Inference in Population-Size-Dependent Branching Processes

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Galton–Watson Branching processes

- ξ : the offspring distribution
- $m := \mathbb{E}[\xi]$ the mean offspring
- Z_n : the population size at generation n,

$$Z_{n+1} = \sum_{i=1}^{Z_n} \xi_{n,i}, \qquad n \geq 0$$

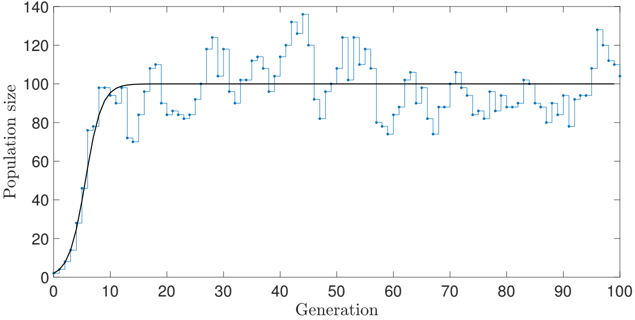
- $\mathbb{E}[Z_n \mid Z_0] = Z_0\, m^n$ (exponential growth)
- The MLE of m based on $Z_0, Z_1, \ldots, Z_n$:

$$\hat{m}_n = \frac{\sum_{i=1}^{n} Z_i}{\sum_{i=1}^{n} Z_{i-1}}$$

- Supercritical case $m > 1$: $\hat{m}_n \to m$ on $\{Z_n \to \infty\}$ (consistency).

In reality...

- Biological populations do not grow exponentially
- Population sizes tend to fluctuate around a carrying capacity
- 99.9% of all species are extinct
- Extinction occurs slowly – often after millions of years



Population-size-dependent branching processes

- $\xi(z)$: the offspring distribution at population size z, $\quad z \geq 1$
- $m(z) := \mathbb{E}[\xi(z)]$ the mean offspring at population size z
- Z_n : the population size at generation n,

$$Z_{n+1} = \sum_{i=1}^{Z_n} \xi_{n,i}(Z_n), \qquad n \geq 0$$

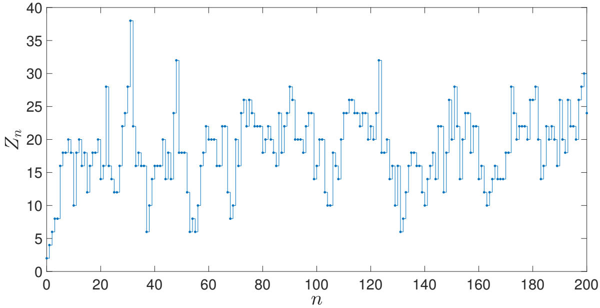
- $\mathbb{E}[Z_n \,|\, Z_{n-1}] = Z_{n-1}\, m(Z_{n-1})$

Example : the Beverton-Holt (B-H) binary splitting model :

- $\xi(z) \sim 2\,\mathrm{Ber}(p(z))$ with $p(z) = \dfrac{K}{K+z}$, where K : carrying capacity
- $m(z) = \dfrac{2K}{K+z}, \quad m(z) \geq 1 \Leftrightarrow z \leq K$

Population-size-dependent branching processes

B-H model with $K = 20$



The MLE of $m(z)$ based on $Z_0, Z_1, \ldots, Z_n$:

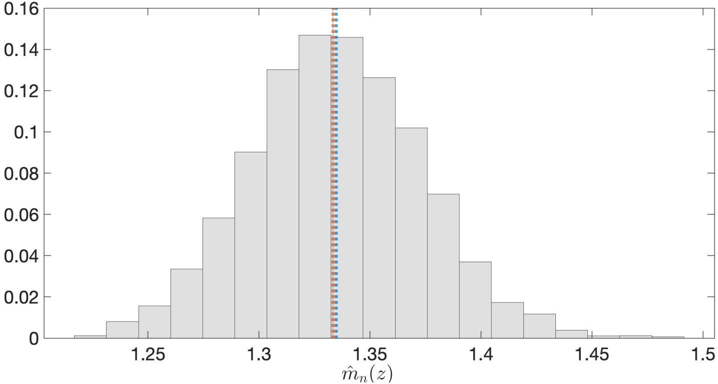
$$\hat{m}_n(z) := \frac{\sum_{i=1}^{n} Z_i \, \mathbb{1}_{\{Z_{i-1}=z\}}}{z \sum_{i=1}^{n} \mathbb{1}_{\{Z_{i-1}=z\}}}$$

Example :

$\hat{m}_{200}(10) = (18 + 14 + 16 + 20 + 10 + 18 + 16 + 14 + 12)/(10 \cdot 9) = 138/90 = 1.53$

Asymptotic properties of the estimator

Histogram of $\hat{m}_n(z)$ for $z = 10$ and $n = 2000$, based on 5000 simulations



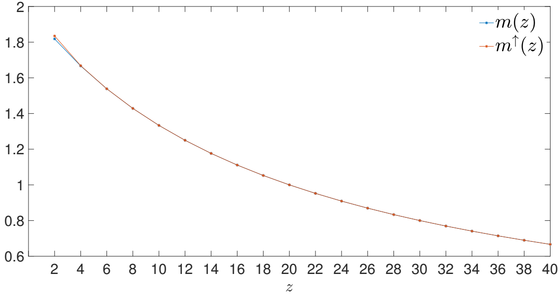
Real value of $m(z) = 1.3333$; Empirical mean of $\hat{m}_n(z) = 1.3349$

Conditional on $Z_n > 0$, $\hat{m}_n(z) \to m^{\uparrow}(z) = 1.3334 \neq m(z)$ as $n \to \infty$

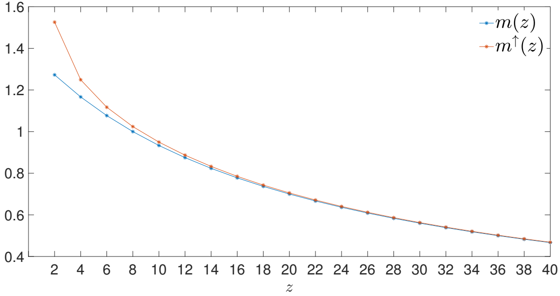
How do $m(z)$ and $m^{\uparrow}(z)$ differ ?

$K = 20, \ v = 1$

(v : efficiency)



$K = 8, \ v = 0.7$



Conditioning on $Z_n > 0$

- Q : the sub-stochastic transition probability matrix of $\{Z_n\}$ restricted to the transient states $\{1, 2, \ldots\}$
- We set the following conditions :

(A1) There exists $z \in \mathbb{N}$ and $n \geq 1$ such that $(Q^n)_{zz} > 0$
(A2) $\limsup_{z\to\infty} m(z) < 1$
(A3) For each $\nu \in \mathbb{N}$, $\sup_{z\in\mathbb{N}} E[\xi_{01}(z)^\nu] < \infty$.

Under these conditions,

- $\mathbb{P}[Z_n \to 0] = 1$ (almost sure extinction)
- $Q^n \sim \rho^n \boldsymbol{v}\boldsymbol{u}^\top$, where $\rho := \lim_{n\to\infty}(Q^n)_{ij}^{1/n}$, and $\boldsymbol{u}, \boldsymbol{v} > \boldsymbol{0}$ such that

$$\boldsymbol{u}^\top Q = \rho \boldsymbol{u}^\top, \quad Q\boldsymbol{v} = \rho\boldsymbol{v}, \quad \boldsymbol{u}^\top \boldsymbol{1} = 1, \quad \text{and} \quad \boldsymbol{u}^\top \boldsymbol{v} = 1.$$

