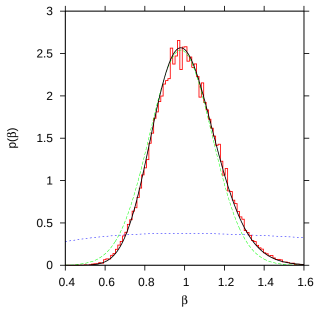
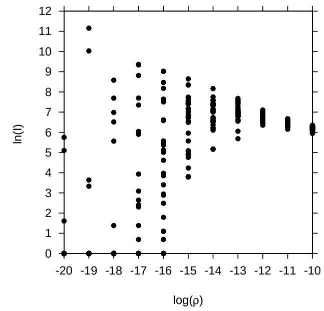
Dynamic noise, chaos and parameter estimation in population biology





Nico Stollenwerk

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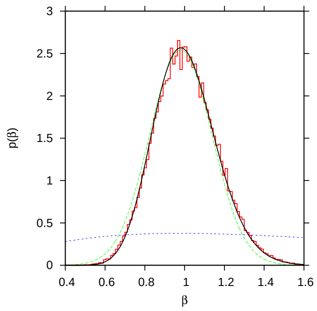

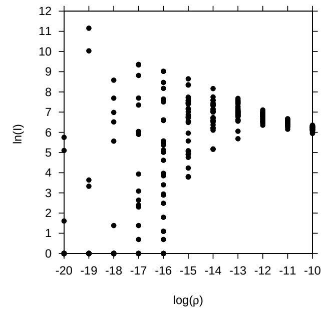

Nico Stollenwerk

joint work with

Maíra Aguiar, Bob Kooi, Sébastien Ballesteros, João Boto and Luis Mateus

SIS epidemic

stochastic process

$$\begin{aligned} S + I &\xrightarrow{\beta} I + I \\ I &\xrightarrow{\alpha} S \end{aligned}$$

for variable I and $S = N - I$ => probab. $p(I,t)$

$$\begin{aligned} \frac{d}{dt}p(I,t) &= \frac{\beta}{N}(I-1)(N-(I-1))p(I-1,t) + \alpha(I+1)p(I+1,t) \\ &\quad - \left(\frac{\beta}{N}I(N-I) + \alpha I\right)p(I,t) \end{aligned}$$

mean $\langle I \rangle := \sum_{I=0}^{N} I \cdot p(I,t)$

$$\frac{d}{dt} \langle I \rangle = (\beta - \alpha)\langle I \rangle - \frac{\beta}{N}\langle I^2 \rangle$$

and only in mean field approx. $var := \langle I^2 \rangle - \langle I \rangle^2 \approx 0$

$$\frac{d}{dt} \langle I \rangle = \frac{\beta}{N}\langle I \rangle (N - \langle I \rangle) - \alpha \langle I \rangle$$

we obtain closed ODE

SIR epidemic

stochastic process

$$\begin{aligned} S+I &\xrightarrow{\beta} I+I \\ I &\xrightarrow{\gamma} R \\ R &\xrightarrow{\alpha} S \end{aligned}$$

for variables S, I and $R = N - S - I$ => probab. $p(S, I, t)$

$$\begin{aligned} \frac{d}{dt}p(S,I,t) &= \frac{\beta}{N}(I-1)(S+1)p(S+1,I-1,t) + \gamma(I+1)p(S,I+1,t) \\ &-\alpha(N-(S+1)-I)p(S+1,I,t) \\ &-\left(\frac{\beta}{N}SI + \gamma I + \alpha(N-S-I)\right)p(S,I,t) \end{aligned}$$

Multi-strain SIR-type model for dengue fever

$$\begin{aligned}
S + I_1 &\xrightarrow{\beta_1} I_1 + I_1 \\
S + I_{21} &\xrightarrow{\phi_1 \beta_1} I_1 + I_{21} \\
I_1 &\xrightarrow{\gamma} R_1 \\
R_1 &\xrightarrow{\alpha} S_1 \\
S_1 + I_2 &\xrightarrow{\beta_2} I_{12} + I_2 \\
S_1 + I_{12} &\xrightarrow{\phi_2 \beta_2} I_{12} + I_{12} \\
I_{12} &\xrightarrow{\gamma} R
\end{aligned}$$

Multi-strain SIR-type model for dengue fever

mean field ODE approximation

$$\frac{dS}{dt} = -\frac{\beta_1}{N}S(I_1 + \phi_1 I_{21}) - \frac{\beta_2}{N}S(I_2 + \phi_2 I_{12}) + \mu(N - S)$$

$$\frac{dI_1}{dt} = \frac{\beta_1}{N}S(I_1 + \phi_1 I_{21}) - (\gamma + \mu)I_1$$

$$\frac{dI_2}{dt} = \frac{\beta_2}{N}S(I_2 + \phi_2 I_{12}) - (\gamma + \mu)I_2$$

$$\frac{dR_1}{dt} = \gamma I_1 - (\alpha + \mu)R_1$$

$$\frac{dR_2}{dt} = \gamma I_2 - (\alpha + \mu)R_2$$

$$\frac{dS_1}{dt} = -\frac{\beta_2}{N}S_1(I_2 + \phi_2 I_{12}) + \alpha R_1 - \mu S_1$$

$$\frac{dS_2}{dt} = -\frac{\beta_1}{N}S_2(I_1 + \phi_1 I_{21}) + \alpha R_2 - \mu S_2$$

$$\frac{dI_{12}}{dt} = \frac{\beta_2}{N}S_1(I_2 + \phi_2 I_{12}) - (\gamma + \mu)I_{12}$$

$$\frac{dI_{21}}{dt} = \frac{\beta_1}{N}S_2(I_1 + \phi_1 I_{21}) - (\gamma + \mu)I_{21}$$

$$\frac{dR}{dt} = \gamma(I_{12} + I_{21}) - \mu R$$

Multi-strain SIR-type model for dengue fever

mean field ODE approximation

can show deterministic chaos in wide parameter regions
(Aguiar, Kooi, Stollenwerk, 2008, 2009)

Multi-strain SIR-type model for dengue fever

real world data

interplay between deterministic skeleton and stochasticity

Multi-strain SIR-type model for dengue fever

real world data

interplay between deterministic skeleton
and stochasticity

first look at a toy example (”linear infection model”)
even simpler than SIS

Linear infection model

SIS model
$$\begin{aligned} S + I &\xrightarrow{\beta} I + I \\ I &\xrightarrow{\alpha} S \end{aligned}$$

with dynamics for the probab. $p(I,t)$

$$\begin{aligned} \frac{d}{dt}p(I,t) &= \frac{\beta}{N}(I-1)(N-(I-1))p(I-1,t) + \alpha(I+1)p(I+1,t) \\ &\quad - \left(\frac{\beta}{N}I(N-I) + \alpha I\right)p(I,t) \end{aligned}$$

simplified to susceptibles infected only outside the considered population of size N, by meeting a constant number of external infected (from much larger system) I^*, and no recovery (or cumulative cases in SIR)

$$S + I^* \xrightarrow{\beta} I + I^*$$

Linear infection model

$$S + I^* \xrightarrow{\beta} I + I^*$$

for variable I and $S = N - I$ => probab. $p(I,t)$

$$\frac{d}{dt}p(I,t) = \frac{\beta}{N}I^* \cdot (N-(I-1))p(I-1,t) - \frac{\beta}{N}I^* \cdot (N-I)p(I,t)$$

hence constant force of infection $\beta^* := \frac{\beta}{N}I^*$

linear infection model easily solvable

Characteristic function

like ordinary mean now mean of a function

$$\langle e^{i\kappa I} \rangle := \sum_{I=0}^{N} e^{i\kappa I} \cdot p(I,t) =: g(\kappa,t)$$

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generates moments

$$(-i)^n \left. \frac{\partial^n}{\partial \kappa^n} g(\kappa,t) \right|_{\kappa=0} = \langle I^n \rangle$$

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$$(-i)^n \left.\frac{\partial^n}{\partial\kappa^n} g(\kappa,t)\right|_{\kappa=0} = \langle I^n\rangle$$

and can be inverted (Fourier transform) with $\kappa =: \frac{2\pi}{N+1}\cdot k$

$$g(\kappa,t) = \sum_{I=0}^{N} e^{i\frac{2\pi}{N+1}k\cdot I}\cdot p(I,t) = \hat{g}(k,t)$$

Characteristic function

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$$g(\kappa,t) = \sum_{I=0}^{N} e^{i\frac{2\pi}{N+1}k\cdot I}\cdot p(I,t) = \hat{g}(k,t)$$

then probability p as function of g

$$p(I,t) = \frac{1}{N+1}\sum_{k=0}^{N} e^{-i\frac{2\pi}{N+1}k\cdot I}\cdot \hat{g}(k,t)$$

Dynamics for $g(\kappa, t)$

use master equation of SIS stochastic system

$$\frac{\partial}{\partial t} g(\kappa, t) = \sum_{I=0}^{N} e^{i\kappa I} \cdot \frac{d}{dt} p(I, t)$$

Dynamics for $g(\kappa, t)$

use master equation of SIS stochastic system

$$\frac{\partial}{\partial t} g(\kappa, t) = \sum_{I=0}^{N} e^{i\kappa I} \cdot \frac{d}{dt} p(I, t)$$

and after some calculation

$$\frac{\partial}{\partial t} g(\kappa, t) \;=\; \beta^* N \left((e^{i\kappa} - 1) \right) \cdot g(\kappa, t) + i\beta^* (e^{i\kappa} - 1) \cdot \frac{\partial g}{\partial \kappa}$$

Solution by separation ansatz

solve partial differential equation

$$\frac{\partial}{\partial t} g(\kappa, t) \ = \ \beta^* N \left((e^{i\kappa} - 1) \right) \cdot g(\kappa, t) + i\beta^*(e^{i\kappa} - 1) \cdot \frac{\partial g}{\partial \kappa}$$

by separation ansatz first with

$$g(\kappa, t) := h(\kappa) \cdot \ell(\kappa, t)$$

giving another simpler PDE for $\ell(\kappa, t)$, and an easily solvable ODE for $h(\kappa)$

$$\frac{\partial \ell}{\partial t} = i\beta^* \left(e^{i\kappa} - 1 \right) \frac{\partial \ell}{\partial \kappa}$$

$$\frac{dh}{d\kappa} = iN \cdot h(\kappa)$$

last one with special solution $h(\kappa) = e^{iN\kappa}$

Solution by separation ansatz

solve the PDE for $\ell(\kappa, t)$

$$\frac{\partial \ell}{\partial t} = i\beta^* \left(e^{i\kappa} - 1\right) \frac{\partial \ell}{\partial \kappa}$$

by another separation ansatz with

$$\ell(\kappa, t) := m(\kappa) \cdot n(t)$$

giving two separate ODEs for $n(t)$ and $m(\kappa)$ with special solutions

$$\frac{dn}{dt} = i\beta^* \cdot n(t) \qquad \Rightarrow \qquad n(t) = e^{i\beta^* t}$$

and

$$\frac{dm}{d\kappa} = \frac{1}{e^{i\kappa} - 1} \cdot m(\kappa) \qquad \Rightarrow \qquad m(\kappa) = e^{-\kappa} \cdot \left(e^{i\kappa} - 1\right)^{-i}$$

Including initial conditions

for transition probabilities take initially exactly I_0 infected at time t_0, hence

$$p(I, t_0) = \delta_{I,I_0}$$

and hence for the characteristic function

$$g(\kappa, t_0) = \sum_{I=0}^{N} e^{i\kappa I} \cdot p(I, t_0) = e^{i\kappa I_0}$$

and include initial conditions into the separation ansatz via another function $\Phi(z)$ with $z(\kappa, t) = m(\kappa) \cdot n(t)$

$$g(\kappa, t) = h(\kappa) \cdot \Phi(z) = h(\kappa) \cdot \Phi(\ell(\kappa, t))$$

and initial condition equation gives functional form of $\Phi(z)$ by inverting $z(\kappa, t_0)$ to $\kappa(z, t_0)$

$$g(\kappa, t_0) = h(\kappa) \cdot \Phi(z(\kappa, t_0)) = e^{i\kappa I_0}$$

Including initial conditions

$$g(\kappa, t_0) = h(\kappa) \cdot \Phi(z(\kappa, t_0)) = e^{i\kappa I_0}$$

resulting in $e^{-i\kappa} = e^{-i\kappa}(z, t_0)$ as function of z and t_0 as

$$e^{-i\kappa} = 1 - z^i e^{\beta^* t_0}$$

and

$$\Phi(z) = \left(1 - z^i e^{\beta^* t_0}\right)^{N - I_0}$$

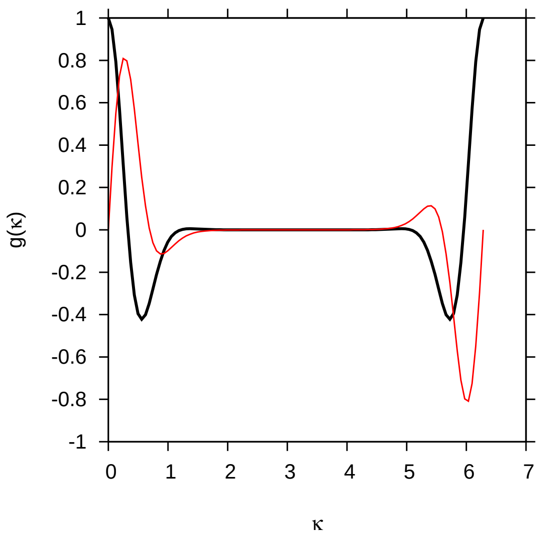
Solution of characteristic function

the solution for all times, including the initial conditions, is now given by

$$g(\kappa, t) = h(\kappa) \cdot \Phi(z(\kappa, t))$$

resulting in

$$g(\kappa, t) = e^{i\kappa N} \cdot \left(e^{-i\kappa} e^{-\beta^*(t-t_0)} + (1 - e^{-\beta^*(t-t_0)}) \right)^{N-I_0}$$



real and imaginary part of $g(\kappa)$ for fixed t

Solution of characteristic function

the solution for all times, including the initial conditions, is now given by

$$g(\kappa, t) = h(\kappa) \cdot \Phi(z(\kappa, t))$$

resulting in

$$g(\kappa, t) = e^{i\kappa N} \cdot \left(e^{-i\kappa} e^{-\beta^*(t-t_0)} + (1 - e^{-\beta^*(t-t_0)}) \right)^{N-I_0}$$

and with $p(I,t) = \frac{1}{N+1} \sum_{k=0}^{N} e^{-i\frac{2\pi}{N+1}k \cdot I} \cdot g(\kappa(k), t)$
(Fourier back-transformation)

$$p(I,t) = \begin{pmatrix} N - I_0 \\ I - I_0 \end{pmatrix} \left(e^{-\beta^*(t-t_0)} \right)^{N-I} \left(1 - e^{-\beta^*(t-t_0)} \right)^{I-I_0}$$

this is also the transition probability $p(I, t | I_0, t_0)$
needed for the likelihood function

