Stochastic population dynamics: the Poisson approximation

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Motivation

- Population Dynamics
- Markov jump processes
- Need for a systematic description as N increases
- Need for error control
- Need for proper handling of "border" states
- Indications about soundness of Poisson approximation

Markov jump processes

- Event-space, event-classes E.
- $X = X_0 + \sum_{j=1}^{E} \delta_j \zeta_j$
- ζ_j nonnegative integer random variable, taking values $n_j \in \{0, \ldots, M_j\}$.
- Kolmogorov forward equation (Master equation)

$$\frac{d}{dt}P(\{n_j\}) = \sum_{j=1}^{E} \Big(W_j(X - \delta_j) P(\{n_j - 1\}) \Big) - \left(\sum_{j=1}^{E} W_j(X) \right) P(\{n_j\})$$

(for given t and X_0).

What is available?

Deterministic limit and gaussian fluctuations:

$\hat{X}(t) = X(t)/n$,

$$\hat{X}_n(t) = \hat{X}_n(0) + \sum_l \frac{\delta_l}{n} Y_l(n\beta(\hat{X}_n)) + \int_0^t W(\hat{X}_n(s))ds,$$

$\lim_{n\to\infty} \hat{X}_n(0) = x_0$ and $d\hat{X}/dt = W(\hat{X})$ then for all $t \geq 0$, $\lim_{n\to\infty} \sup_{s\leq t} |\hat{X}_n(s) - \hat{X}(s)| = 0$ a.s.

$Y_l(n\beta(\hat{X}_n)) = Y_l(\beta(X_n))$ standard Poisson process, β is the time-scale factor.

Letting $X_n(t) = X(t) + V_n(t)/\sqrt{n}$, we have $V_n(t) \to V(t)$ with U a Brownian motion and

$$V(t) = V(0) + U(t) + \int_0^s \partial W(X(s))V(s)ds$$

Kurtz 1971–1986 (with Ethier), Andersson and Britten 2000.

Drawbacks

- Little predictive value: Solution of jump equation requires knowledge of the history of the system.
- Little or no details about rate of convergence to the limit.

Truncated Poisson approximation

- *Admissible*, *non-admissible* and *border* states B_j.
- Admissible $\{n\} \notin B_j$:
  $\bar{P}(\{n_j\}) = \Pi_j e^{-\lambda_j} \lambda_j^{n_j} / n_j!$
- Border states collect what remains.
- Mass-action law: $W_j(X) = \Omega w_j(X/\Omega)$.

$$\mathcal{N}_j(t, X_0) \frac{d\lambda_j}{dt} = \sum_{\{n\} \notin B_j} W_j(X) \bar{P}(\{n_j\}) \equiv f_j(\lambda) \mathcal{N}_j(t, X_0)$$

$$\lambda(0) = 0$$

$$X = X_0 + \sum_j^E \delta_j n_j$$

Error estimates I

- Pointwise convergence of generating functions implies convergence *in distribution*.

$$\Phi(z,t;X_0) = \Psi(z,t;X_0) + \Delta(z,t;X_0)$$

$$\begin{aligned}\Delta(z,t;X_0) &= -\int_0^t \frac{d\left(e^{\mathcal{L}(X_0)(t-s)}\Psi(z,s;X_0)\right)}{ds}ds \\ &= \int_0^t e^{\mathcal{L}(X_0)(t-s)}\left(\mathcal{L}(X_0) - \frac{d}{ds}\right)\Psi(z,s;X_0)ds\end{aligned}$$

$|\Delta - E| \leq C$, where:

Error estimates II

$$
\begin{aligned}
E &= \int_0^t \left(\sum_{j=1\ldots E} \sum_{\{n\} \notin B_j} z^n \bar{P}(n,s)(W_j(X) - f_j) \right. \\
&\qquad \left. (z_j - 1)\Phi(z, t-s; X) \right) ds \\
C &= \int_0^t (t-s)ds \left(\sum_{j=1\ldots E} \sum_{\{n\} \notin B_j} z^n \bar{P}(n,s)|W_j(X) - f_j| \right. \\
&\qquad \{\sum_k (1 - z_k)\} \sup_{kY} |W_k(Y + \delta_j) - W_k(Y)| \\
&\qquad \left. \exp((t-s) \sum_l \sup_{kY} |W_k(Y + \delta_l) - W_k(Y)|) \right)
\end{aligned}
$$

Results I

Theorem 1: Let V_j be the minimum distance to the j-border states, i.e., the minimum of all n such that $X_0 + \sum_{k \neq j} n_k \delta_k + n\delta_j \in B_j$. Assume also that the generalized mass-action law holds and that $|W_j(X) - W_j(Y)| \leq C_j |X - Y|$ with C_j $(j = 1 \ldots E)$ finite. Then, for $\epsilon > 0$ sufficiently small and $-\epsilon < \nu_i \leq 0$, $H_x(\nu)$ converges uniformly to $\Psi_X(\exp(\sum_j \nu_j / \Omega))$ in the limit $\Omega \to \infty$, provided that $\forall j$, $\lambda_j / V_j < 1$.

