PERSISTENCE IN POPULATION BIOLOGY MODELS

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This note contains copies of illustrations used in the Large Deviations Conference, Ann Arbor, June 2007.

Overview
Quasi-stationarity and persistence
The SIS model:
  Asymptotic approximations of QSD
  Uniform results
The classic endemic model

Birth-death process, with origin absorbing
State space: S={0,1,2,. . . ,N}
Transition rates: λ_n and μ_n, with $\lambda_0 = \mu_0 = 0$
Generator: A
$p = (p_0, p_1, \ldots, p_N)$
Master equation: $p' = pA$

Partition the state space and condition the state probabilities
$S = S_0 \cup S_Q, \quad S_0 = \{0\}, \quad S_Q = \{1, 2, \ldots, N\}$
$p = (p_0, p_Q), \quad p_Q = (p_1, \ldots, p_N)$
$p_0' = \mu_1 p_1$
$p_Q' = p_Q A_Q$
$q_Q(t) = p_Q(t)/(1 - p_0(t))$

QSD = stationary conditional distribution on S_Q
The stationary distribution of q_Q is denoted q
q is an eigenvector of A_Q: $qA_Q = -\mu_1 q_1 q$
The original process has degenerate stationary distribution: $p_0 = 1$

The original process with $p_Q(0) = q$
$p_Q(t) = q \exp(-\mu_1 q_1 t)$
$p_0(t) = 1 - \exp(-\mu_1 q_1 t)$

Can use this case to derive ODE for pgf $G_Q(x)$ of q from PDE of pgf $G(x,t)$ of $p(t)$

Two auxiliary processes with nondegenerate stationary distributions
$X^{(0)}$: replace μ_1 by 0
$X^{(1)}$: replace μ_n by μ_{n-1}
The stationary distributions $p^{(0)}$ and $p^{(1)}$ are known functions of λ_n and μ_n
A recursion relation for q involves $p^{(0)}$ and $p^{(1)}$

Time to extinction τ
$P\{\tau < t\} = p_0(t)$
Persistence: Time to exctinction from QSD, τ_Q, has exponential distribution with expectation $\mathrm{E}\tau_Q = 1/\mu_1 q_1$
Time to extinction from state 1, τ_1, has expectation $\mathrm{E}\tau_1 = 1/\mu_1 p_1^{(0)}$

Logistic models
Verhulst model has density dependence in both birth rate and death rate: $\lambda_n = \lambda(1-\alpha_1 n/N)n, \quad \mu_n = \mu(1+\alpha_2 n/N)n, \quad R_0 = \lambda/\mu$
Special case: Logistic epidemic (aka SIS model, with recovered individuals susceptible): $\lambda_n = \lambda(1-n/N)n, \quad \mu_n = \mu n$

The deterministic SIS model
$X' = \mu(R_0 - 1 - R_0 X/N)X$
The model has a threshold at $R_0 = 1$: $X(t) \to K = (1-1/R_0)N$ if $R_0 > 1$ and $X(t) \to 0$ if $R_0 < 1$
The counterpart to the threshold in the stochastic model is sought

The SIS model
Asymptotic approximations of QSD as $N \to \infty$ show qualitatively different behaviors in three parameter regions: $R_0 > 1$, $R_0 < 1$, and transition region near $R_0 = 1$, where $\rho = (R_0 - 1)\sqrt{N}$ is constant
Uniform approximations across the three regions are found for $\mathrm{E}\tau_1$, $\mathrm{E}\tau_Q$, $\mathrm{E}X^{(0)}$, $\mathrm{E}X^{(1)}$, $\mathrm{E}X^{(Q)}$

The classic endemic model
Famous model for measles since the 1950's
SIR model: recovered individuals are immune

$S' = \mu N - \beta SI/N - \mu S$
$I' = \beta SI/N - (\gamma + \mu)I$
$\alpha = (\gamma + \mu)/\mu, \quad R_0 = \beta/(\gamma + \mu)$

The classic endemic model
The stochastic version of the model is bivariate: $\{S(t), I(t)\}$
The states $(S, 0)$ are absorbing
QSD is denoted q_{si}
$\mathrm{E}\tau_Q = 1/\mu\alpha q_{\cdot i}$

The classic endemic model
The marginal distribution $q_{\cdot i}$ behaves in qualitatively different ways in three parameter regions
With large α, the transition region is wide
$q_{\cdot i}$ is close to geometric in a large part of the transition region