Stochastic simulation

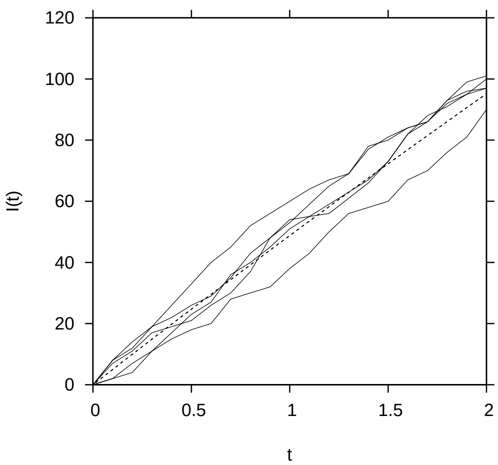
linear infection model as stochastic process

$$S + I^* \xrightarrow{\beta} I + I^*$$

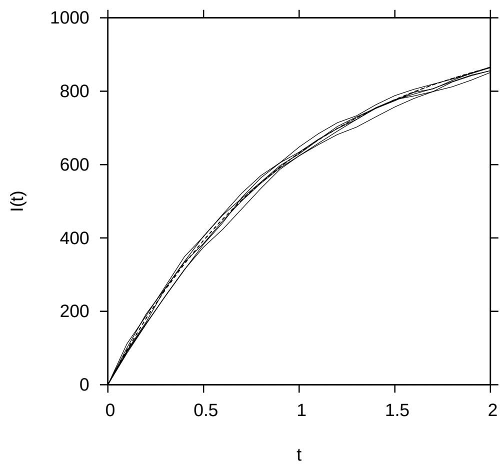
for variable I and $S = N - I$ => probab. $p(I,t)$

$$\frac{d}{dt}p(I,t) = \beta^*(N-(I-1))p(I-1,t) - \beta^*(N-I)p(I,t)$$

simulated by e.g. Gillespie algortithm



$\beta^* = 0.05$



$\beta^* = 1.0$

Stochastic simulation

linear infection model as stochastic process

$$S + I^* \xrightarrow{\beta} I + I^*$$

for variable I and $S = N - I$ => probab. $p(I,t)$

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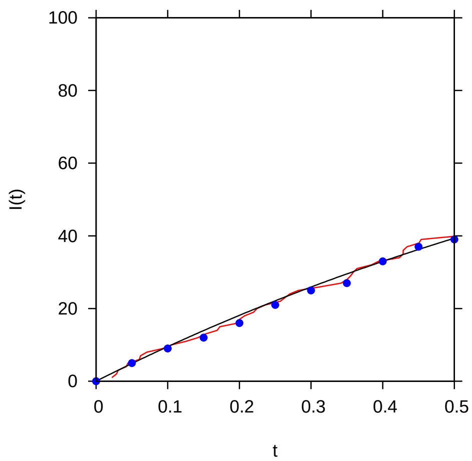

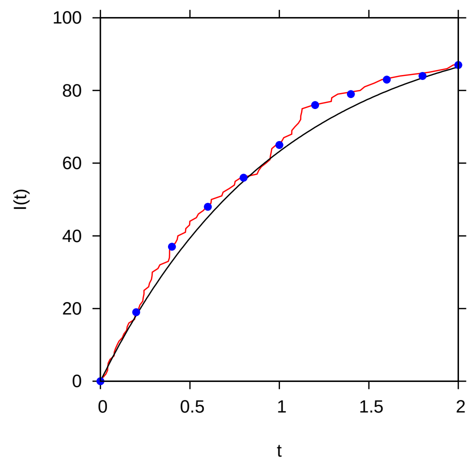

take data points for parameter estimation

Likelihood function from data $(I_0, I_1, ... I_n)$

joint probability of data points

$$p(I_n, t_n, I_{n-1}, t_{n-1}, ..., I_1, t_1, I_0, t_0) = \prod_{\nu=0}^{n-1} p(I_{\nu+1}, t_{\nu+1} | I_\nu, t_\nu) \cdot p(I_0, t_0)$$

Likelihood function from data $(I_0, I_1, ...I_n)$

joint probability of data points

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inserting solution of stochastic process

$$p(I, t | I_0, t_0) = \binom{N - I_0}{I - I_0} \left(e^{-\beta(t-t_0)}\right)^{N-I} \left(1 - e^{-\beta(t-t_0)}\right)^{I-I_0}$$

Likelihood function from data $(I_0, I_1, ... I_n)$

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inserting solution of stochastic process

$$p(I, t | I_0, t_0) = \begin{pmatrix} N - I_0 \\ I - I_0 \end{pmatrix} \left(e^{-\beta(t-t_0)} \right)^{N-I} \left(1 - e^{-\beta(t-t_0)} \right)^{I-I_0}$$

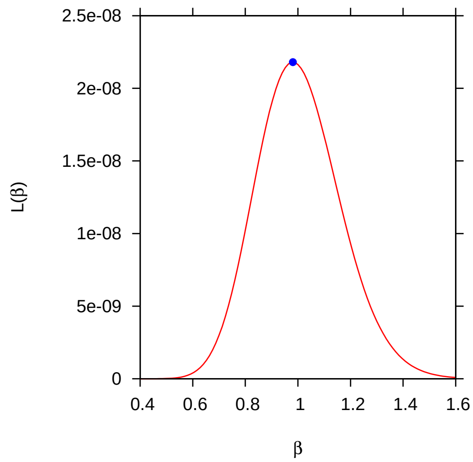
gives likelihood function

$$L(\beta) = \prod_{\nu=0}^{n-1} \begin{pmatrix} N - I_\nu \\ I_{\nu+1} - I_\nu \end{pmatrix} \left(e^{-\beta(\Delta t)} \right)^{N-I_{\nu+1}} \left(1 - e^{-\beta(\Delta t)} \right)^{I_{\nu+1}-I_\nu}$$

Likelihood function from data $(I_0, I_1, ...I_n)$

likelihood function

$$L(\beta) = \prod_{\nu=0}^{n-1} \binom{N - I_\nu}{I_{\nu+1} - I_\nu} \left(e^{-\beta(\Delta t)}\right)^{N - I_{\nu+1}} \left(1 - e^{-\beta(\Delta t)}\right)^{I_{\nu+1} - I_\nu}$$



Likelihood function from data $(I_0, I_1, ... I_n)$

likelihood function

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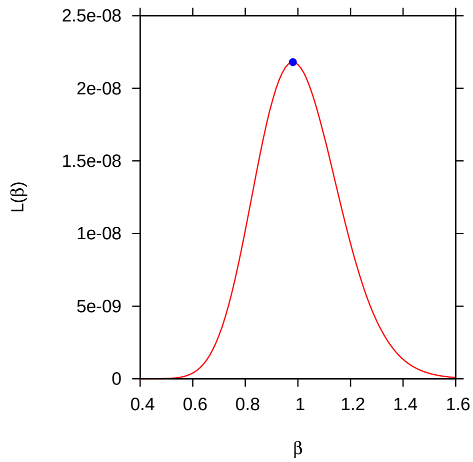


maximizing the likelihood $\frac{\partial L}{\partial \beta} = 0$ gives best estimator

$$\hat{\beta} = \frac{1}{\Delta t} \cdot ln \left(\frac{N - \frac{1}{n} \sum_{\nu=0}^{n-1} I_\nu}{N - \frac{1}{n} \sum_{\nu=0}^{n-1} I_{\nu+1}} \right)$$

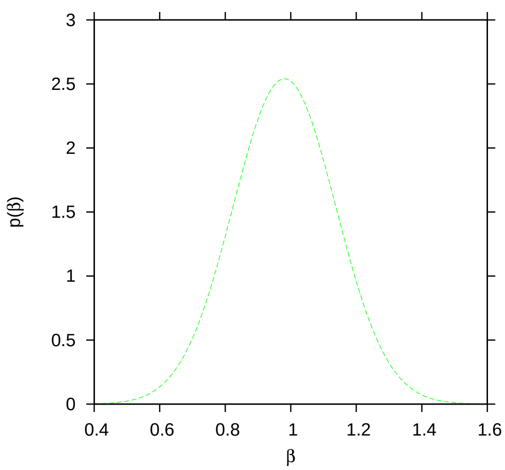
Confidence intervals via Fisher information

assume Gaussianity around the maximum of likelihood

$$p(\beta) := \frac{1}{\sigma\sqrt{2\pi}} e^{\frac{(\beta-\hat{\beta})^2}{2\sigma^2}}$$

second derivative around maximum gives σ

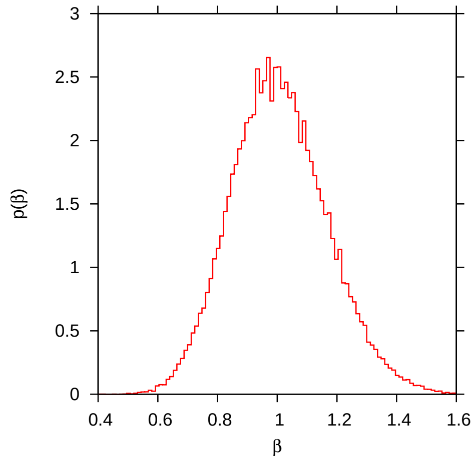
$$\left.\frac{\partial^2 p(\beta)}{\partial \beta^2}\right|_{\beta=\hat{\beta}} = -\frac{1}{\sigma} \quad , \quad \sigma = -\frac{1}{\left.\frac{\partial^2 L(\beta)}{\partial \beta^2}\right|_{\beta=\hat{\beta}}}$$



Experiment: many realizations

simulate many realizations of stochastic process

take histogram of best estimates



Gaussian approximation compares relatively well

Experiment: many realizations

simulate many realizations of stochastic process

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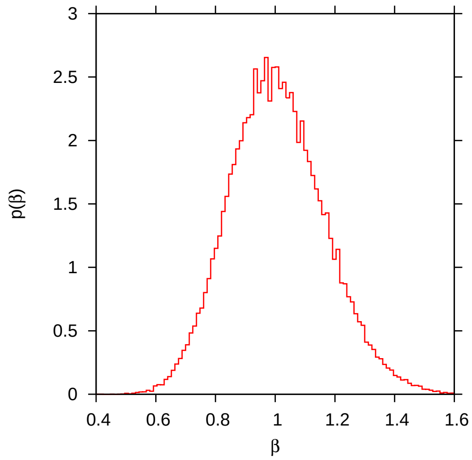

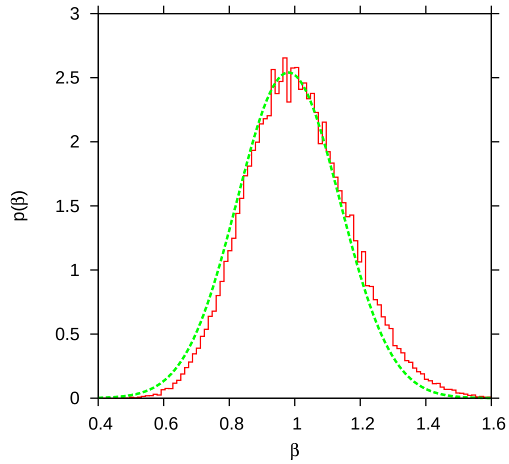

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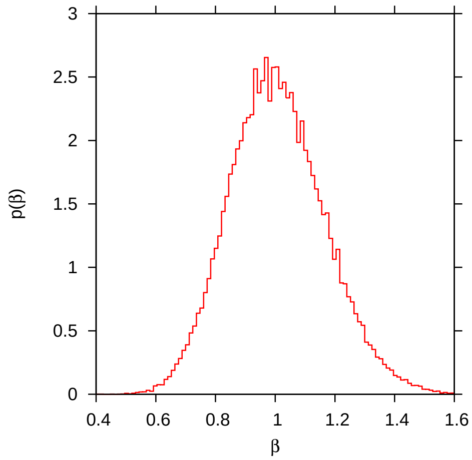
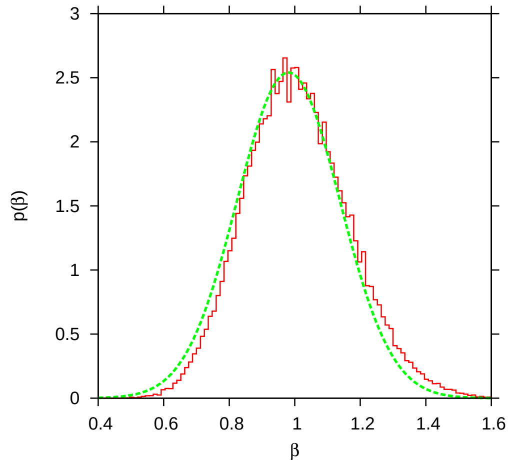




Gaussian approximation compares relatively well

but can be improved :-)

Bayesian approach to improve conf. int.

as before data vector $\underline{I} = (I_0, I_1, ...I_n)$ consider joint probability of data and parameter

$$p(\beta, \underline{I}) = p(\underline{I}, \beta)$$

gives via conditional probabilities $p(\beta|\underline{I}) \cdot p(\underline{I}) = p(\underline{I}|\beta) \cdot p(\beta)$ the probabiltiy of the parameter given the data $p(\beta|\underline{I})$, the Bayesian posterior

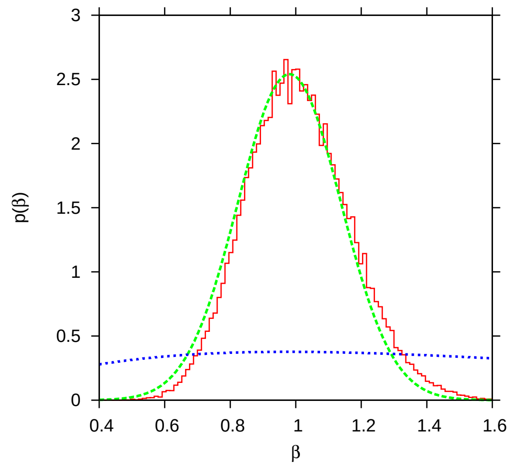
$$p(\beta|\underline{I}) = \frac{p(\underline{I}|\beta)}{p(\underline{I})}\, p(\beta)$$

again with previously used likelihood funcition $p(\underline{I}|\beta)$

Bayesian approach to improve conf. int.

$$p(\beta|\underline{I}) = \frac{p(\underline{I}|\beta)}{p(\underline{I})}\, p(\beta)$$

with previously used likelihood funcition $p(\underline{I}|\beta)$



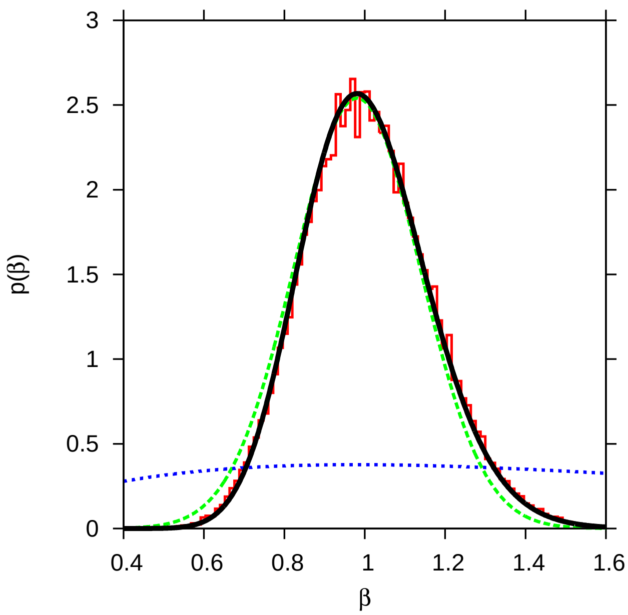
conjugate prior is a beta-distribution with parameters a and b

Bayesian posterior

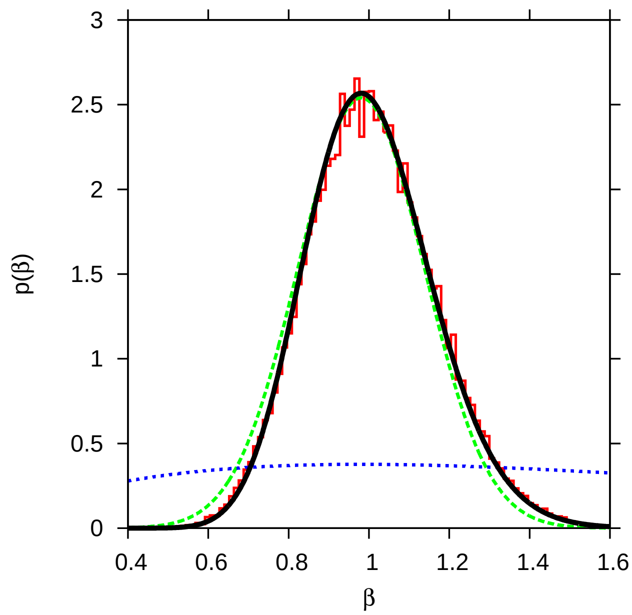
after some calculation

$$p(\beta|\underline{I}) \;=\; \frac{\Gamma(a+b+\sum_{\nu=0}^{n-1}(N-I_\nu))}{\Gamma(a+\sum_{\nu=0}^{n-1}(I_{\nu+1}-I_\nu))\;\Gamma(b+\sum_{\nu=0}^{n-1}(N-I_{\nu+1}))}$$

$$\cdot\left(1-e^{-\beta\Delta t}\right)^{a+\sum_{\nu=0}^{n-1}(I_{\nu+1}-I_\nu)-1}\;\left(e^{-\beta\Delta t}\right)^{b+\sum_{\nu=0}^{n-1}(N-I_{\nu+1})-1}\cdot e^{-\beta\Delta t}\cdot\Delta t$$