Conditioning on $Z_n > 0$

- For n fixed : the process $\{Z_\ell\}_{0\le\ell\le n}$ conditioned on $Z_n > 0$ is a time-inhomogeneous Markov chain :

$$\begin{aligned}\mathbb{P}[Z_\ell^{(n)} = j \mid Z_{\ell-1}^{(n)} = i] &:= \mathbb{P}[Z_\ell = j \mid Z_{\ell-1} = i,\ Z_n > 0] \\ &= Q_{ij} \frac{\boldsymbol{e}_j^\top Q^{n-\ell}\mathbf{1}}{\boldsymbol{e}_i^\top Q^{n-\ell+1}\mathbf{1}}.\end{aligned}$$

- As $n \to \infty$:

$$\begin{aligned}\mathbb{P}[Z_\ell^\uparrow = j \mid Z_{\ell-1}^\uparrow = i] &:= \lim_{n\to\infty} \mathbb{P}[Z_\ell = j \mid Z_{\ell-1} = i,\ Z_n > 0] \\ &= Q_{ij} \frac{\boldsymbol{e}_j^\top \rho^{n-\ell}\,\boldsymbol{v}}{\boldsymbol{e}_i^\top \rho^{n-\ell+1}\,\boldsymbol{v}} \\ &= Q_{ij} \frac{v_j}{\rho v_i}.\end{aligned}$$

$\{Z_\ell^\uparrow\}_{\ell\ge 0}$ is a positive recurrent time-homogeneous Markov chain called the Q-process

The Q-process and 'Q-consistency'

- In $\{Z_n\}$: $m(z) = z^{-1} \sum_{j \geq 1} j \, Q_{zj}$
- In $\{Z_n^{\uparrow}\}$: $m^{\uparrow}(z) = z^{-1} \sum_{j \geq 1} j \, Q_{zj}^{\uparrow}$ with $Q_{ij}^{\uparrow} := Q_{ij} \, \frac{v_j}{\rho v_i}$

Theorem (Braunsteins, H., Minuesa (2019))

Under Assumptions (A1)–(A3), for any $z \in \mathbb{N}$, initial state i, and $\varepsilon > 0$, $\hat{m}_n(z)$ satisfies

$$\lim_{n \to \infty} \mathbb{P}_i[|\hat{m}_n(z) - m^{\uparrow}(z)| > \varepsilon \,|\, Z_n > 0] = 0 \qquad \text{'Q-consistency'}$$

Asymptotic normality

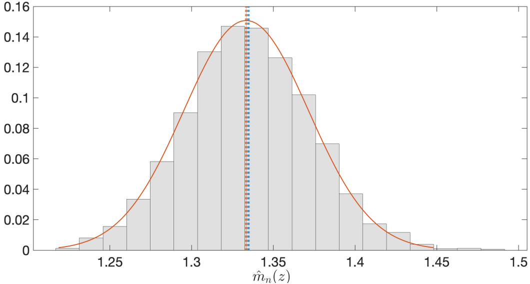
$(u_i v_i)_{i\geq 1}$: stationary distribution of $\{Z_n^{\uparrow}\}$, $\quad \sigma^{2\uparrow}(z) = \frac{\sum_{k=1}^{\infty} k^2 Q_{zk}^{\uparrow}}{z^2} - (m^{\uparrow}(z))^2$

Theorem (Braunsteins, H., Minuesa (2019))

Under Assumptions (A1)–(A3), for any $z \in \mathbb{N}$, initial state i, and $x \in \mathbb{R}$, $\hat{m}_n(z)$ satisfies

$$\lim_{n\to\infty} \mathbb{P}_i[\{n\, u_z v_z / \sigma^{2\uparrow}(z)\}^{1/2} \left(\hat{m}_n(z) - m^{\uparrow}(z)\right) \leq x \mid Z_n > 0] = \Phi(x),$$

where $\Phi(x)$ is the standard normal distribution.