The classic endemic model
The persistence threshold is related to the critical community size
The large deviation problem of determining $q_{\cdot i}$ for $R_0 > 1$ is open

Persistence
Deterministic modellers use the term persistence to describe various ways in which the solution of a deterministic model can avoid getting close to zero
The deterministic persistence concept is at complete odds with the stochastic one.
Persistence measured by time to extinction cannot be studied in the deterministic framework

References
(1) I. Nåsell: The quasi-stationary distribution of the closed endemic SIS model, Adv Appl Prob, 28, 895–932, 1996.
(2) I. Nåsell: Extinction and quasi-stationarity in the Verhulst logistic model, J Theor Biol, 211, 11–27, 2001.
(3) `www.math.kth.se/~ingemar/forsk/verhulst/verhulst.html`, 2006. This is an extended and updated version of (2).
(4) I. Nåsell: On the time to extinction in recurrent epidemics, J Roy Stat Soc B, 61, 309–330, 1999.
(5) I. Nåsell, A new look at the critical community size for childhood infections, Theor Pop Biol, 67, 203–216, 2005.

The well-known expression for expected time to extinction from state n is rewritten in terms of the stationary distributions $p^{(0)}$ and $p^{(1)}$ of the two auxiliary processes:

$$\mathrm{E}\tau_n = \frac{1}{\mu_1} \sum_{k=1}^{n} \frac{1}{p_k^{(1)}} \sum_{j=k}^{N} p_j^{(0)} \ \frac{p_1^{(1)}}{p_1^{(0)}}.$$

The QSD obeys the following recursion relation. The similarity with the above expression for $\mathrm{E}\tau_n$ is noted.

$$q_n = p_n^{(0)} \sum_{k=1}^{n} \frac{1}{p_k^{(1)}} \sum_{j=k}^{N} q_j \ \frac{p_1^{(1)} q_1}{p_1^{(0)}}.$$

Notation that is used to express the uniform approximation results for the SIS model is summarized as follows:

$$\begin{aligned}
f_1 &= \max\left(\frac{\beta_1}{\rho}, \frac{1}{R_0}\right), \\
f_Q &= \min\left(\frac{R_0 \beta_1^2}{\rho^2}, 1\right), \\
\widetilde{\rho} &= \rho \min\left(\frac{\beta_1}{\rho}, 1\right), \\
\rho &= (R_0 - 1)\sqrt{N}, \\
\beta_1 &= \mathrm{sgn}(R_0 - 1)\sqrt{2N[\log(R_0 - 1) - 1 + 1/R_0]}.
\end{aligned}$$

Definitions of the functions H_1, H_0, H that are needed to express the uniform results for the SIS model are as follows:

$$\begin{aligned}
H_1(y) &= \frac{\Phi(y)}{\phi(y)}, \\
\phi(y) &= \frac{1}{\sqrt{2\pi}} \exp(-y^2/2), \\
\Phi(y) &= \int_{-\infty}^{y} \phi(t)dt,
\end{aligned}$$

$$H(y) = \frac{1}{y + 1/H(y)} \int_{-1/H(y)}^{y} H_1(t)dt,$$

$$H_a(y) = -\log|y| - \frac{1}{2y^2} + \frac{3}{4y^4} - \frac{5}{2y^6},$$

$$H_0(y) = \begin{cases} H_a(y), & \text{if } y \le -3, \\ H_a(-3) + \int_{-3}^{y} H_1(t)dt, & \text{if } y > -3. \end{cases}$$

Uniform approximations for the expected times to extinction from the state 1 and from the quasi-stationary distribution for the SIS model:

$$
\begin{aligned}
\mathrm{E}\tau_1 &\approx \frac{1}{\mu} f_1 \left[\log \sqrt{N} + H_0(\widetilde{\rho})\right], \\
\mathrm{E}\tau_Q &\approx \frac{1}{\mu} f_Q H(\widetilde{\rho}) \sqrt{N}.
\end{aligned}
$$