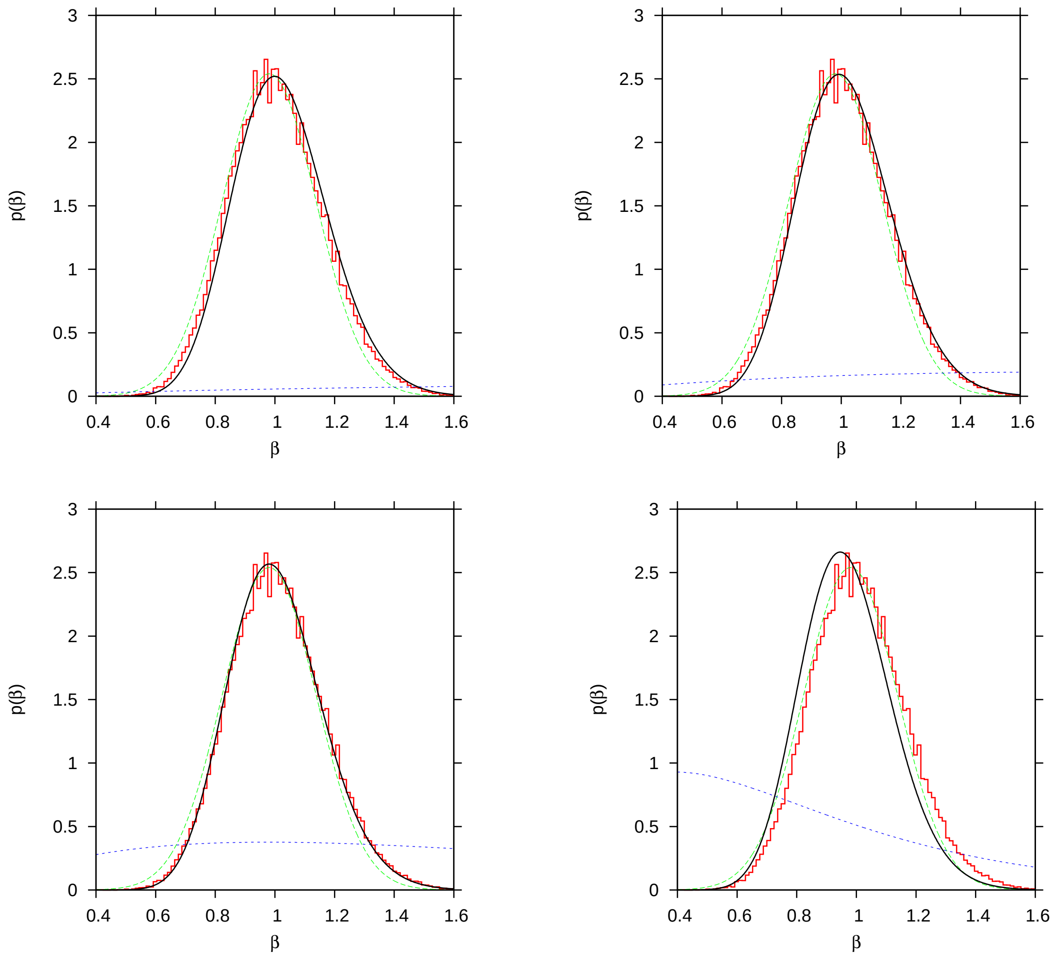


Bayesian posterior

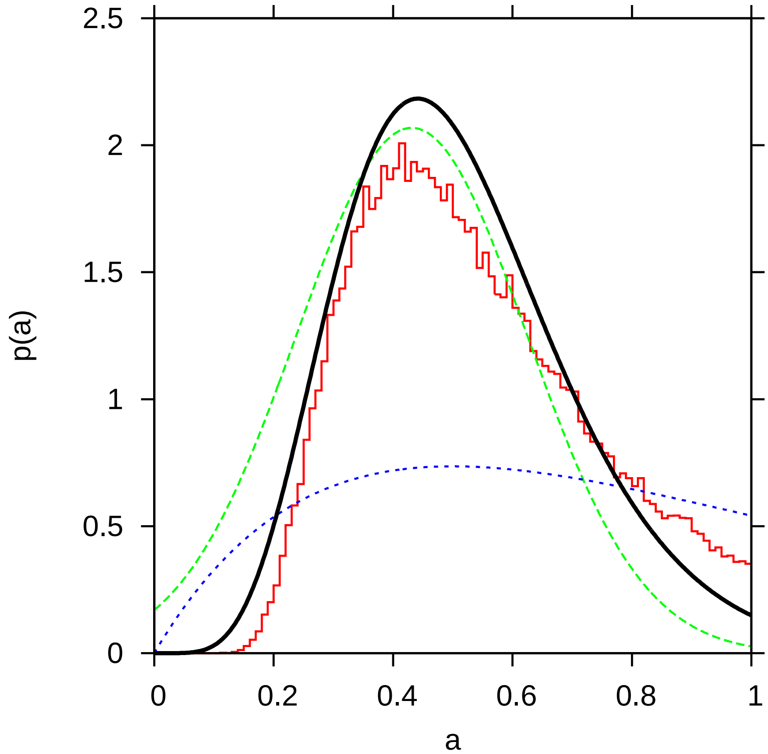


when using soft prior and with good data, the likelihood function carries most of the information

Changing Bayesian prior



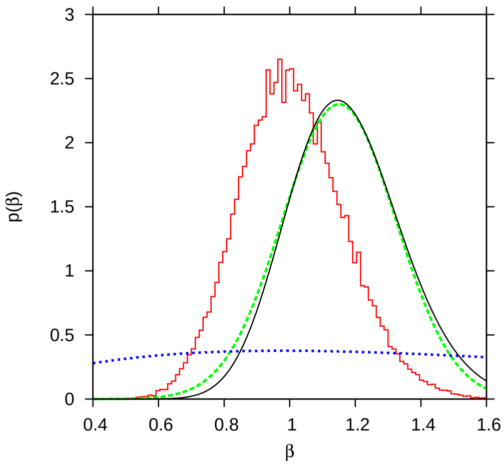
Another example: estimating exponential distribution



the effects are even more pronounced

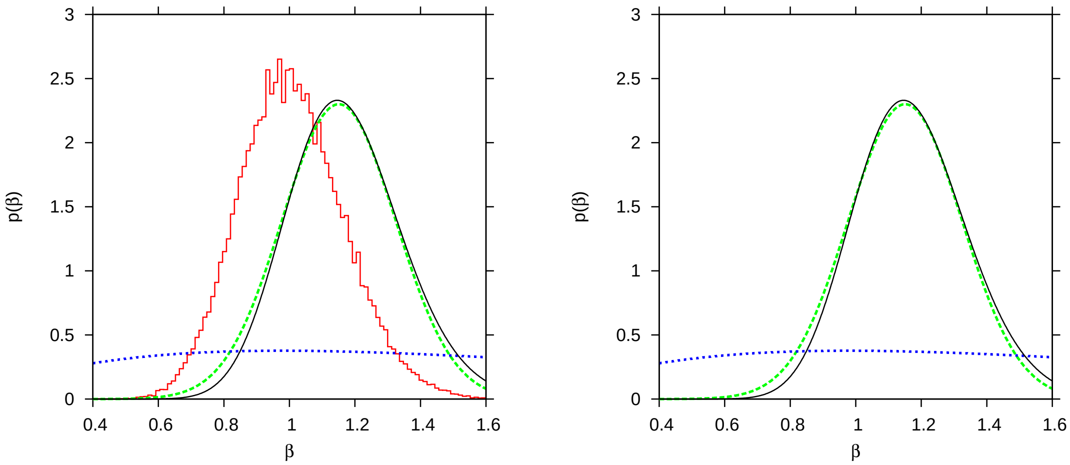
Empirical situation

observed realisation might be "atypical"



Empirical situation

observed realisation might be "atypical"



and we might never know how atypical our data are

Likelihood function from data $(I_0, I_1, ... I_n)$

joint probability of data points

$$p(I_n, t_n, I_{n-1}, t_{n-1}, ..., I_1, t_1, I_0, t_0) = \prod_{\nu=0}^{n-1} p(I_{\nu+1}, t_{\nu+1} | I_\nu, t_\nu) \cdot p(I_0, t_0)$$

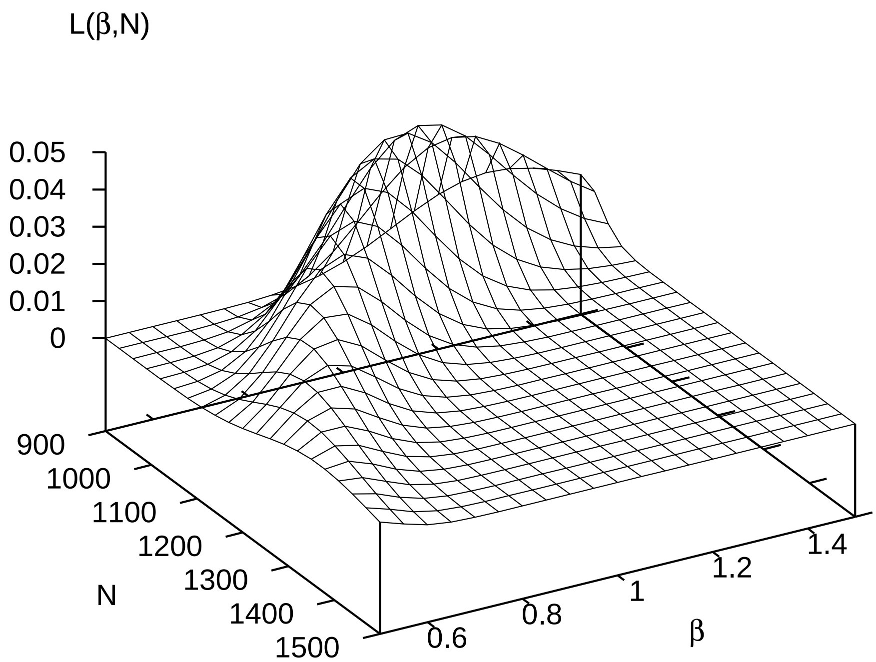
inserting solution of stochastic process

$$p(I, t | I_0, t_0) = \begin{pmatrix} N - I_0 \\ I - I_0 \end{pmatrix} \left(e^{-\beta(t-t_0)}\right)^{N-I} \left(1 - e^{-\beta(t-t_0)}\right)^{I-I_0}$$

gives likelihood function

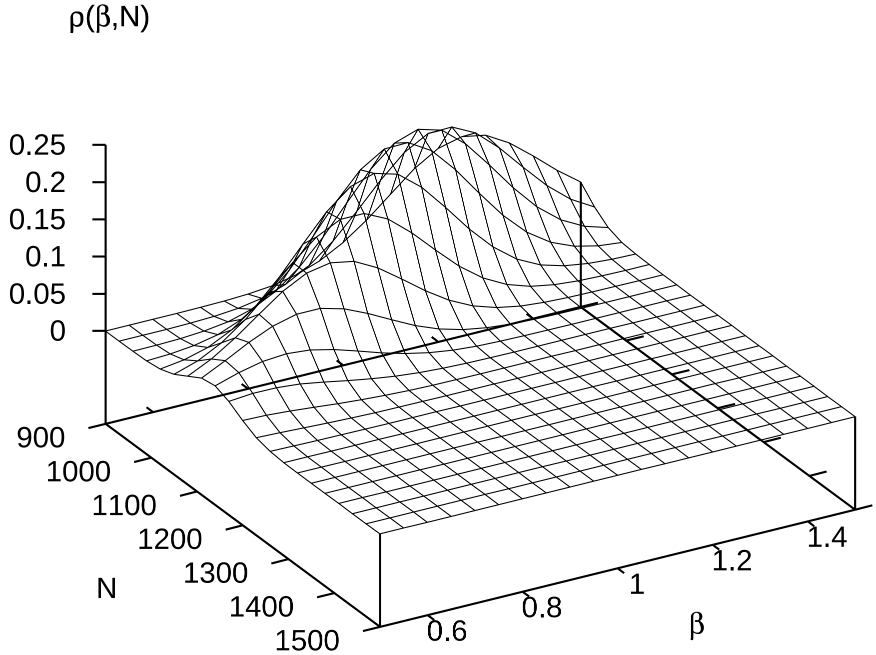
$$L(\beta, N) = \prod_{\nu=0}^{n-1} \begin{pmatrix} N - I_\nu \\ I_{\nu+1} - I_\nu \end{pmatrix} \left(e^{-\beta(\Delta t)}\right)^{N-I_{\nu+1}} \left(1 - e^{-\beta(\Delta t)}\right)^{I_{\nu+1}-I_\nu}$$

Likelihood function



Likelihood per data point

Likelihood function



Gaussian approximation

Generalization to further models: Euler-multinomial approximation

approximation for small time steps $\Delta t = t - t_0$

$$S + I_0 \xrightarrow{\beta} I + I_0$$

gives stochastic process for decay of suseptibles S

$$\frac{d}{dt} p(S,t) \; = \; \frac{\beta}{N} I_0 (S+1) p(S+1,t) - \frac{\beta}{N} I_0 S p(S,t)$$

giving

$$p(S,t|S_0,t_0) = \left(\begin{array}{c} S_0 \\ S \end{array} \right) \left(e^{-\frac{\beta}{N} I_0 (t-t_0)} \right)^{S} \left(1 - e^{-\frac{\beta}{N} I_0 (t-t_0)} \right)^{S_0 - S}$$

updating at time t_1 to $S_1 = S$ and $I_1 = I_0 + (S_0 - S_1)$ giving

$$p(S_1, t_0 + \Delta t|S_0,t_0) = \left(\begin{array}{c} S_0 \\ S_1 \end{array} \right) \left(e^{-\frac{\beta}{N} I_0 \Delta t} \right)^{S_1} \left(1 - e^{-\frac{\beta}{N} I_0 \Delta t} \right)^{S_0 - S_1}$$

Generalization to further models: Euler-multinomial approximation

approximation for small time steps $\Delta t = t - t_0$

$$S + I_0 \xrightarrow{\beta} I + I_0$$

gives stochastic process for decay of suseptibles S

$$\frac{d}{dt}p(S,t) \;=\; \frac{\beta}{N}I_0(S+1)p(S+1,t) - \frac{\beta}{N}I_0 S p(S,t)$$

giving

$$p(S,t|S_0,t_0) = \begin{pmatrix} S_0 \\ S \end{pmatrix} \left(e^{-\frac{\beta}{N}I_0(t-t_0)}\right)^S \left(1 - e^{-\frac{\beta}{N}I_0(t-t_0)}\right)^{S_0 - S}$$

updating at time t_1 to $S_1 = S$ and $I_1 = I_0 + (S_0 - S_1)$ giving

$$p(I_1, t_0 + \Delta t|I_0,t_0) = \begin{pmatrix} N - I_0 \\ N - I_1 \end{pmatrix} \left(e^{-\frac{\beta}{N}I_0 \Delta t}\right)^{N - I_1} \left(1 - e^{-\frac{\beta}{N}I_0 \Delta t}\right)^{I_1 - I_0}$$

Generalization to further models: Euler-multinomial approximation

in the same way "decay of infected"

$$I \xrightarrow{\alpha} S$$

gives stochastic process for decay of infected I

$$\frac{d}{dt}p(I,t) \; = \; \alpha(I+1)p(I+1,t) - \alpha I p(S,t)$$

updating at time $t_0 + \Delta t$ to I_2 and $S_2 = S_0 + (I_0 - I_1)$ giving

$$p(I_2, t_0 + \Delta t | I_0, t_0) = \begin{pmatrix} I_0 \\ I_2 \end{pmatrix} \left(e^{-\alpha \Delta t}\right)^{I_2} \left(1 - e^{-\alpha \Delta t}\right)^{I_0 - I_2}$$