Results II

$$
\begin{aligned}
& |\Delta(\exp(\nu/\Omega), t, X_0) - O(\epsilon t\sqrt{\widehat{\lambda}}/\sqrt{\Omega})| \\
\leq \quad & \sum_{j=1\ldots E} \left(\sqrt{\widehat{\lambda}_j} C_j |\delta_j|\right) O(t^2 \epsilon/\sqrt{\Omega})
\end{aligned}
$$

Results III

Theorem 2: Under the conditions of the previous theorem and if, additionally, $\lim_{\Omega\to\infty} \lambda_j/V_j = b_j < 1$ then $\Psi_X(\exp(\nu/\Omega))$ converges uniformly to $\exp(\sum_j \nu_j \hat{\lambda}_j)$, where $\hat{\lambda}_j = \lim_{\Omega\to\infty} \lambda_j/\Omega$ satisfies the differential equation

$$\frac{d\hat{\lambda}_j}{dt} = \lim_{\Omega\to\infty} \frac{f_j}{\Omega}.$$

$\Psi_X(e^{\nu/\Omega}) - e^{\sum_j \lambda_j (e^{\nu_j/\Omega} - 1)} \to 0$
exponentially fast with Ω.

$$e^{\sum_j \lambda_j (e^{\nu_j/\Omega} - 1)} = e^{\sum_j \hat{\lambda}_j \nu_j} + O(\nu^2/\Omega)$$

Results IV

Corollary (Deterministic limit): In the conditions of the above theorems, the fluctuation of the variables x_i are zero; i.e., the variables have a deterministic behavior in the limit $\Omega \to \infty$.

Theorem 3: Under the assumption of the mass-action law and if $|W_j(X) - W_j(Y)| \leq C_j|X - Y|$ with C_j ($j = 1 \ldots E$) finite, then $\Phi(z, t; X_0; \Omega) - \Psi(z, t; X_0; \Omega)$ converges uniformly to zero as a function of z in $[0, 1]$ in the limit $\Omega \to \infty$, $t \to 0$, while λ_j is kept bounded.

Results V

Theorem 4: The fluctuations of n_j around its mean value, $< n_j >$, in the scale $\sqrt{\Omega}$, i.e., $(n_j - < n_j >)/\sqrt{\Omega})$ converge towards a Brownian process under the conditions of Theorems 1, 2, in the limit $\Omega \to \infty$ for any fixed $t < t^*$ and the proper does the motion in phase space for the variable $(X - < X >)/\sqrt{\Omega}$.

$$\Xi(\nu) = \exp(\sum_j (\nu_j^2 \hat{\lambda}_j)/2 + O(|\nu|^3 \hat{\lambda}/\sqrt{\Omega})) + \sum_{j=1 \ldots E} \left(\sqrt{\hat{\lambda}_j} C_j |\delta_j| \right) O(t^2 \epsilon')$$

Interpretation

$$\frac{dx}{dt} = \sum_j \delta_j w_j(x)$$

letting $x_0 = \lim_{\Omega\to\infty} X_0/\Omega$, we have:

$$x = x_0 + \sum_j \delta_j \hat{\lambda}_j$$

$x = X/\Omega = (X_0 + \sum_j(\delta_j n_j))/\Omega$ obeys:

$$dx = \left(\sum_j \delta_j w_j(x) + \zeta(t)/\sqrt{\Omega}\right) dt$$

ζ is "normally distributed with zero mean".

Interpretation II

Recast the last equation in terms of X:

$$dX = \left(\Omega \sum_j \delta_j w_j(x) + \sqrt{\Omega}(\zeta(t) + O(1/\sqrt{\Omega})) \right) dt$$
$$+ O(\Omega dt^2)$$

- X is a discrete variable
- Errors negligible if Ω is large and Ωdt^2 is small.
- There is a definite sequence in the limit procedure: *First* $\Omega \to \infty$ (to get a continuous variable $x = X/\Omega$, *then* $t \to 0$ (to get a differential equation)
- It is not possible to invert the sequence
- What is the proper interpretation of ζ ?

Example I

$$\frac{\partial \Phi(z,t)}{\partial t} = (z-1)(V - z\frac{\partial}{\partial z})\Phi(z,t)$$

$$P_n(t) = \binom{V}{n} (\exp(-t))^{V-n}(1-\exp(-t))^n$$

$$\Psi(z,t;X_0) = z^V + \sum_{z=0}^{V-1} \exp(-\lambda)\frac{\lambda^n}{n!}(z^n - z^V)$$

$\lambda(t)$ satisfies $\lambda(0) = 0$ and

$$\frac{d\lambda}{dt} = V - \lambda \left(1 - \frac{\lambda^{V-1}/(V-1)!}{\sum_{k=0}^{V-1} \lambda^k/k!}\right).$$

Example II

Deterministic limit of n/V for $V \to \infty$ is

$$n/V \to \hat{\lambda} = (1 - \exp(-t)),$$

which is the solution of
$d\hat{\lambda}/dt = 1 - \hat{\lambda} = 1 - \lim_{V\to\infty} < n >_{\lambda} /V$.