Uniform approximations for expectations of the stationary distributions of the two auxiliary processes and of the qsd for the SIS model:

$$
\begin{aligned}
\mathrm{E}X^{(1)} &\sim \min\left(\frac{1}{R_0}, 1\right) \frac{1+\rho H_1(\rho)}{H_1(\rho)} \sqrt{N}, \\
\mathrm{E}X^{(0)} &\approx \min\left(\frac{1}{R_0}, R_0\right) \frac{H_1(\rho)}{\log \sqrt{N} + H_0(\rho)} \sqrt{N}, \\
\mathrm{E}X^{(Q)} &\approx \min\left(\frac{1}{R_0}, 1\right) \frac{H_1(\rho) - H_1(-1/H(\rho))}{1+\rho H(\rho)} \sqrt{N}.
\end{aligned}
$$

Approximations of $\mathrm{E}\tau_Q$ for the SIS model in different parameter regions:

$$
\begin{aligned}
\mathrm{E}\tau_Q &\approx \frac{1}{\mu} f_Q H(\widetilde{\rho}) \sqrt{N}, \\
\mathrm{E}\tau_Q &\approx \frac{1}{\mu} \frac{R_0 \beta_1^2}{\rho^2} H(\beta_1) \sqrt{N}, \quad R_0 \geq 1, \\
\mathrm{E}\tau_Q &\approx \frac{1}{\mu} \sqrt{\frac{2\pi}{N}} \frac{R_0}{(R_0-1)^2} \exp(\beta_1^2/2), \quad R_0 > 1, \\
\mathrm{E}\tau_Q &\approx \frac{1}{\mu} H(\rho) \sqrt{N}, \quad R_0 \leq 1, \\
\mathrm{E}\tau_Q &\approx \frac{1}{\mu} \frac{1}{1-R_0}, \quad R_0 < 1, \\
\mathrm{E}\tau_Q &\approx \frac{1}{\mu} H(\rho) \sqrt{N}, \quad \rho = \mathrm{O}(1).
\end{aligned}
$$

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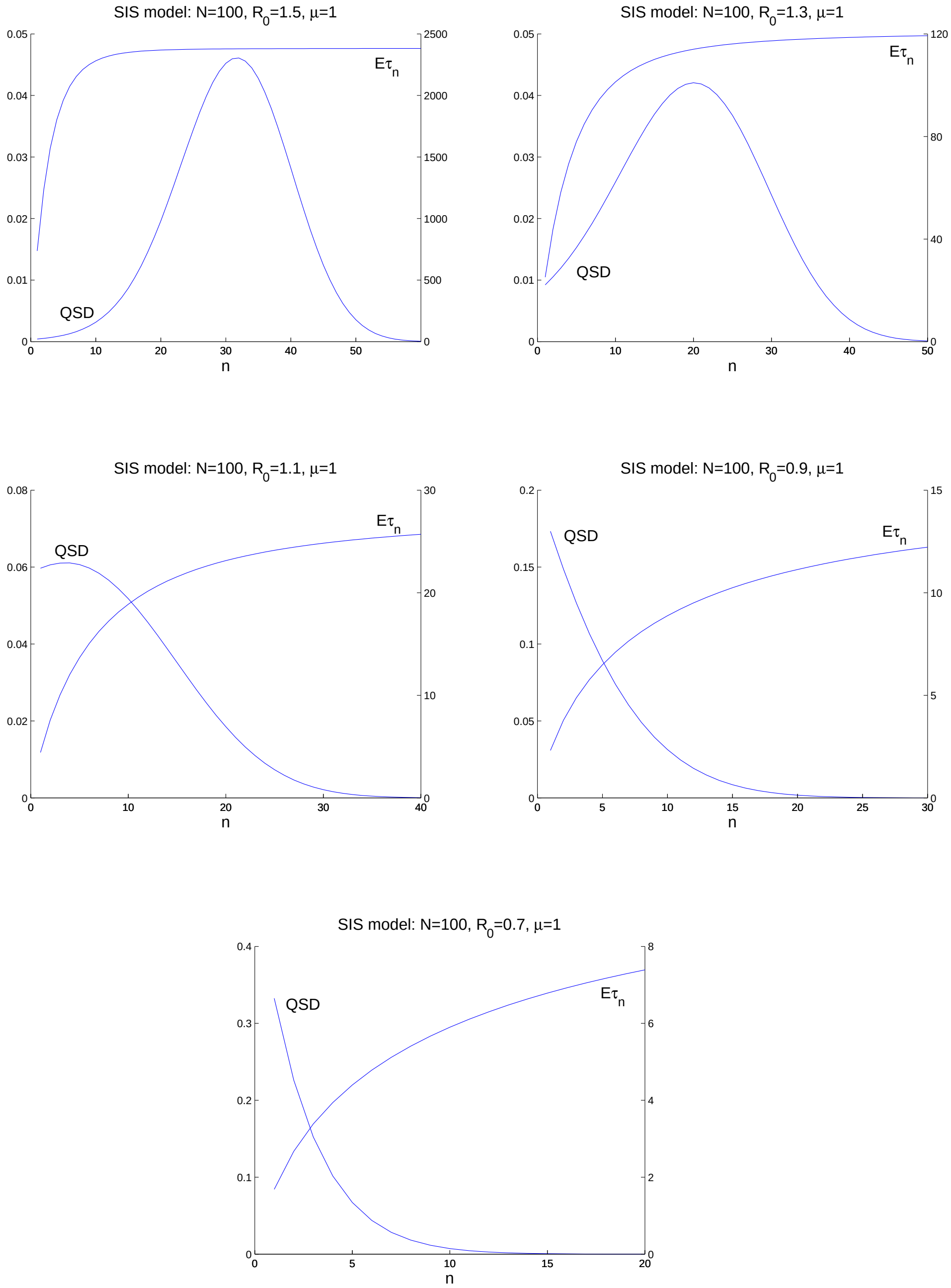