Generalization to further models: Euler-multinomial approximation

and putting everything together to the final update for the full SIS model

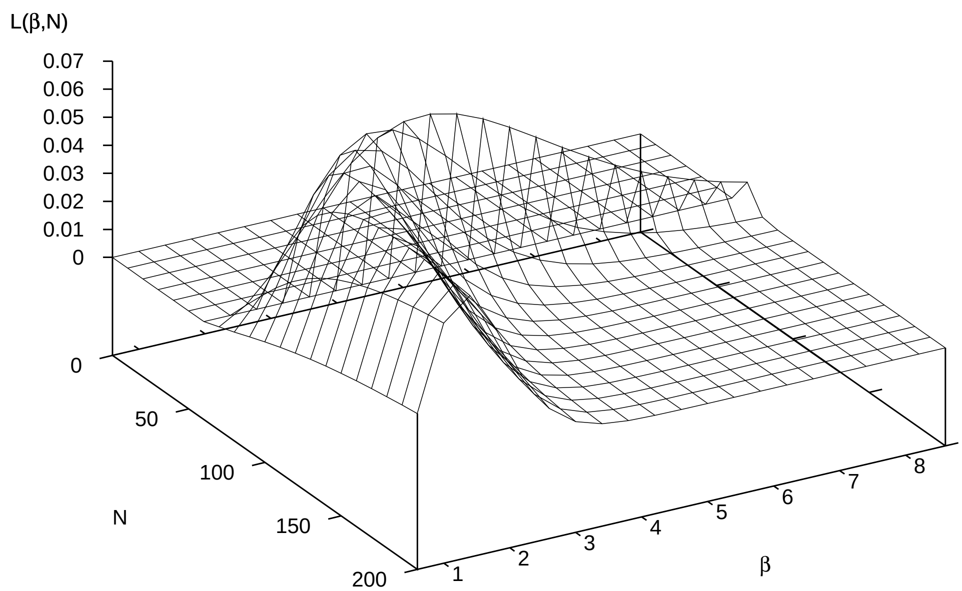
$$S + I_0 \xrightarrow{\beta} I + I_0$$
$$I \xrightarrow{\alpha} S$$

gives with update rules $I_t = I_0 + I_1 - (N - I_2)$ and its stocahstic version $p(I_t|I_1, I_2) = \delta_{I_2, N-I_0+I_t-I_1}$

$$p(I_t, t|I_0, t_0) = \sum_{I_1=0}^{N-I_0} \sum_{I_2=0}^{I_0} p(I_t|I_1, I_2) \cdot p(I_2, t_0 + \Delta t|I_0, t_0) \cdot p(I_1, t_0 + \Delta t|I_0, t_0)$$

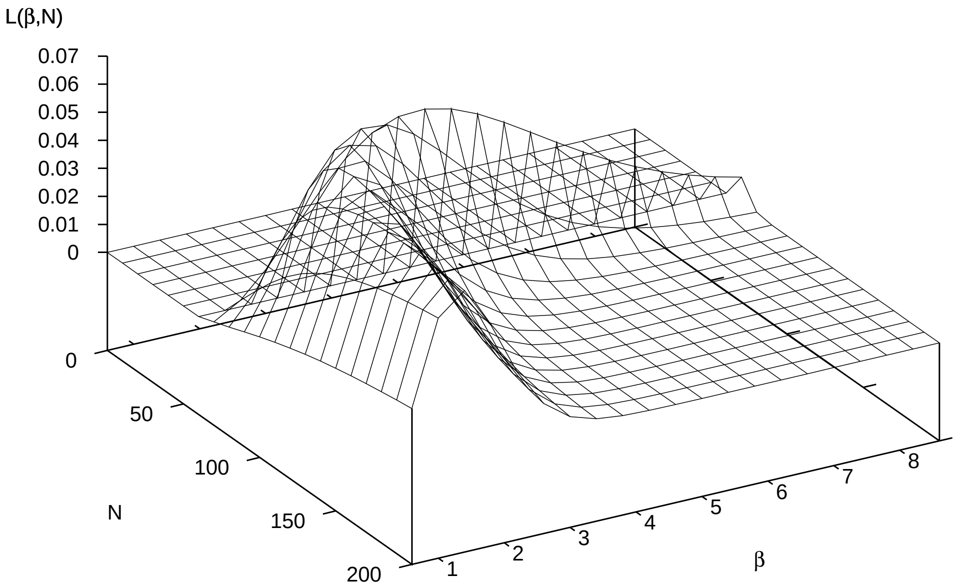
and from this again the likelihood, but sticking with eventually large summations in it

Likelihood function: Euler-multinomial approximation



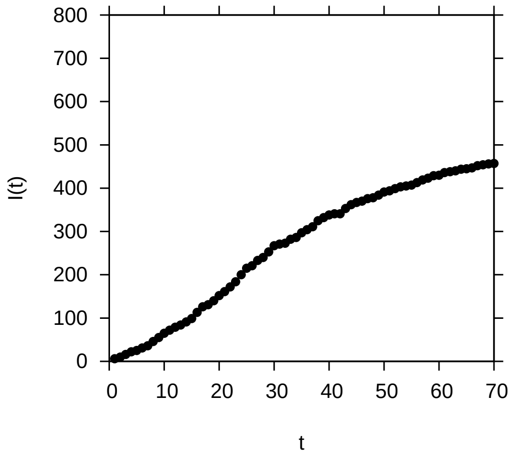
Likelihood per data point

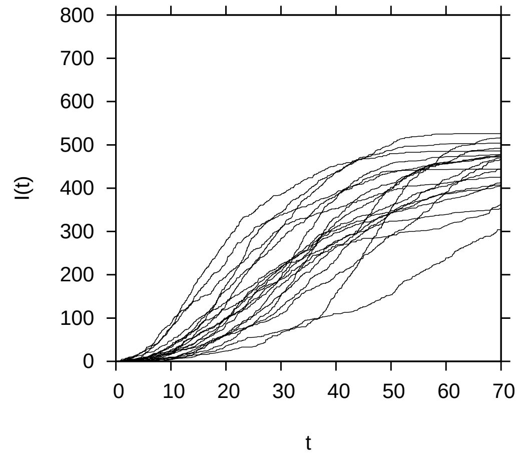
Likelihood function: Euler-multinomial approximation



likelihood profile versus likelihood section

Comparison of data with simulations





flu data cumulative **simulations of SIR-system**

number of simulations in η-ball vicinity to data set gives likelihood of data under this model parameter set

=> estimate of likelihood function (Stollenwerk, Briggs 2000)

Comparison of data with simulations

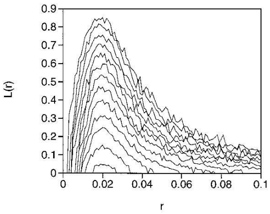


Fig. 4. Empirical likelihood curves for the one parameter r for various values of η-neighbourhoods. The maximum does not change much with varying η, showing that the estimate for the parameter is rather robust.

mates of the parameters used for our likelihood sections are obtained with this method.

From the Padé approximation in Section 6 instead of likelihood sections we could also easily generate likelihood profiles as described for example in Ref. [12]. These profiles are calculated by varying one parameter and maximizing the likelihood in respect to all other model parameters, which is rather cumbersome for the Empirical Likelihood Method due to the fluctuations around the empirical likelihood maximum (see Fig. 4). In biological systems one often has information about some of the model parameters from other experiments and searches for an otherwise difficult obtainable parameter like the contact rate, which is r in our case. In such situations the Empirical Likelihood Method is easiest and best applicable. However, we have also investigated empirical likelihoods with variation of two parameters [11].

8. Summary and prospect

We have solved the Master equation for a plant disease model analytically and also obtained numerically stable solutions over the whole range of states, which was previously not possible using the matrix exponential.

The solution is used for constructing likelihood sections from empirical microcosm data. The Master equation approach can be easily generalized to more complex models, allowing for likelihood estimations on the basis of simulated trajectories. Further research on this Empirical Likelihood Method is in progress.

The form of the Master equation we use here gives exponential waiting times between events and in the Gillespie algorithm this property is used explicitly to construct stochastic realizations of the process. However, the exponential waiting time is not a principal restriction, but arbitrary waiting time distributions can be included in a Master equation with time-convolution [13,14]. It would be an interesting extension of the present work to combine numerically this time-convolved Master equation with our Empirical Likelihood Method.

Also the Master equation approach opens naturally the way to a Fock space formulation of stochastic processes [15] which is easily generalizable to the field theoretic treatment of spatial epidemic systems see Ref. [16], and related Refs. [17–21]). Such a field theory is needed to describe the underlying experimental system more appropriately, as first experiments by Bailey et al. indicate [22]). The time decaying susceptibility drives the system through a threshold region between a simple spreading regime and a non-spreading regime.

Acknowledgements

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[3] A. Kleczkowski, D.J. Bailey, C.A. Gilligan, Proc. R. Soc. (London) B 263 (1996) 777.
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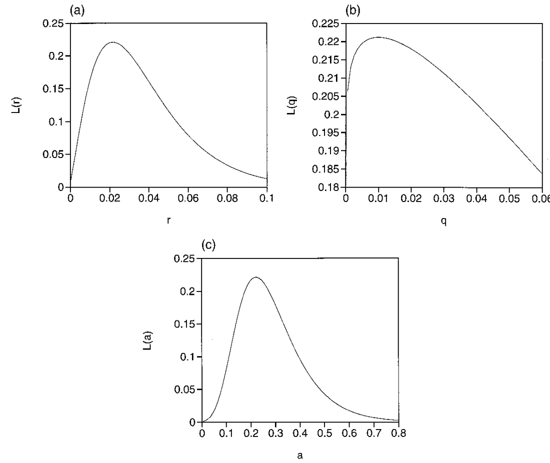


Fig. 3. Likelihood sections for all three parameters, i.e. variation of one parameter, keeping the others fixed at their maximal values, as obtained from the likelihood maximization. The estimates are: $r = 0.022$, $q = 0.0099$ and $a = 0.22$.

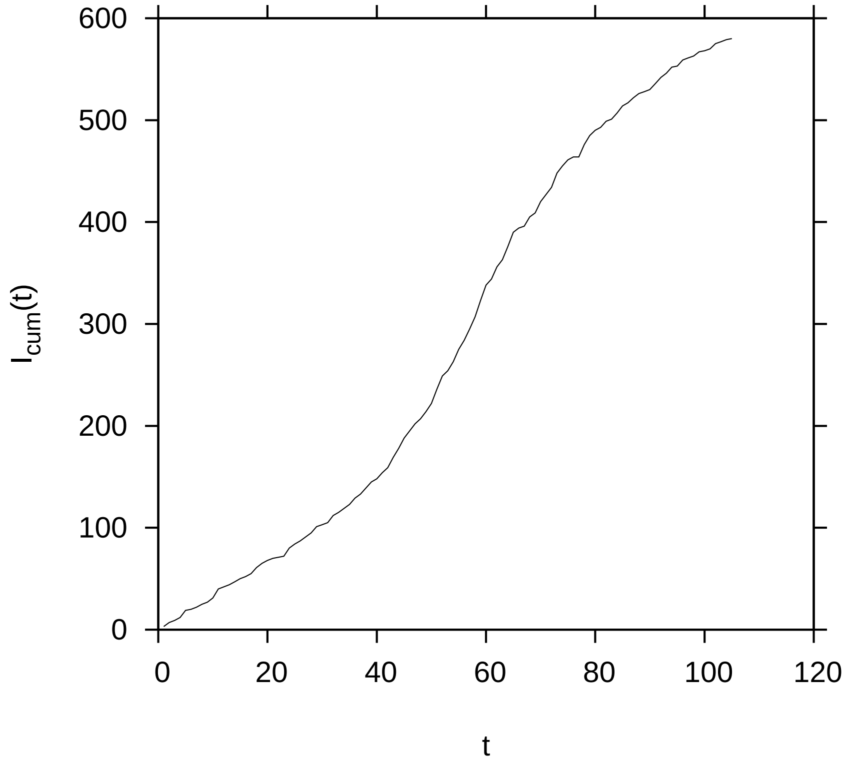
using the β-recursion, i.e. using Eq. (14). We obtained in this way the same value for L from both methods. Only the machine precision prevented using the β-recursion for higher values of k_i.

7. Empirical likelihood

The above mentioned solution cannot be carried through to more general Master equations, which have different time-dependent transition rates for different transitions as likely in multicompartmental models, for example models with an additional exposed class (SEI models) between susceptible and infected classes (as in the SI models we consider here). Still, the single trajectory simulation method holds for time-dependent multicompartment models and even can be used for constructing empirically obtained likelihoods. We experimented with such a method by estimating the joint probability of the data, that is, Eq. (12), directly from simulated stochastic trajectories. In the space of dimensionality of the number of data points the estimate is given by using balls around the measured data with radius η (η-balls) and counting the number of simulated trajectories inside these neighborhoods (for details see a forthcoming article by Stollenwerk [11]). The esti-

estimate of likelihood function (Stollenwerk, Briggs 2000)

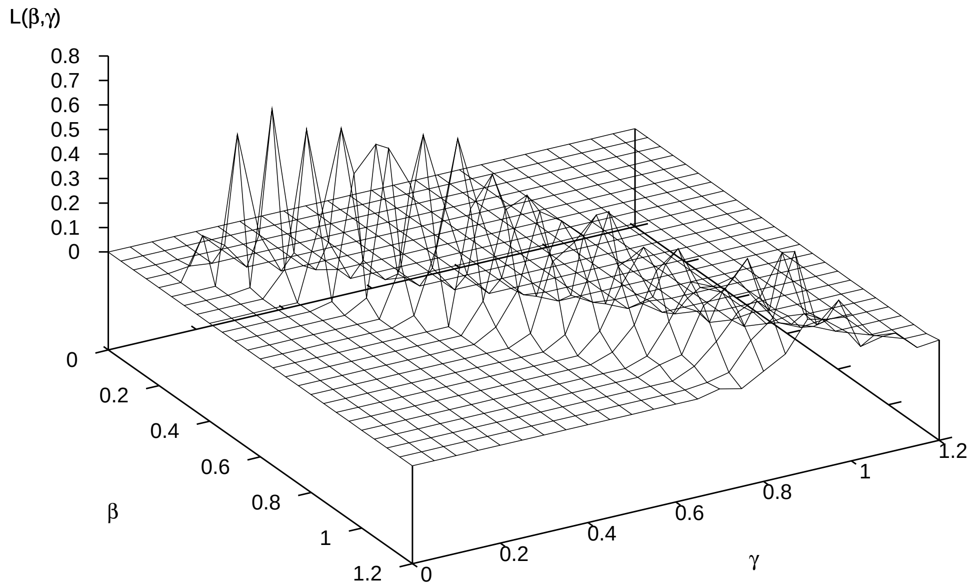
η-ball method for Dutch influenza data



daily influenza data between 1st of January and 15th of April 2007 for the Netherlands (from InfluenzaNet, EPIWORK project)

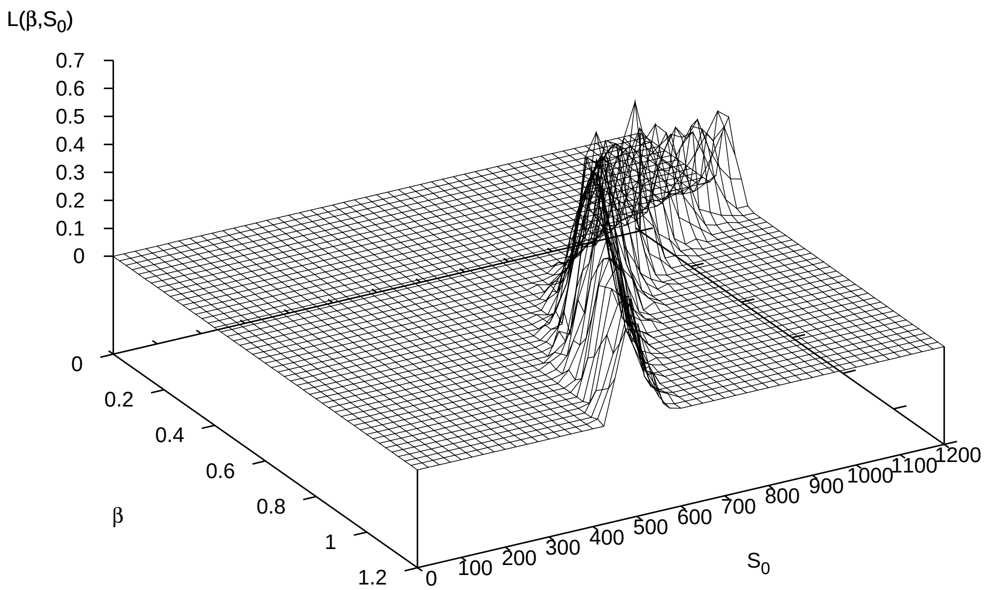
... to be compared with SIR stochastic simulations for various parameter values

