$$\frac{1}{2}\frac{d\rho_{11}}{dt} = \frac{b}{24}\left(1+7q_{1/0}+16\tilde{q}_{1/0}\right)(\rho_1-\rho_{11})P_F^{Surv}\, e^{-\delta[1+7q_{1/0}]} - \alpha\rho_{11}$$

$$\frac{1}{2}\frac{d\tilde{\rho}_{11}}{dt} = \frac{b}{24}\left(8q_{1/0}+1+15\tilde{q}_{1/0}\right)(\rho_1-\tilde{\rho}_{11})P_F^{Surv} e^{-8\delta q_{1/0}} - \alpha\tilde{\rho}_{11}$$

$$q_{1/0} = \frac{\rho_1 - \rho_{11}}{1-\rho_1} \qquad \tilde{q}_{1/0} = \frac{\rho_1 - \tilde{\rho}_{11}}{1-\rho_1} \qquad P_F^{Surv} = 1 - \frac{\left((1-h)c(1-\rho_1)\right)^w}{(c\sigma)^w + \left((1-h)c(1-\rho_1)\right)^w}$$

$b = 11.7$ $\alpha = 0.00746$ $\sigma =$ user determined

$\delta = 1.1$ $c = 322$ $g =$ control parameter

$w = 14$

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

A viability problem based on MF approx.

$$\frac{d\rho_1}{dt} = be^{-\delta z_n \rho_1} \frac{\sigma}{\sigma + 1 - \rho_1}(\rho_1 - \rho_1^2) - \alpha \rho_1 = \phi(\rho_1, h)$$

where $\hat{\sigma} = \sigma / (1 - h)$

Redefine system to include dynamics of control:

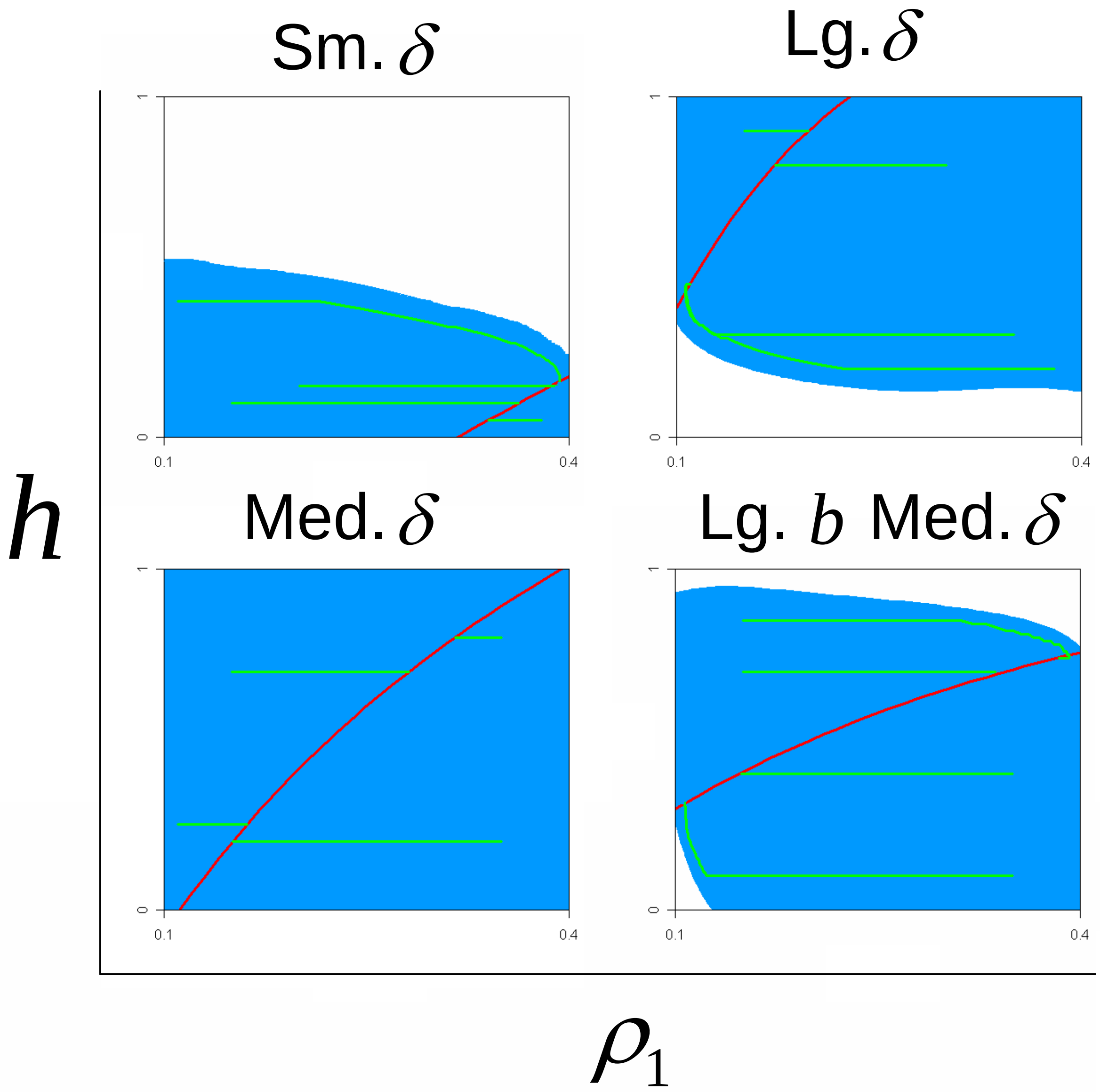
$$\rho_1(t+dt) = \rho_1(t) + \phi(\rho_1(t), h(t))dt$$
$$h(t+dt) = h(t) + u(t)dt$$