Proof approach : coupling and martingale CLT

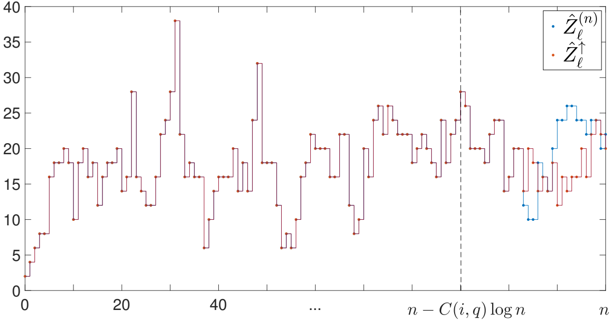
We use a MEXIT coupling $(\{\widehat{Z}_\ell^{(n)}\}, \{\widehat{Z}_\ell^{\uparrow}\})$ of

- $\{Z_\ell^{(n)}\}_{0\le\ell\le n}$: the time-inhomogeneous Markov chain $\{Z_\ell\}_{0\le\ell\le n}$ conditioned on $Z_n > 0$
- $\{Z_\ell^{\uparrow}\}_{0\le\ell\le n}$: the time-homogeneous Markov chain $\{Z_\ell\}_{0\le\ell\le n}$ conditioned on $Z_\infty > 0$

Let $\tau := \min\{\ell \le n : \widehat{Z}_\ell^{(n)} \ne \widehat{Z}_\ell^{\uparrow}\}$ (un-coupling time)

$$\hat{\mathbb{P}}(\tau \le k) = d_{TV}\left(\{Z_\ell^{(n)}\}_{0\le\ell\le k}, \{Z_\ell^{\uparrow}\}_{0\le\ell\le k}\right), \qquad k \le n$$

Proof approach : coupling and martingale CLT



Theorem (Braunsteins, H., Minuesa (2019))

Under Assumptions (A1)–(A3), for any initial state i and any $q > 0$, there exist constants $C(i,q)$ and $N(i,q)$ such that

$$\hat{\mathbb{P}}(\tau \leq n - C(i,q)\log n) \leq \frac{1}{n^q} \qquad \textit{for all } n \geq N(i,q).$$

'Q-consistency' versus C-consistency

- 'Q-consistency' : for any $\varepsilon > 0$,

$$\lim_{n\to\infty} \mathbb{P}[|\hat{m}_n(z) - m^{\uparrow}(z)| > \varepsilon \mid Z_n > 0] = 0$$

- C-consistency : for any $\varepsilon > 0$,

$$\lim_{n\to\infty} \mathbb{P}[|\tilde{m}_n(z) - m(z)| > \varepsilon \mid Z_n > 0] = 0$$

The estimator $\hat{m}_n(z)$ is Q-consistent but not C-consistent

Thankfully, in our PSDBP, $m^{\uparrow}(z) \approx m(z)$ because $\{Z_\ell^{\uparrow}\} \approx \{Z_\ell\}$

Are there situations where we may prefer C-consistency ?

'Q-consistency' versus C-consistency

- 'Q-consistency' : for any $\varepsilon > 0$,

$$\lim_{n\to\infty} \mathbb{P}[|\hat{m}_n(z) - m^{\uparrow}(z)| > \varepsilon \,|\, Z_n > 0] = 0$$

- C-consistency : for any $\varepsilon > 0$,

$$\lim_{n\to\infty} \mathbb{P}[|\tilde{m}_n(z) - m(z)| > \varepsilon \,|\, Z_n > 0] = 0$$

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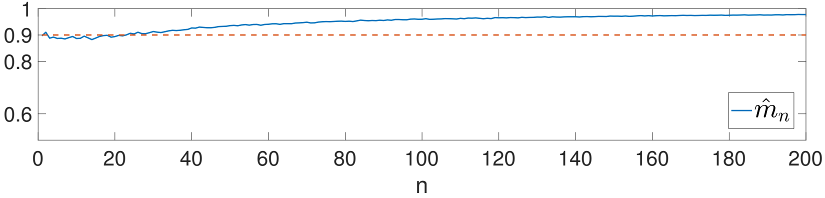
Are there situations where we may prefer C-consistency ?