Estimated likelihood function



Likelihood per data point

Estimated likelihood function



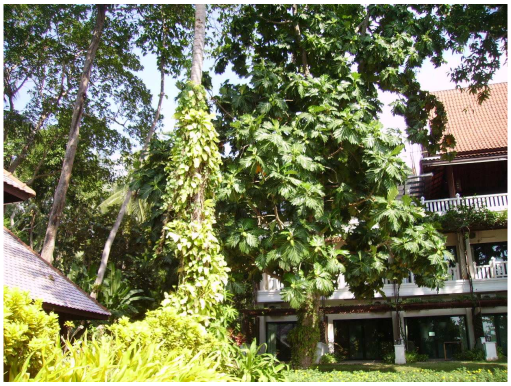
Likelihood per data point

Application to dengue data from Thailand

rural

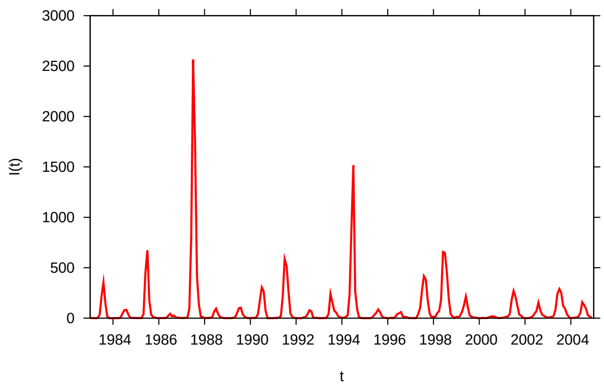
urban

Application to dengue data from Thailand

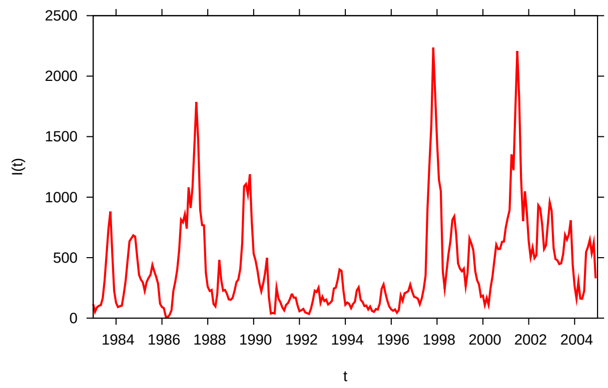


rural **urban**

Application to dengue data from Thailand



Chiang Mai province

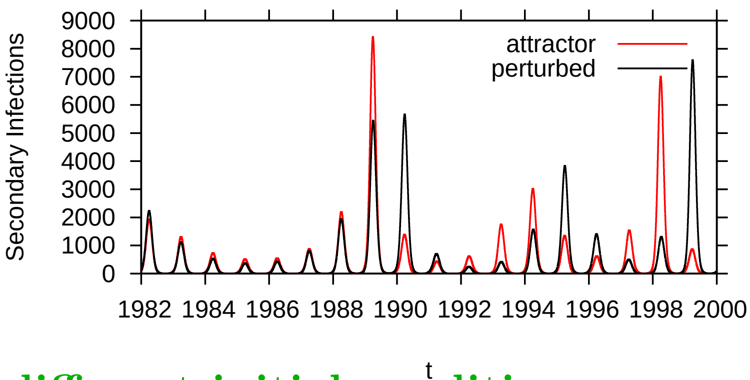


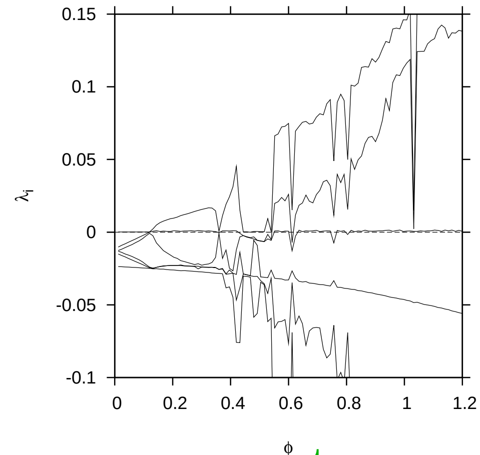
Bangkok

Deterministic Chaos (UPCA):

short term predictability, long term unpred.

example dengue without seasonality and import (Aguira et al. 2011)



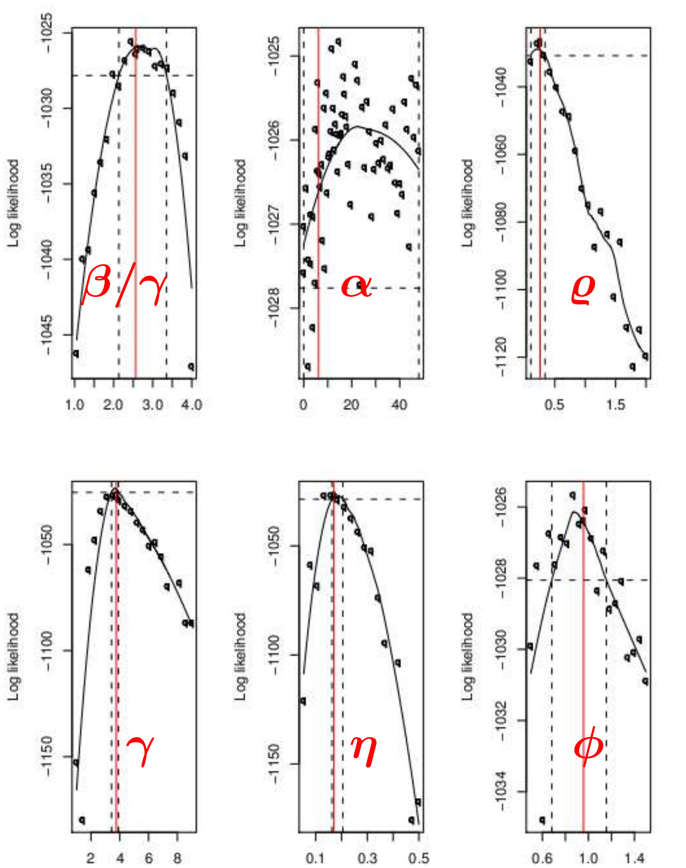


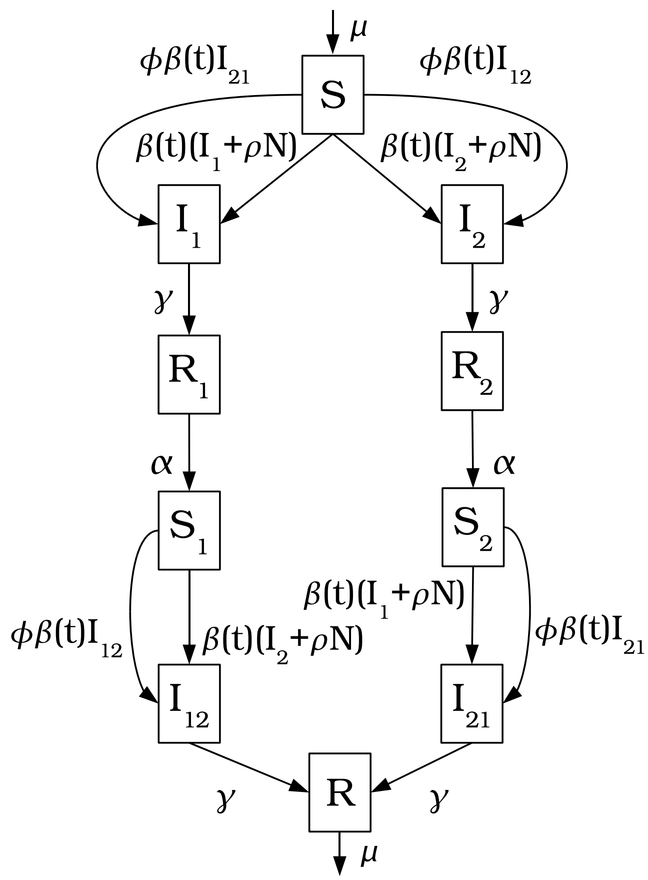
different initial conditions

Lyapunov spectrum

implications for data analysis: Maximum Likelihood Iterated Filtering (MIF) is choice for such systems (Ionides et al 2006/ Bretó et al. 2009),

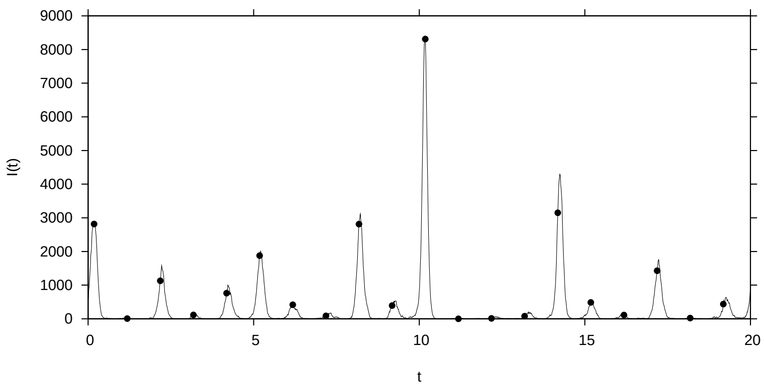
Likelihood profiles for Chiang Mai



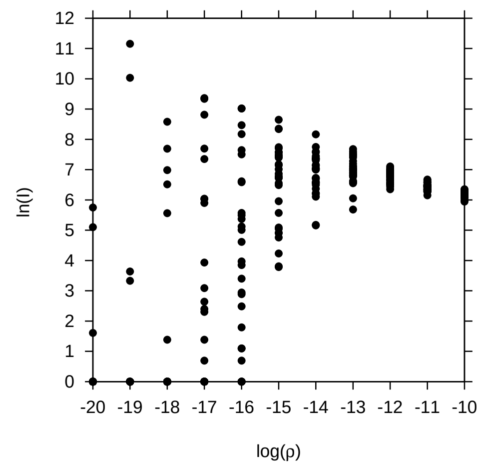


scattered likelihood estimates, large confidence intervals

Stochastic simulations with estimated parameters

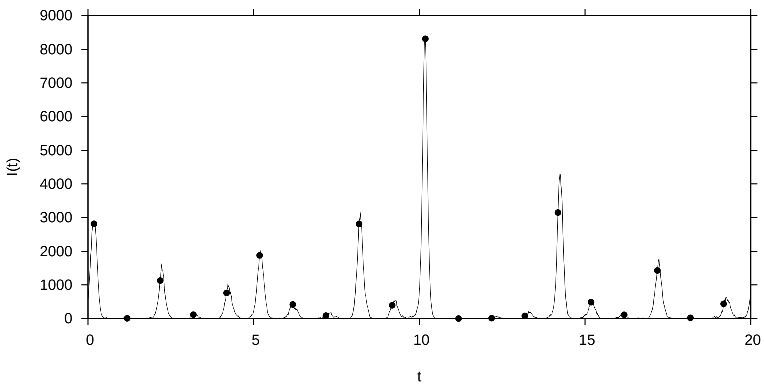


time series simulation

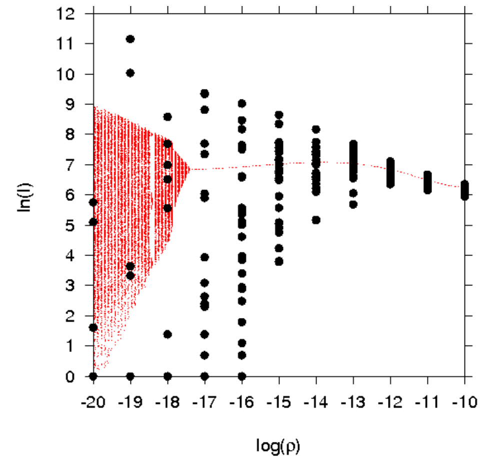


stoch. bif. diag.

Stochastic simulations with estimated parameters



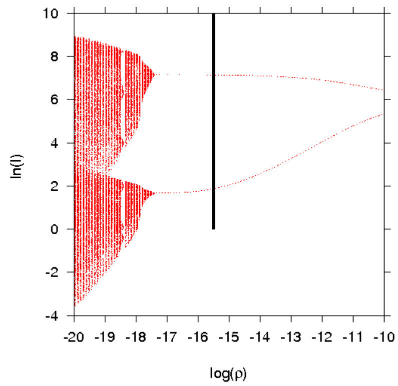
time series simulation



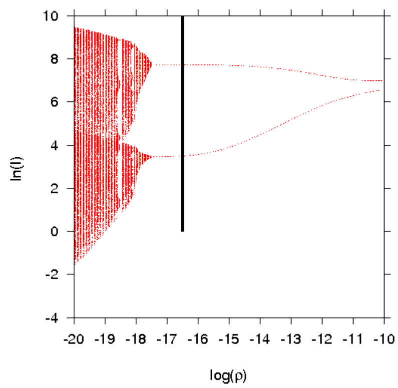
stoch. bif. diag.

Estimating import at different spatial scales

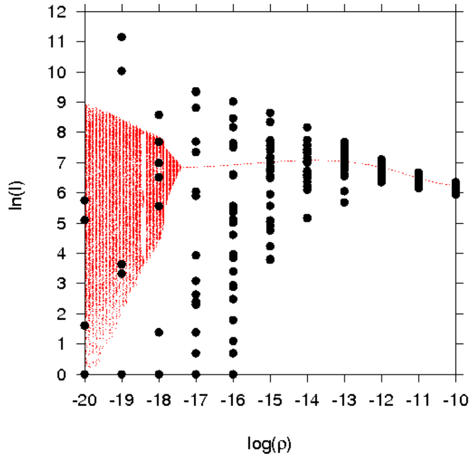
estimates from Chiang Mai

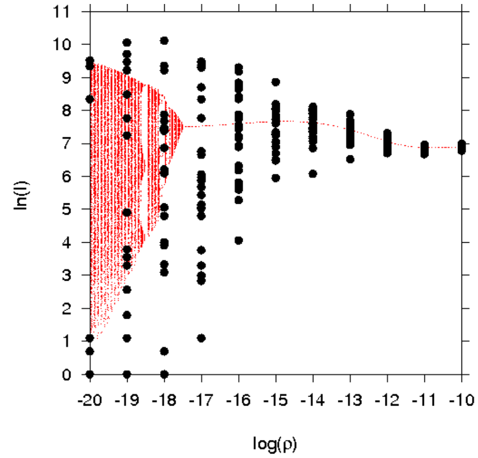


estimates from 9 Northern Thai Provinces



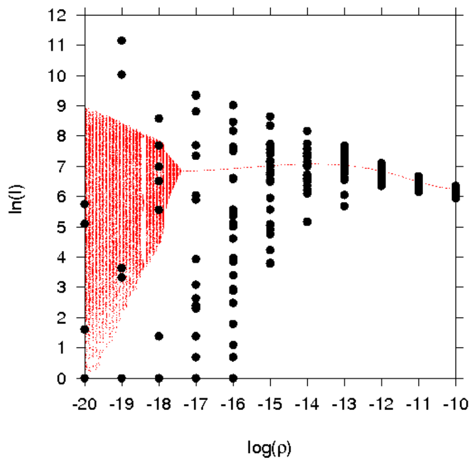
Parameter estimation in dengue: scaling with noise



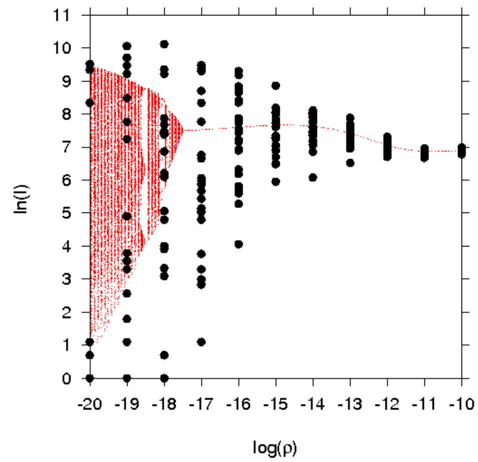


Chiang Mai $N \approx 1$ mio.　　**North $N \approx 6$ mio**

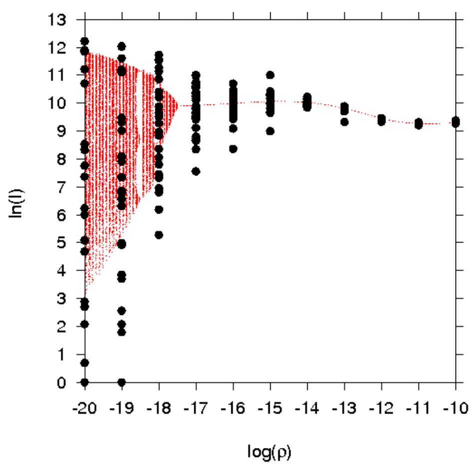
Parameter estimation in dengue: scaling with noise



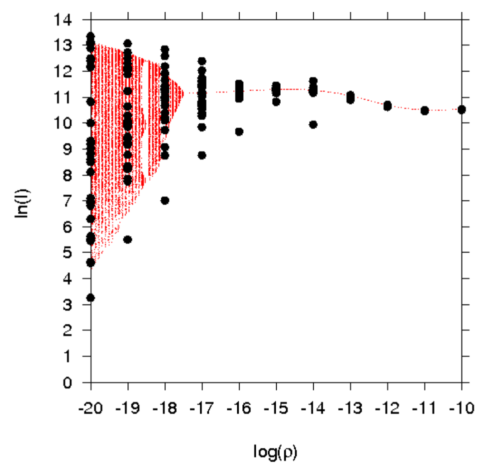
Chiang Mai $N \approx 1$ mio.