FIGURE 1. The quasi-stationary distribution and the expected time to extinction from the state n are shown for the SIS model for several values of R_0.

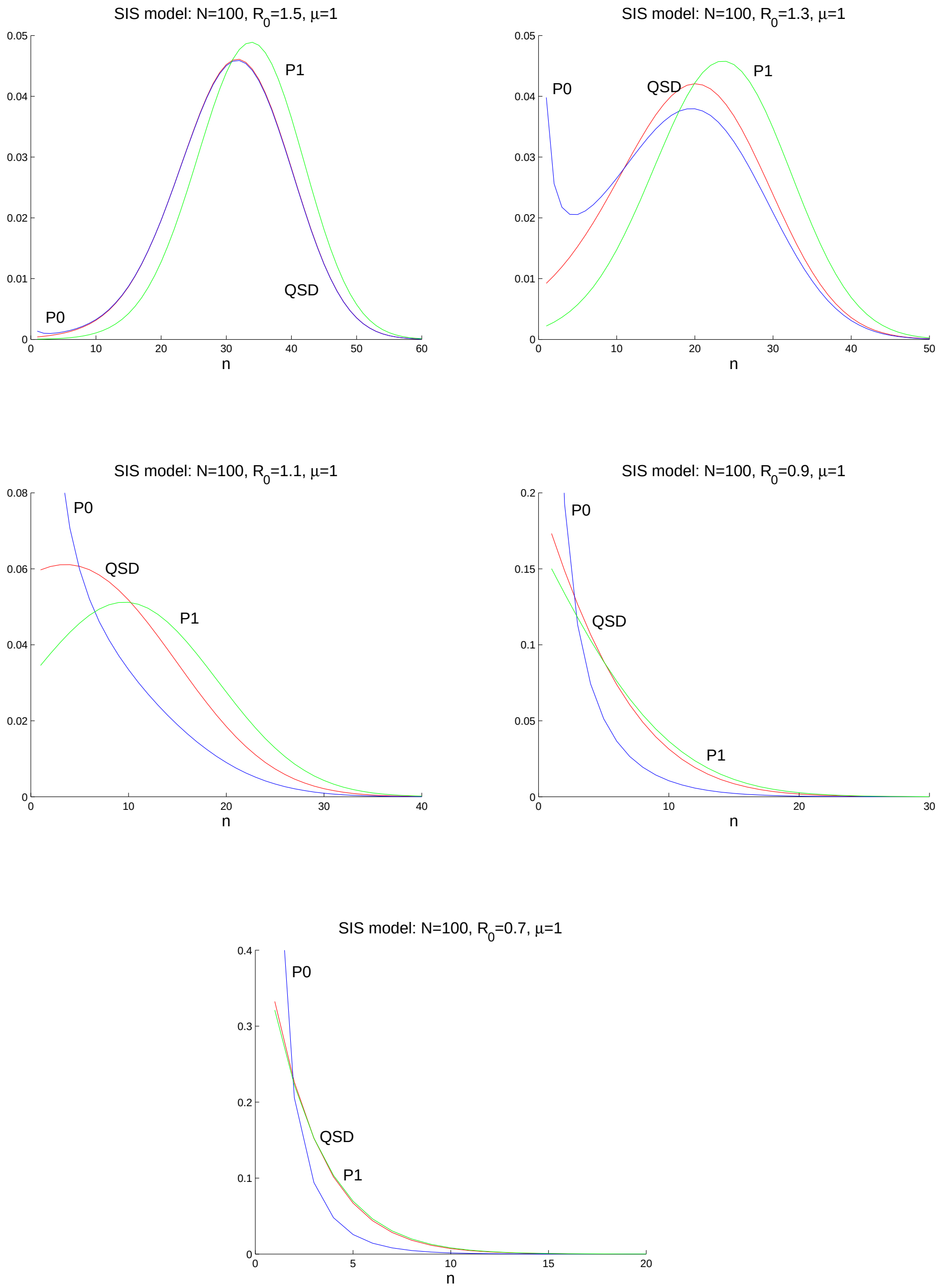

FIGURE 2. The quasi-stationary distribution and the stationary distributions of the two auxiliary processes are shown for the SIS model for several values of R_0.

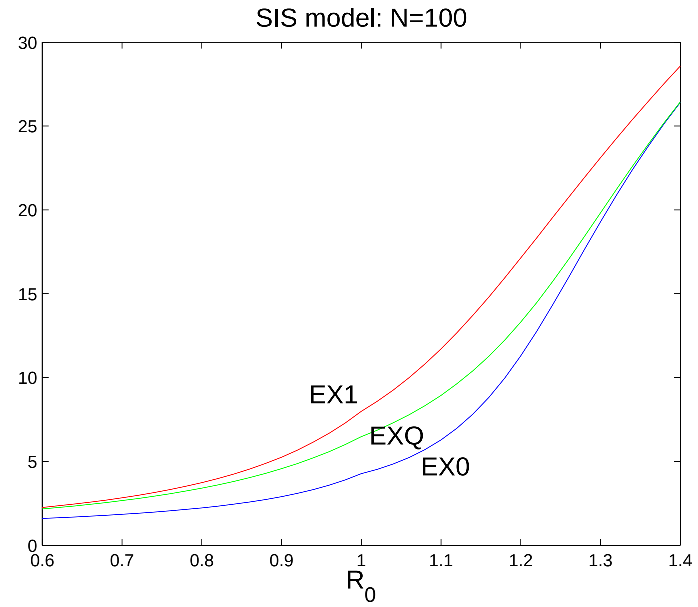