Subject to constraints:

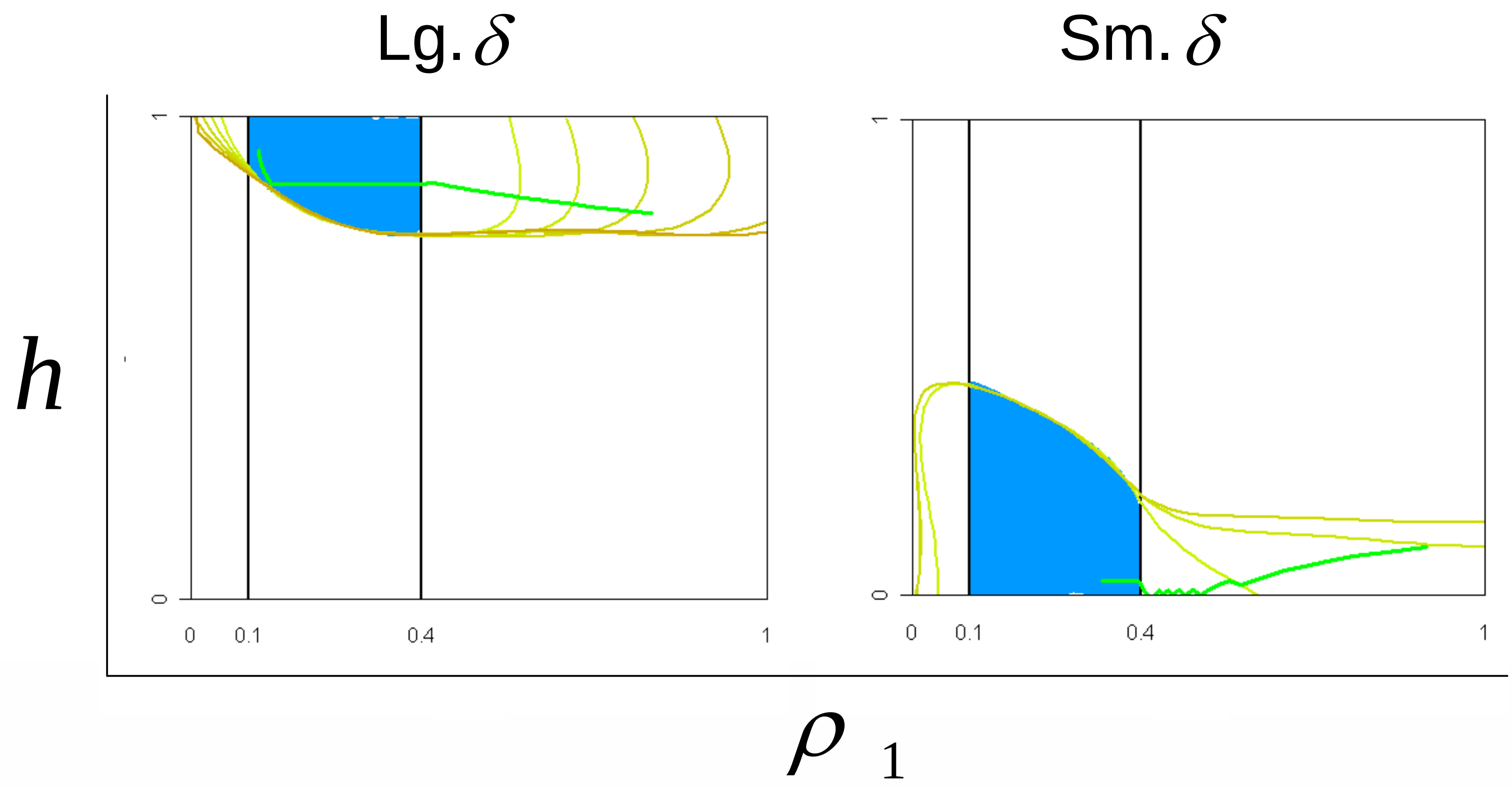
$$\rho_{1Min} \leq \rho_1(t) \leq \rho_{1Max} \qquad |u(t)| \leq h'_{Max}$$

HELMHOLTZ CENTRE FOR ENVIRONMENTAL RESEARCH – UFZ

Viability kernels



Quantifying resilience



Conclusions

Path from Jeltsch mod. to viab. analysis is long & winding

Formal approximation frameworks (e.g., moment equations) cannot be applied directly to models of arbitrary complexity

Main value of this exercise is as a proof of concept

Next step is to apply a control policy identified using the approx. mod. to the full Jeltsch mod.

Thanks!

PATRES
PATTERN RESILIENCE
EU FRAMEWORK 6 NEST PROJECT

justin.calabrese@ufz.de

HELMHOLTZ
CENTRE FOR
ENVIRONMENTAL
RESEARCH – UFZ