North $N \approx 6$ mio

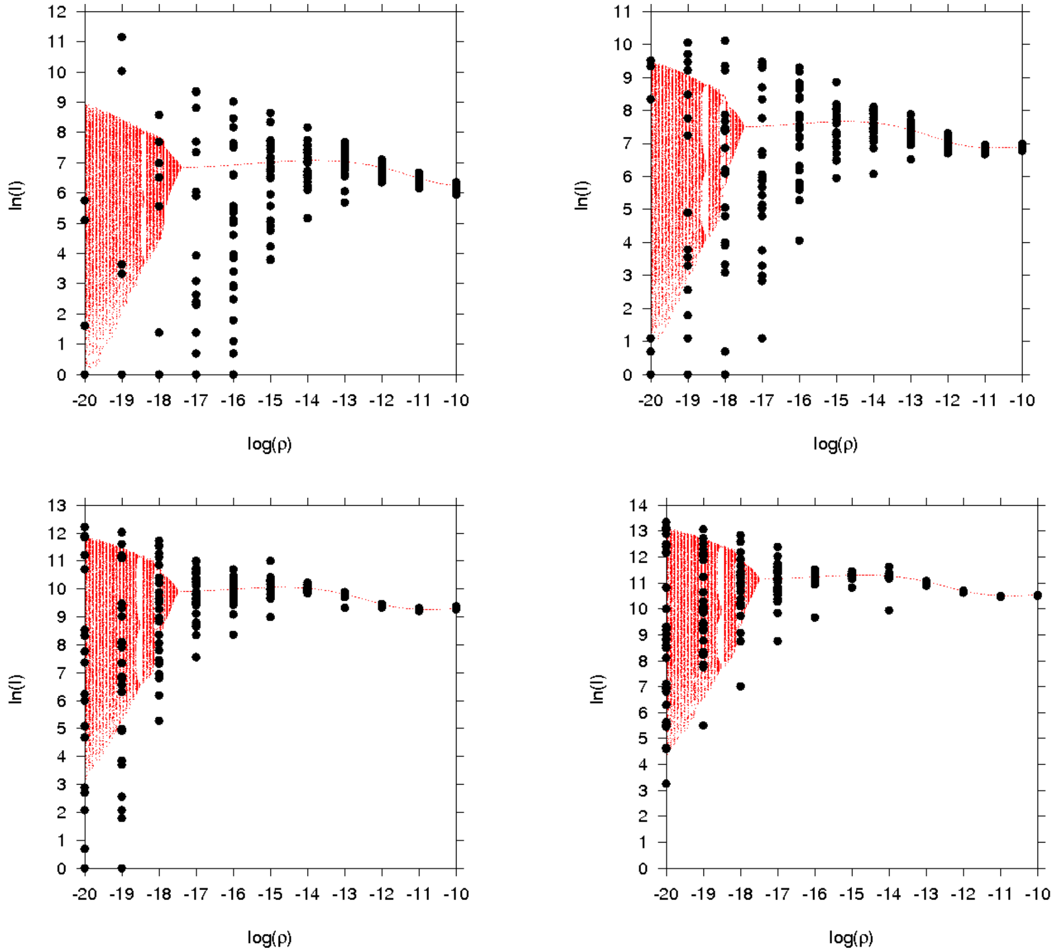


Thailand $N \approx 60$ mio.



East Asia $N \approx 250$ mio

Parameter estimation in dengue: scaling with noise



A fresh look to Iterated Filtering

to include dynamic noise appropriately

algorithmic descritption after Bretó et al. 2009:

MODEL INPUT: $f(\cdot)$, $g(\cdot|\cdot)$, $y_1, ..., y_N$, $t_0, ..., t_N$

ALGORITHMIC PARAMETERS: integers J, L, M;
scalars $0 < a < 1$, $b > 0$; vectors $X_I^{(1)}$, $\theta^{(1)}$;
positive definite symmetric matrices Σ_I ,Σ_θ.

1. FOR $m = 1$ to M
2. $\quad X_I(t_0, j) \sim N[X_I^{(m)}, a^{m-1}\Sigma_I], \quad j = 1, ..., J$
3. $\quad X_F(t_0, j) = X_I(t_0, j)$
4. $\quad \theta(t_0, j) \sim N[\theta^{(m)}, ba^{m-1}\Sigma_\theta]$
5. $\quad \bar{\theta}(t_0) = \theta^{(m)}$
6. $\quad$ FOR $n = 1$ to N
7. $\quad\quad X_P(t_n, j) = f(X_F(t_{n-1}, j), t_{n-1}, t_n, \theta(t_{n-1}, j), W)$
8. $\quad\quad w(n, j) = g(y_n | X_P(t_n, j), t_n, \theta(t_{n-1}, j))$
9. $\quad\quad$ draw $k_1, ..., k_J$ such that $\text{Prob}(k_j = i) = w(n, i) / \sum_\ell w(n, \ell)$
10. $\quad\quad X_F(t_n, j) = X_P(t_n, k_j)$
11. $\quad\quad X_I(t_n, j) = X_I(t_{n-1}, k_j)$
12. $\quad\quad \theta(t_n, j) \sim N[\theta(t_{n-1}, k_j), a^{m-1}(t_n - t_{n-1})\Sigma_\theta]$
13. $\quad\quad$ Set $\bar{\theta}_i(t_n)$ to be the sample mean of $\{\theta_i(t_{n-1}, k_j), \ j = 1, ..., J\}$
14. $\quad\quad$ Set $V_i(t_n)$ to be the sample variance of $\{\theta_i(t_n, j), \ j = 1, ..., J\}$
15. $\quad$ END FOR
16. $\quad \theta_i^{(m+1)} = \theta_i^{(m)} + V_i(t_1) \sum_{n=1}^{N} V_i^{-1}(t_n)(\bar{\theta}_i(t_n) - \bar{\theta}_i(t_{n-1}))$
17. $\quad$ Set $X_I^{(m+1)}$ to be the sample mean of $\{X_I(t_L, j), \ j = 1, ..., J\}$
18. END FOR

RETURN
maximum likelihood estimate for parameters, $\hat{\theta} = \theta^{(M+1)}$
maximum likelihood estimate for initial values, $\hat{X}(t_0) = X_I^{(M+1)}$
maximized conditional log likelihood estimates, $\ell_n(\hat{\theta}) = log(\sum_j w(n, j)/J)$
maximized log likelihood estimate, $\ell(\hat{\theta}) = \sum_n \ell_n(\hat{\theta})$

A fresh look to Iterated Filtering

to include dynamic noise appropriately

algorithmic descritption after Bretó et al. 2009:

MODEL INPUT: $f(\cdot)$, $g(\cdot|\cdot)$, $y_1, ..., y_N$, $t_0, ..., t_N$

ALGORITHMIC PARAMETERS: integers J, L, M;
scalars $0 < a < 1$, $b > 0$; vectors $X_I^{(1)}$, $\theta^{(1)}$;
positive definite symmetric matrices Σ_I ,Σ_θ.

FOR $m = 1$ to M
- $X_I(t_0, j) \sim N[X_I^{(m)}, a^{m-1}\Sigma_I], \quad j = 1, ..., J$
- $X_F(t_0, j) = X_I(t_0, j)$
- $\theta(t_0, j) \sim N[\theta^{(m)}, ba^{m-1}\Sigma_\theta]$
- $\bar{\theta}(t_0) = \theta^{(m)}$
- FOR $n = 1$ to N
  - $X_P(t_n, j) = f(X_F(t_{n-1}, j), t_{n-1}, t_n, \theta(t_{n-1}, j), W)$
  - $w(n, j) = g(y_n | X_P(t_n, j), t_n, \theta(t_{n-1}, j))$
  - draw $k_1, ..., k_J$ such that Prob$(k_j = i) = w(n, i) / \sum_\ell w(n, \ell)$
  - $X_F(t_n, j) = X_P(t_n, k_j)$
  - $X_I(t_n, j) = X_I(t_{n-1}, k_j)$
  - $\theta(t_n, j) \sim N[\theta(t_{n-1}, k_j), a^{m-1}(t_n - t_{n-1})\Sigma_\theta]$
  - Set $\bar{\theta}_i(t_n)$ to be the sample mean of $\{\theta_i(t_{n-1}, k_j), \;\; j = 1, ..., J\}$
  - Set $V_i(t_n)$ to be the sample variance of $\{\theta_i(t_n, j), \;\; j = 1, ..., J\}$
- END FOR
- $\theta_i^{(m+1)} = \theta_i^{(m)} + V_i(t_1) \sum_{n=1}^{N} V_i^{-1}(t_n)(\bar{\theta}_i(t_n) - \bar{\theta}_i(t_{n-1}))$
- Set $X_I^{(m+1)}$ to be the sample mean of $\{X_I(t_L, j), \;\; j = 1, ..., J\}$

END FOR

RETURN
maximum likelihood estimate for parameters, $\hat{\theta} = \theta^{(M+1)}$
maximum likelihood estimate for initial values, $\hat{X}(t_0) = X_I^{(M+1)}$
maximized conditional log likelihood estimates, $\ell_n(\hat{\theta}) = log(\sum_j w(n, j)/J)$
maximized log likelihood estimate, $\ell(\hat{\theta}) = \sum_n \ell_n(\hat{\theta})$

A fresh look to Iterated Filtering

to include dynamic noise appropriately

algorithmic descritption after Bretó et al. 2009:

MODEL INPUT: $f(\cdot)$, $g(\cdot|\cdot)$, $y_1, ..., y_N$, $t_0, ..., t_N$

ALGORITHMIC PARAMETERS: integers J, L, M;
scalars $0 < a < 1$, $b > 0$; vectors $X_I^{(1)}$, $\theta^{(1)}$;
positive definite symmetric matrices Σ_I ,Σ_θ.

FOR $m = 1$ to M
    $X_I(t_0, j) \sim N[X_I^{(m)}, a^{m-1}\Sigma_I], \quad j = 1, ..., J$
    $X_F(t_0, j) = X_I(t_0, j)$
    $\theta(t_0, j) \sim N[\theta^{(m)}, ba^{m-1}\Sigma_\theta]$
    $\bar{\theta}(t_0) = \theta^{(m)}$
    FOR $n = 1$ to N
        $X_P(t_n, j) = f(X_F(t_{n-1}, j), t_{n-1}, t_n, \theta(t_{n-1}, j), W)$
        $w(n, j) = g(y_n | X_P(t_n, j), t_n, \theta(t_{n-1}, j))$
        draw $k_1, ..., k_J$ such that $\text{Prob}(k_j = i) = w(n, i) / \sum_\ell w(n, \ell)$
        $X_F(t_n, j) = X_P(t_n, k_j)$
        $X_I(t_n, j) = X_I(t_{n-1}, k_j)$
        $\theta(t_n, j) \sim N[\theta(t_{n-1}, k_j), a^{m-1}(t_n - t_{n-1})\Sigma_\theta]$
        Set $\bar{\theta}_i(t_n)$ to be the sample mean of $\{\theta_i(t_{n-1}, k_j), \ \ j = 1, ..., J\}$
        Set $V_i(t_n)$ to be the sample variance of $\{\theta_i(t_n, j), \ \ j = 1, ..., J\}$
    END FOR
    $\theta_i^{(m+1)} = \theta_i^{(m)} + V_i(t_1) \sum_{n=1}^{N} V_i^{-1}(t_n)(\bar{\theta}_i(t_n) - \bar{\theta}_i(t_{n-1}))$
    Set $X_I^{(m+1)}$ to be the sample mean of $\{X_I(t_L, j), \ \ j = 1, ..., J\}$
END FOR

RETURN
maximum likelihood estimate for parameters, $\hat{\theta} = \theta^{(M+1)}$
maximum likelihood estimate for initial values, $\hat{X}(t_0) = X_I^{(M+1)}$
maximized conditional log likelihood estimates, $\ell_n(\hat{\theta}) = log(\sum_j w(n, j)/J)$
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6. FOR $n = 1$ to N
7. $X_P(t_n, j) = f(X_F(t_{n-1}, j), t_{n-1}, t_n, \theta(t_{n-1}, j), W)$
8. $w(n, j) = g(y_n | X_P(t_n, j), t_n, \theta(t_{n-1}, j))$
9. draw $k_1, ..., k_J$ such that $\text{Prob}(k_j = i) = w(n, i) / \sum_\ell w(n, \ell)$

...