$$x = (n - V(1 - e^{-t}))/\sqrt{V\hat{\lambda}(t)e^{-t}}$$

for $|x| \leq A$ and A arbitrary but fixed and independent of V is approximately $N(0, 1)$ in $|x| \leq A$ when $V \to \infty$.
Convergence: $O(1/\sqrt{V})$ for fixed A.
$(n - V(1 - e^{-t}))/\sqrt{V}$ is $N(0, \hat{\lambda}e^{-t})$.
Theorem 4: $(n - V(1 - e^{-t}))/\sqrt{V}$ is $N(0, \hat{\lambda})$ for $V \to \infty$ and fixed $t*$ sufficiently small.

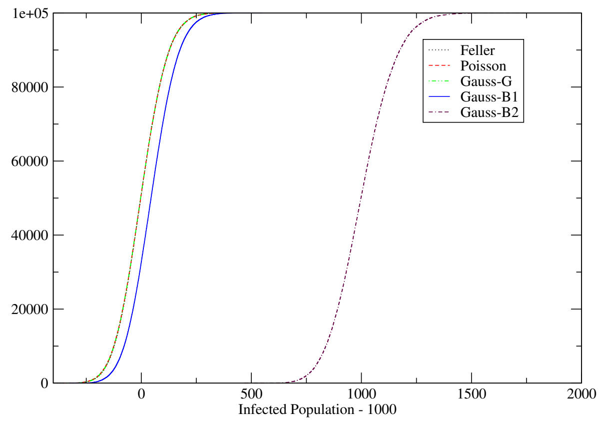
Example III

Epidemics of measles: (S,I).

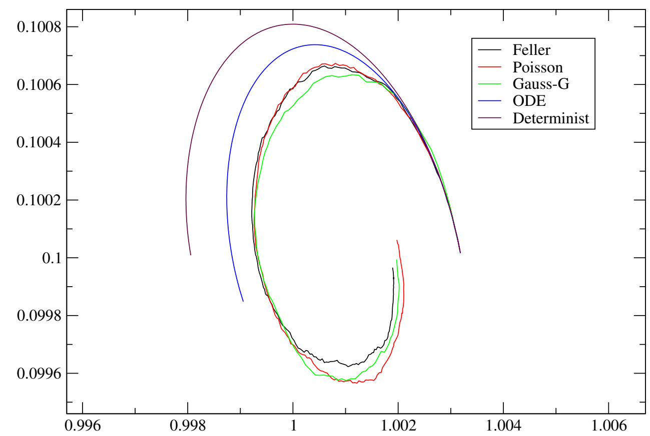
- Event-type 1: *Birth:* Susceptible are born at a constant rate $a = \Theta \bar{a}$.
- Event-type 2: *Contagion:* The susceptible population decreases by one while the infected population increases by one at a rate $\beta SI = \bar{\beta} SI/\Theta$.
- Event-type 3: *Recovery*: Infected individuals are removed at a rate $bI = \bar{b}I$.

The time between events is exponentially distributed with frequency
$\tau^{-1} = a + \beta SI + bI$.

Example IV



Cumulative statistics of $I(2)$



Average orbit (10^5 runs)

Example V

Dataset pair	λ_2	λ_3	$\lambda_2 - \lambda_3$
P0 T1	0.054448	0.705083	0.000196
P0 T2	0.181261	0.507998	0.087076
P0 T3	0.720376	0.916048	0.002592
P11 T1	0.766497	0.366515	0.845375
P11 T2	0.269222	0.101213	0.302322
P11 T3	0.959234	0.802967	0.632484
P12 T1	0.138791	0.020574	0.112523
P12 T2	0.381672	0.169256	0.910722
P12 T3	0.027510	0.110272	0.858000
P13 T1	0.349022	0.082855	0.182363
P13 T2	0.338261	0.221951	0.752806
P13 T3	0.779957	0.211652	0.929525

Table I Comparison of Poisson and Feller runs (see text).

Example VI

Dataset pair	λ_2	λ_3	$\lambda_2 - \lambda_3$
P11 G	0.252950	0.218046	0.025207
P12 G	0.001751	0.000470	0.026063
P13 G	0.008090	0.003931	0.006170
T1 G	0.106936	0.272261	0.004607
T2 G	0.090212	0.026501	0.017923
T3 G	0.064702	0.069907	0.007258
P11 B	0.000000	0.000000	0.000000
P12 B	0.000000	0.000000	0.000000
P13 B	0.000000	0.000000	0.000000
T1 B	0.000000	0.000000	0.000000
T2 B	0.000000	0.000000	0.000000
T3 B	0.000000	0.000000	0.000000

Table II Comparison of G and B runs with P and Feller runs (see text).

Concluding remarks

- "Heuristic diffusion approximation" derived as a limit procedure.
- Error estimates allow for a practical approximation scheme.
- Possibility of deciding which level of approximation suffices for given tolerance.