We often study endangered populations because they are still alive !

Subcritical Galton–Watson branching processes

- Mean offspring $m < 1$ (almost sure extinction – rapid extinction)
- Conditional on $Z_n > 0$, regardless the value of $m < 1$

$$\hat{m}_n = \frac{\sum_{i=1}^{n} Z_i}{\sum_{i=1}^{n} Z_{i-1}} \longrightarrow 1 \qquad \text{as } n \to \infty \qquad \text{(Q-consistency)}$$



Geometric offspring distribution with mean $m = 0.9$, and $Z_0 = 100$

- For small values of n and large values of Z_0, $\hat{m}_n$ is a decent (but not efficient) estimator of n
- For large values of n, the sample $Z_0, Z_1, \ldots, Z_n > 0$ is too biased

Subcritical Galton–Watson branching processes

Assume that

$$\frac{Var[\xi]}{m} = am + b$$

This holds if ξ is geometric, Poisson, binomial (and more ?)

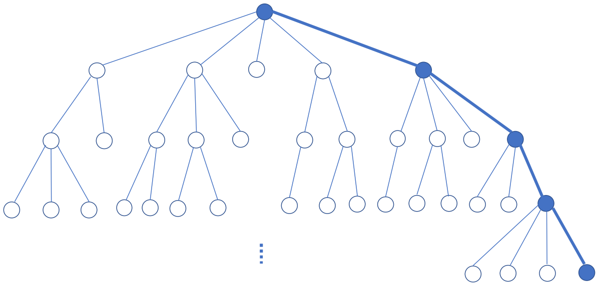
Theorem (Braunsteins, H., Minuesa (2019))

A C-consistent estimator for m is given by

$$\tilde{m}_n := \frac{\sum_{i=1}^{n}(Z_i - b)}{\sum_{i=1}^{n}(Z_{i-1} + a)}.$$

The Q-process $\{Z_\ell^{\uparrow}\}$ of a GW process

The size-biased tree



White nodes have offspring distribution ξ

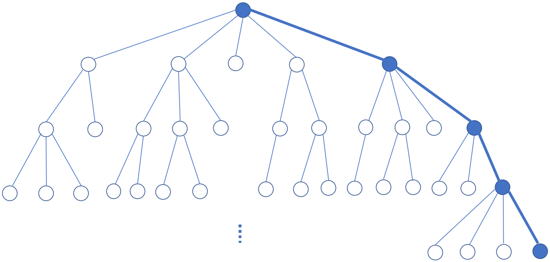
Blue nodes have offspring distribution SB[ξ] (size-biased distribution of ξ)

$$E[Z_\ell^{\uparrow} \mid Z_{\ell-1}^{\uparrow}] \;=\; (Z_{\ell-1}^{\uparrow} - 1)\, m + (E[\xi^2]/m) \;=\; Z_{\ell-1}^{\uparrow}\, m + (Var[\xi]/m)$$

$$\frac{Var[\xi]}{m} = am + b \quad \Rightarrow \quad m = \frac{E[Z_\ell^{\uparrow} \mid Z_{\ell-1}^{\uparrow}] - b}{Z_{\ell-1}^{\uparrow} + a}$$

Unbiasing

$$\frac{Var[\xi]}{m} = am + b, \qquad \tilde{m}_n := \frac{\sum_{i=1}^{n}(Z_i - b)}{\sum_{i=1}^{n}(Z_{i-1} + a)} = \frac{\text{children}}{\text{parents}}$$



$\xi \sim \text{Poi}(m)$: $a = 0,\ b = 1,$ $\text{SB}[\xi] \overset{d}{=} 1 + \xi$