use e.g. η-balls to construct likelihood

Example study for particle filter: SIRS with seasonality and import

stochastic process

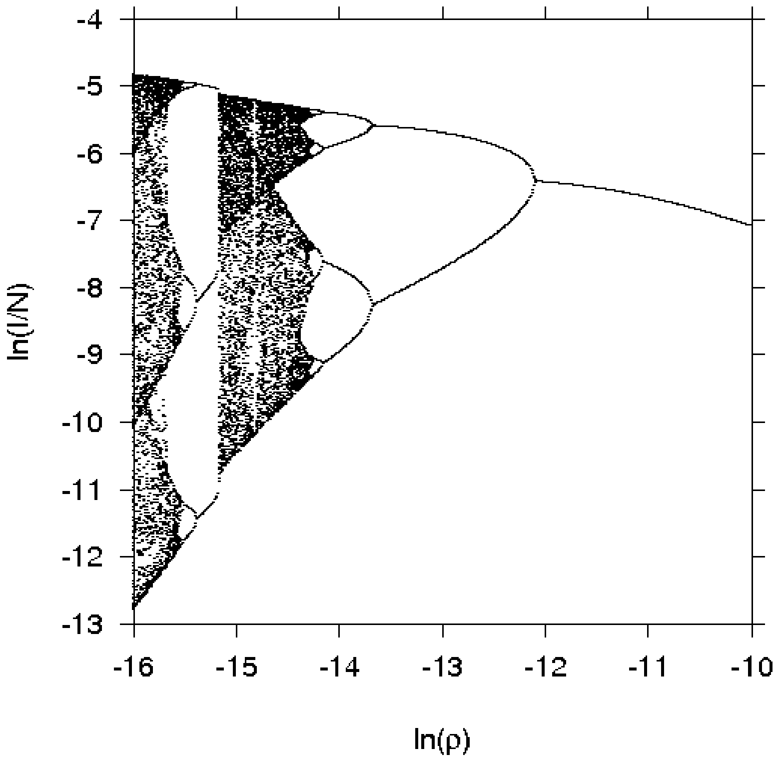
$$\begin{aligned} S + I &\xrightarrow{\beta(t)} I + I \\ I &\xrightarrow{\gamma} R \\ R &\xrightarrow{\alpha} S \\ S &\xrightarrow{\varrho} I \end{aligned}$$

with seasonal forcing given by

$$\beta(t) = \beta \cdot (1 + \theta \cdot \cos(\omega t))$$

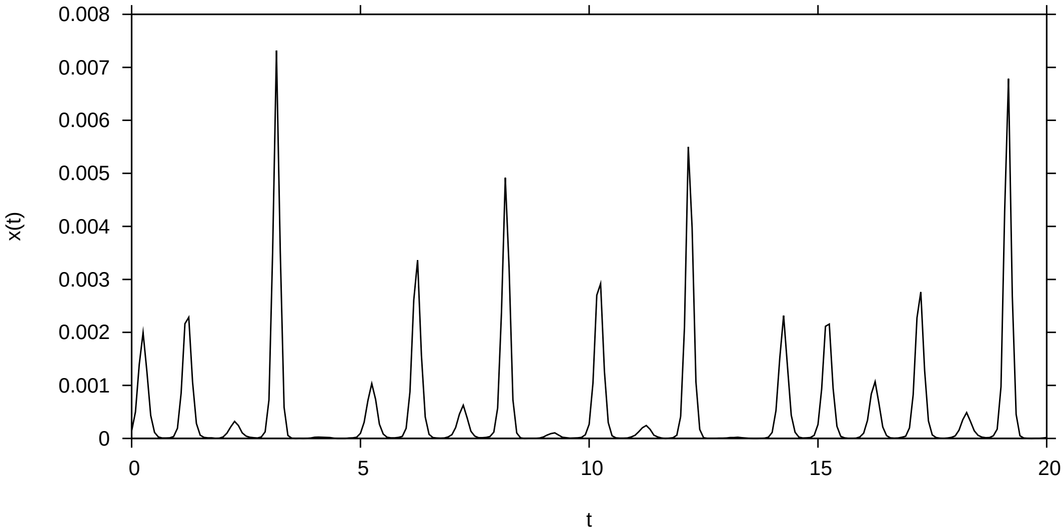
and parameters in the UPCA region, relevant for influenza, $\alpha = \frac{1}{6\text{y}}$, $\gamma = \frac{1}{3\text{d}} = \frac{365}{3}\text{y}^{-1}$, $\beta = 1.5 \cdot \gamma$, $\theta = 0.12$, $\ln(\varrho) = -15$

Example study for particle filter: SIRS with seasonality and import



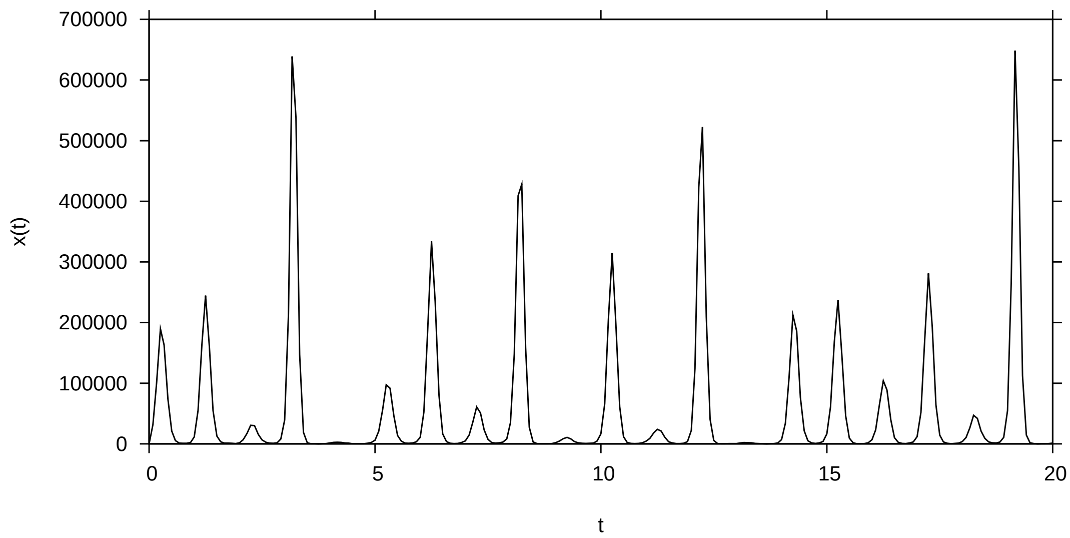
Bifurcation diagram for import $\ln(\varrho)$

Time series generated via Gillespie algorithm



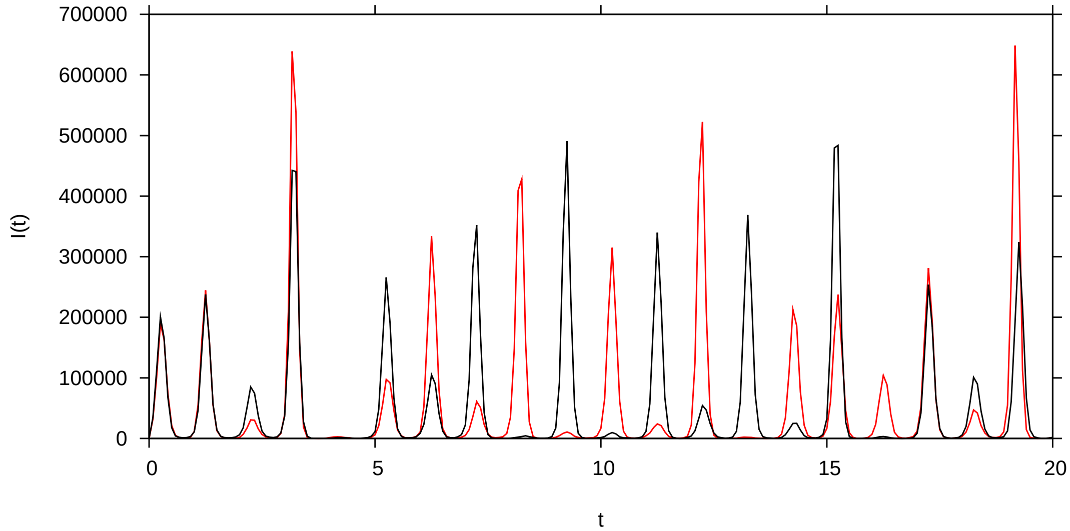
stochastic simulation with exact method, typical run

Time series generated via Gillespie algorithm



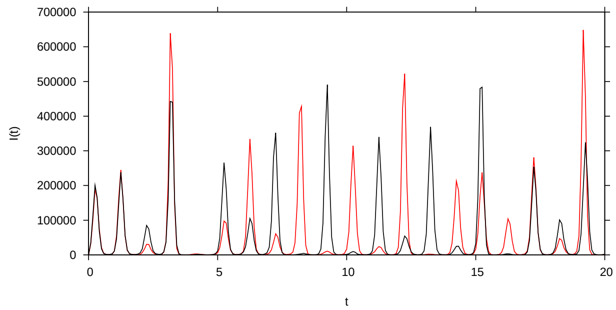
total number of incidences, serves as toy data set
monthly sampled over 20 years

Comparison with Euler-multinomial approx.

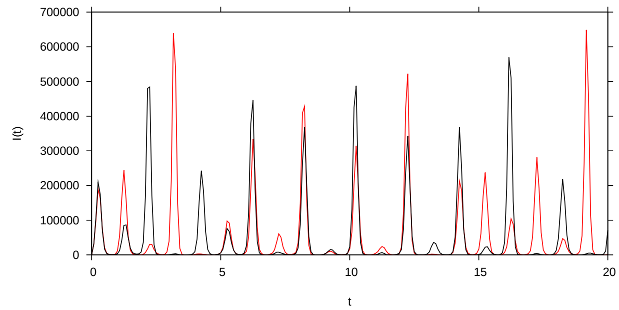


Euler multinomial approximation in black, $\Delta t = 0.001\text{d} = (0.001/365)\text{y}$

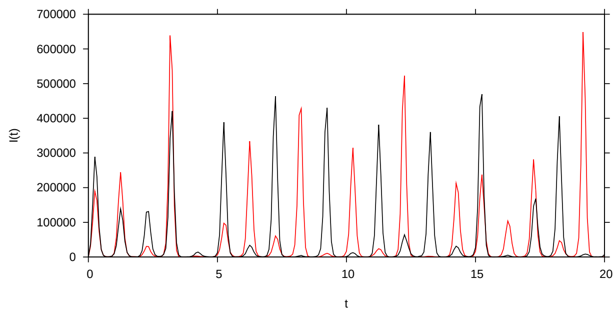
Euler-multinomial approximation: changing Δt



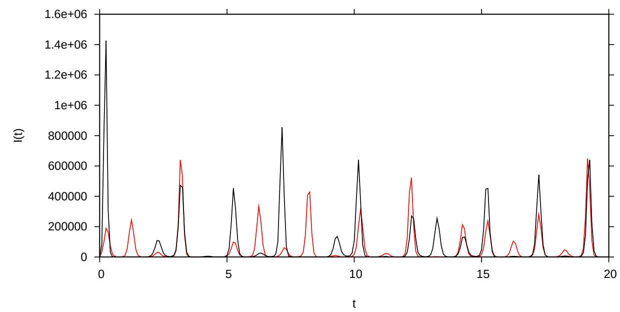
$\Delta t = 0.001\text{d}$



$\Delta t = 0.01\text{d}$

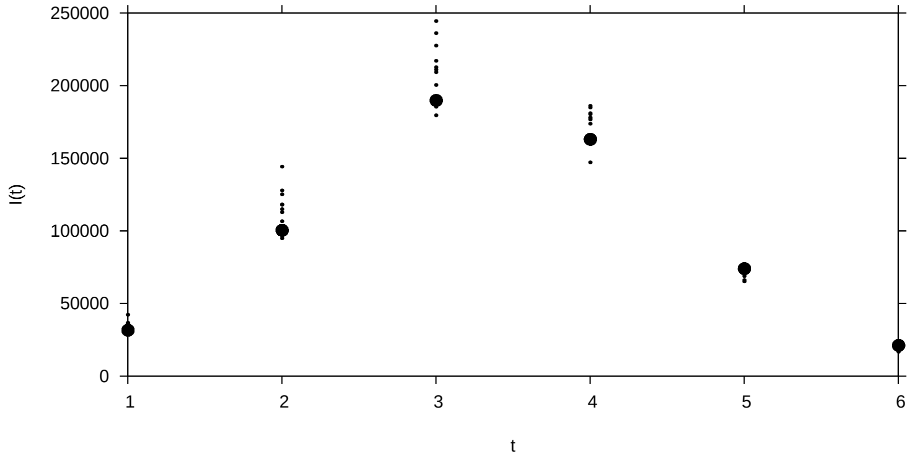


$\Delta t = 0.1\text{d}$



$\Delta t = 1\text{d}$

Constructing particle filter: particle weights from dynamic noise



cloud of simulations around the first 6 months of data
Euler-multinomial with $\Delta t = 0.01$d

Constructing particle filter: particle weights from dynamic noise

compare the data set $\underline{I}_E = (I_1, I_2, ..., I_E)$, with dimension E (here $E = 6$ months) with K Euler-multinomial simulations $\underline{I}_k(\underline{\theta}_j)$ performed with parameter set $\underline{\theta}_j$ ("particles")

$$\hat{p}(\underline{I}_E|\underline{\theta}_j) = \frac{1}{K}\sum_{k=1}^{K} H\left(\eta - ||\underline{I}_E - \underline{I}_k(\underline{\theta}_j)||_E\right)$$

simulations in η-ball around the data, with $H(x)$ being the Heaviside step function, give estimate of the time-local likelihood function $p(\underline{I}_E|\underline{\theta}_j)$, hence for $K \to \infty$ and $\eta \to 0$

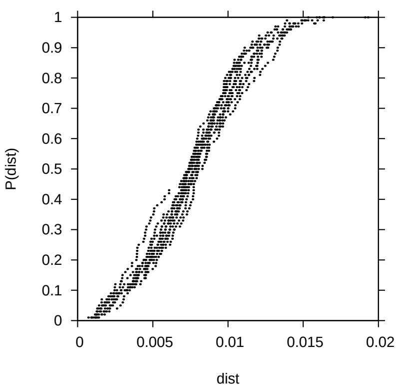
$$w_j := \hat{p}(\underline{I}_E|\underline{\theta}_j) \to p(\underline{I}_E|\underline{\theta}_j)$$

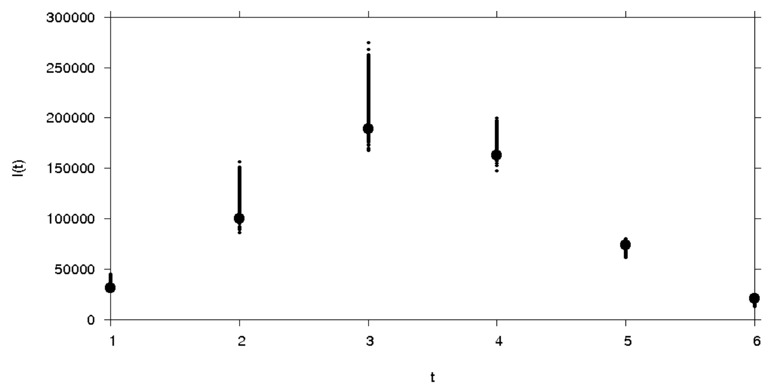
giving the weights of particles w_j for the particle filter

Constructing particle filter: distribution of distances

compare the data set $\underline{I}_E = (I_1, I_2, ..., I_E)$, with dimension E (here $E = 6$ months) with K Euler-multinomial simulations $\underline{I}_k(\underline{\theta}_j)$ performed with parameter set $\underline{\theta}_j$ ("particles")

$$\hat{p}(\underline{I}_E|\underline{\theta}_j) = \frac{1}{K}\sum_{k=1}^{K} H\left(\eta - ||\underline{I}_E - \underline{I}_k(\underline{\theta}_j)||_E\right)$$





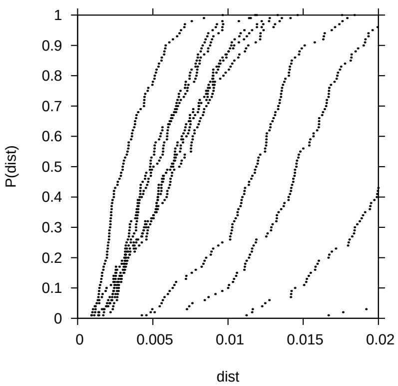
$J = 10$ particles, original parameter set $\underline{\theta}_j$, with $K = 100$ simulations each, distances $dist := ||\underline{I}_E - \underline{I}_k(\theta_j)||$

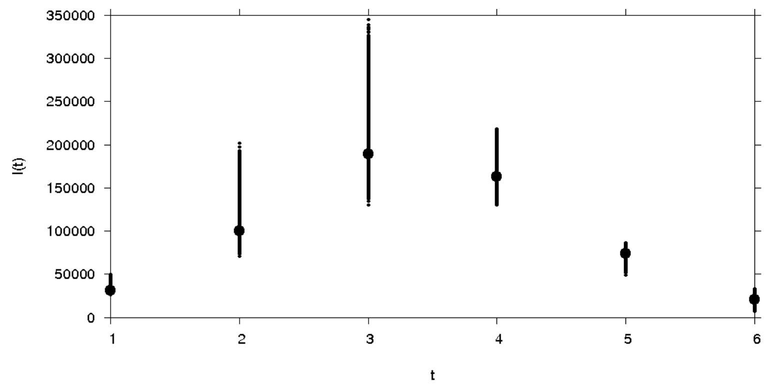
Constructing particle filter: variation of parameters

vary e.g. seasonality θ by 10% with a Gaussian distribution

$$p(\theta) = \frac{1}{\sigma\sqrt{2\pi}}\, e^{-\frac{(\theta-\mu)^2}{2\cdot\sigma^2}}$$

with $\mu = \theta_{orig} = 0.12$, the original value, and $\sigma = \mu/10$ (acts like a Gaussian prior)