FIGURE 3. Uniform approximations of the expectations of the QSD and of the stationary distributions of the two auxiliary processes for the SIS model are shown as functions of R_0.

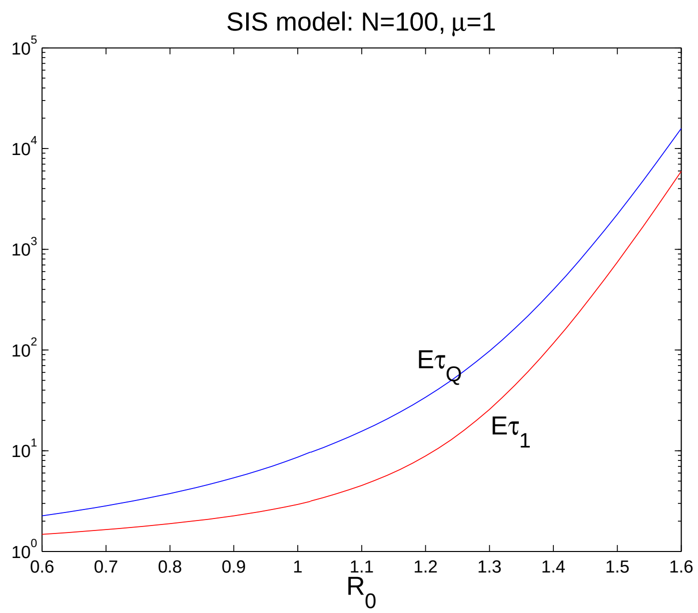

FIGURE 4. Uniform approximations of the expectations of the time to extinction from the state 1 and from the quasi-stationary distribution for the SIS model are shown as functions of R_0.