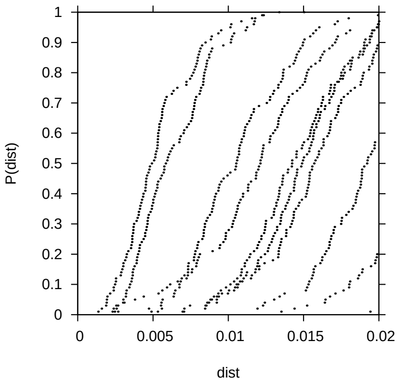


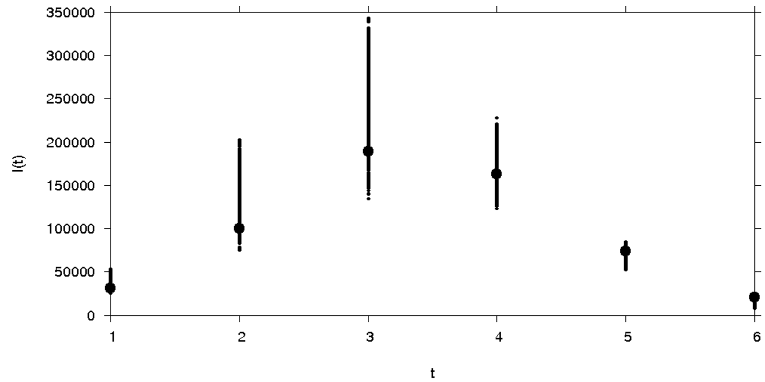
$J = 10$ particles, with $K = 100$ simulations each, most distances are larger, but some even smaller now :-)

Constructing particle filter: variation of several param. and initial cond.

vary seasonality θ, import $ln(\varrho)$ and intital conditions I_0 and R_0, all Gaussian, same order of magnitude

$$\underline{\theta} = (\theta, \varrho, I_0, R_0)$$



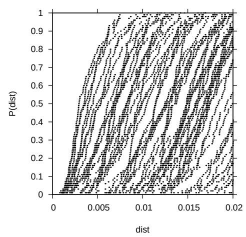


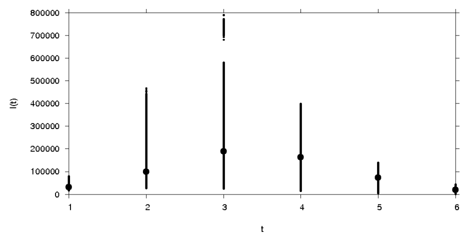
$J = 10$ particles, with $K = 100$ simulations each

Constructing particle filter: calculation of weights of each particle

weight w_j of particle $\underline{\theta}_j$ from estimating time-local likelihood function for dynamic noise

$$w_j := \hat{p}(\underline{I}_E|\underline{\theta}_j) = \frac{1}{K}\sum_{k=1}^{K} H\left(\eta - ||\underline{I}_E - \underline{I}_k(\underline{\theta}_j)||_E\right)$$





$J = 100$ particles, with $K = 100$ simulations each

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weight w_j of particle $\underline{\theta}_j$ from estimating time-local likelihood function for dynamic noise

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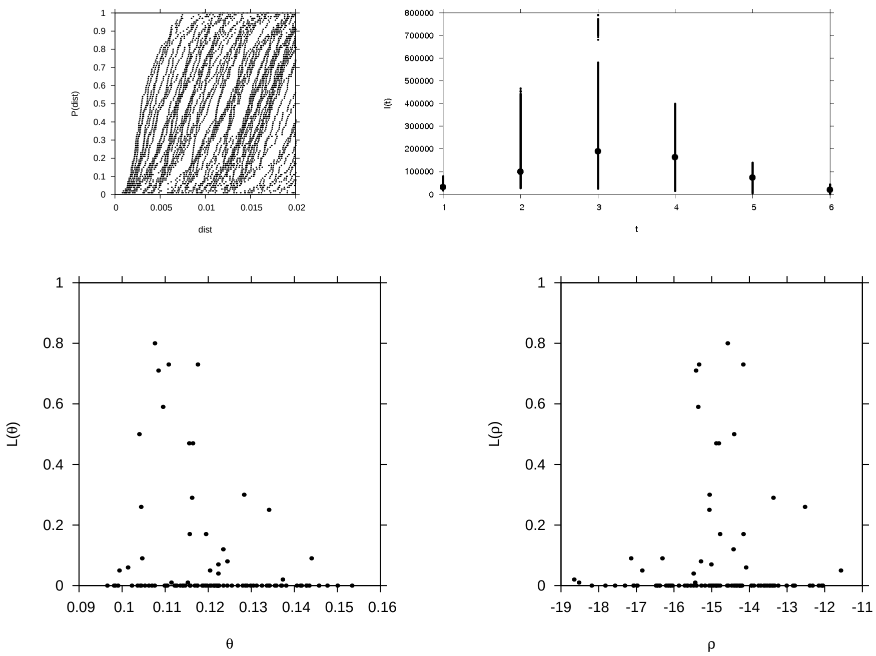
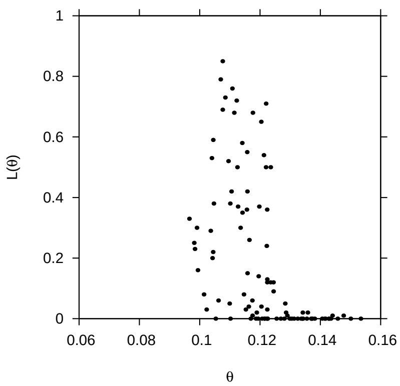
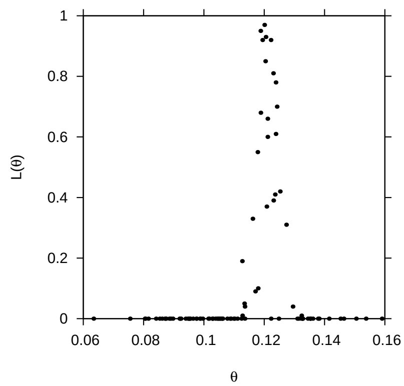


Constructing particle filter: filtering after each 6 months slice

filtering (resample) proportionally to weights w_j of particles $\underline{\theta}_j$ after each 6 months time slice, η-ball size of $\eta = 0.005$





initial distribution   final distribution of θ

Particle filter in action

now going $M = 5$ times through the time series with each $\mathcal{L} = 40$ time slices of 6 months,

starting parameter values now not any more $\theta = 0.12$, but $\theta = 0.14$, and not $ln(\varrho) = -15.0$ but $ln(\varrho) = -13.0$

simulated annealing parameters $a = 0.8$ and at each m-tour initial variance factor $b = 2$ (for details see e.g. Bretó et al. 2009), update rule with sample mean over particles $\bar{\theta}_i^{(m)}(\ell)$ at each time slice

$$\theta_i^{(m+1)} = \sum_{\ell=1}^{\mathcal{L}} \bar{\theta}_i^{(m)}(\ell)$$

Particle filter in action

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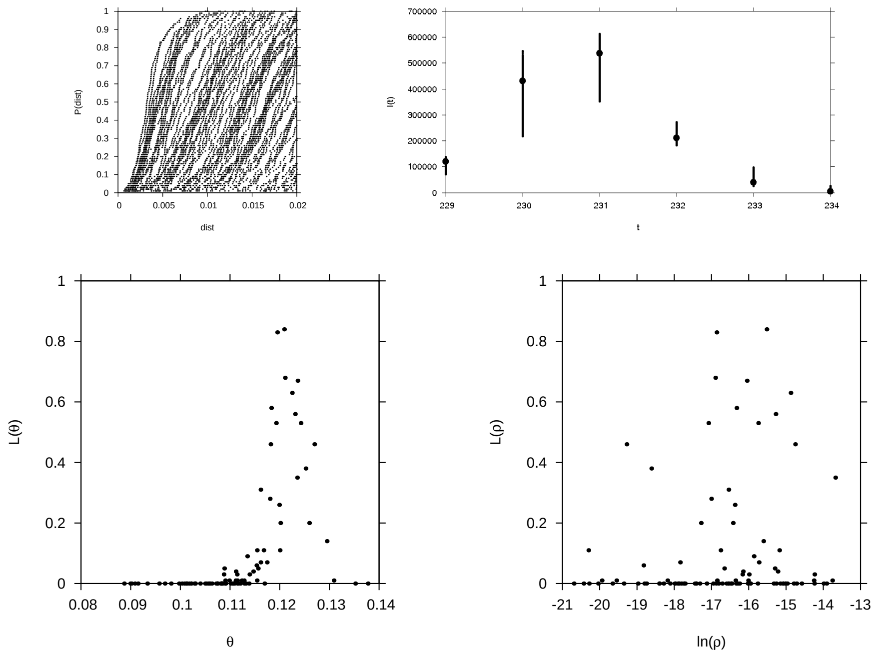
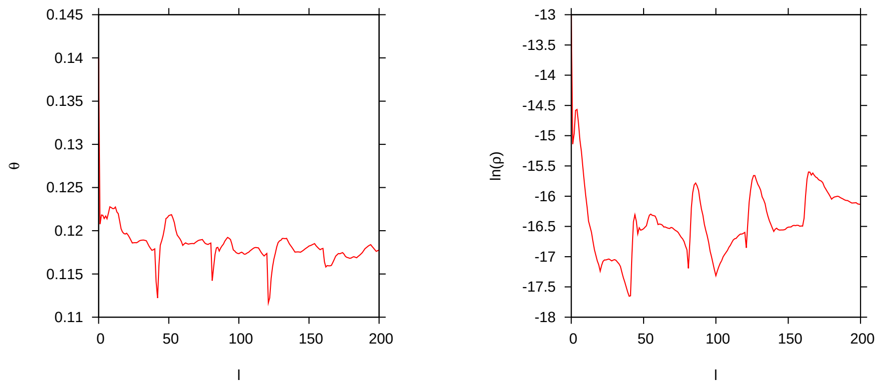


results of final time slice

Particle filter in action: convergence in parameter space

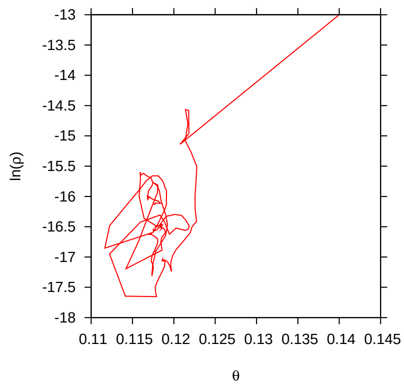
now going $M = 5$ times through the time series with each $\mathcal{L} = 40$ time slices of 6 months,



estimates of the parameters along the $M = 5$ runs through the time series with 5×40 time slices covered

Particle filter in action: convergence in parameter space

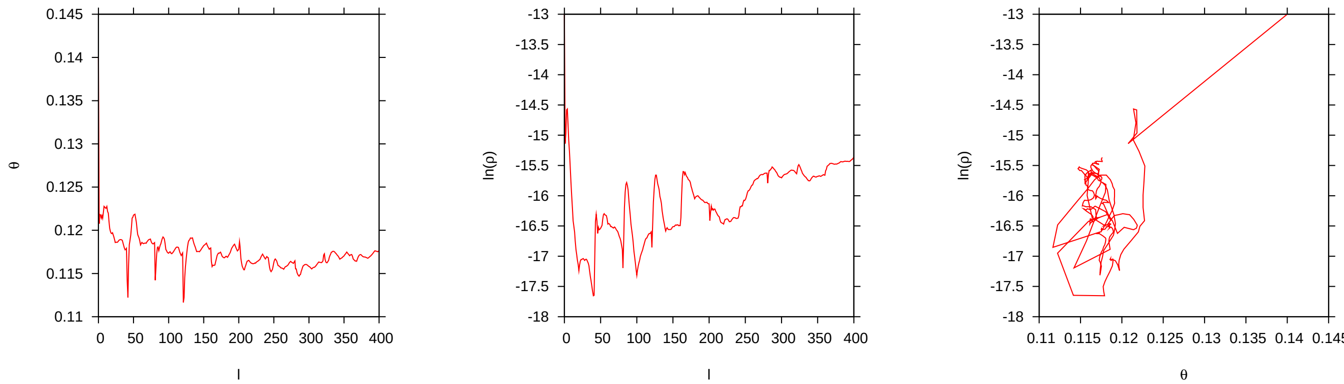
now going $M = 5$ times through the time series with each $\mathcal{L} = 40$ time slices of 6 months,



estimates of two parameters jointly

Particle filter in action: convergence in parameter space

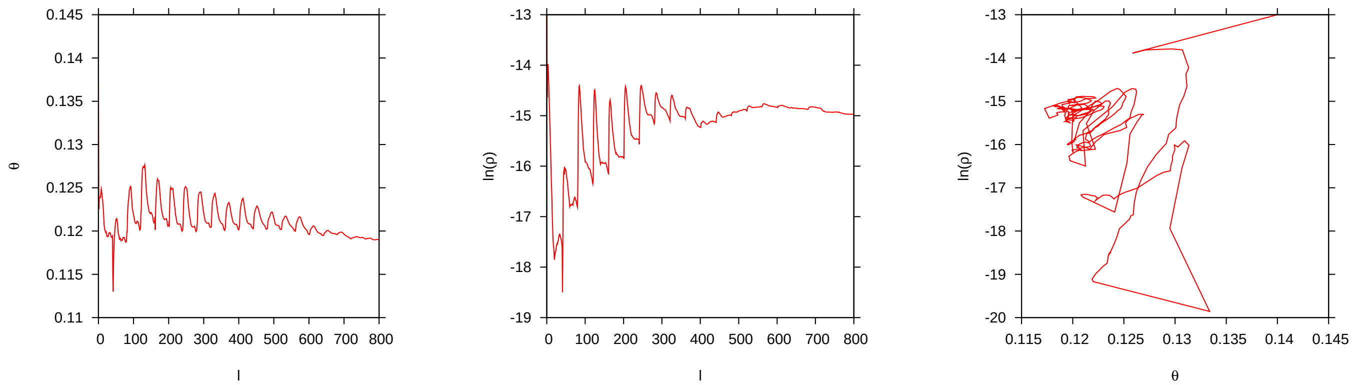
now going $M = 10$ times through the time series



effect of simulated annealing now visible

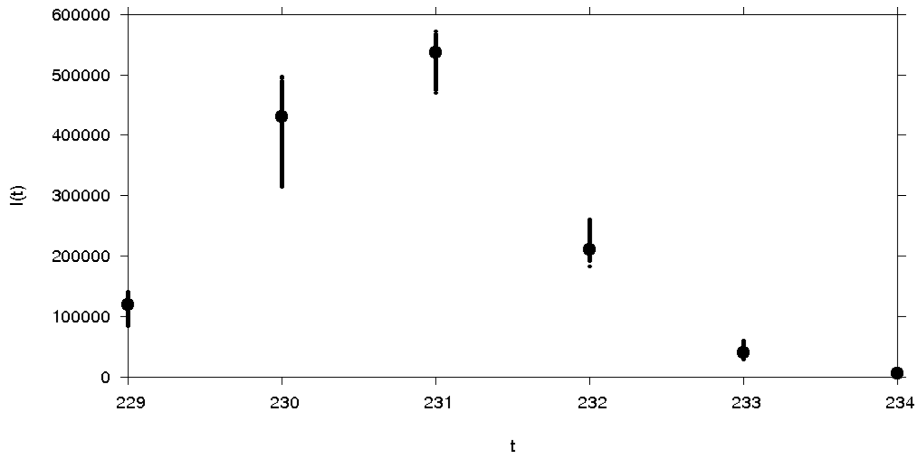
Particle filter in action: convergence in parameter space

now going 20 times through the time series and more particles, better η resolution etc.



completing the iterated filtering for dynamic noise in chaotic population systems

Particle filter in action: good description of the data



cloud of simulations stay colse to the data
for the selected parameter sets (particles)

Parameter estimation in dengue: scaling with noise