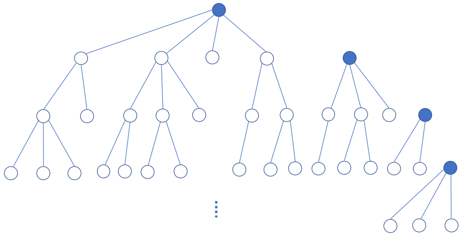
$\xi \sim \text{Geom}(1/(m+1))$: $a = 1,\ b = 1,$ $\text{SB}[\xi] \overset{d}{=} 1 + \xi + \xi'$

$\xi \sim 2\,\text{Ber}(m/2)$: $a = -1,\ b = 2,$ $\text{SB}[\xi] = 2$

Another useful interpretation of $\{Z_\ell^\uparrow\}$

$\{Z_\ell^\uparrow - 1\}$: GW process with immigration and offspring law ξ

Law of the number of immigrants : $\mathrm{SB}[\xi] - 1$



Theorem (Braunsteins, H., Minuesa (2019))

A C-consistent estimator for m is given by

$$\bar{m}_n := 1 - \frac{1}{2}\frac{\sum_{i=1}^n (Z_i - Z_{i-1})^2}{\sum_{i=1}^n (Z_{i-1} - \bar{Z}_n)^2}, \qquad \text{where } \bar{Z}_n := \frac{\sum_{i=1}^n Z_{i-1}}{n}$$

+ a C-consistent estimator for $Var[\xi]$.

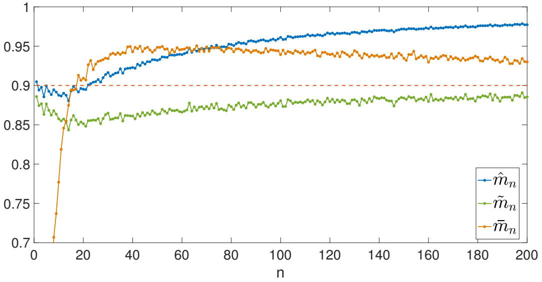
Comparison of the estimators

Given $Z_n > 0$,

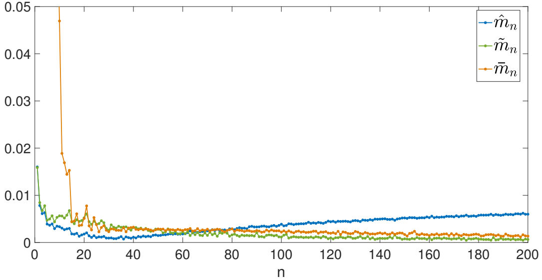
$$\hat{m}_n = \frac{\sum_{i=1}^n Z_i}{\sum_{i=1}^n Z_{i-1}} \to 1,$$

$$\tilde{m}_n := \frac{\sum_{i=1}^n (Z_i - b)}{\sum_{i=1}^n (Z_{i-1} + a)} \to m\ ,$$

$$\bar{m}_n := 1 - \frac{1}{2} \frac{\sum_{i=1}^n (Z_i - Z_{i-1})^2}{\sum_{i=1}^n (Z_{i-1} - \bar{Z}_n)^2} \to m$$



Mean squared error :



Geometric offspring distribution with mean $m = 0.9$, and $Z_0 = 100$

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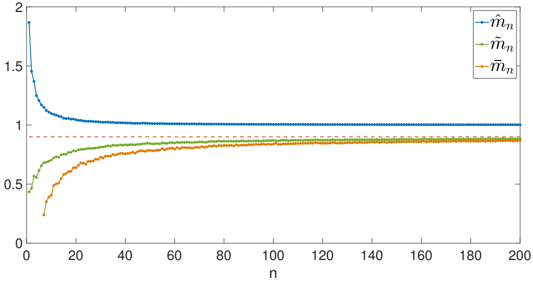

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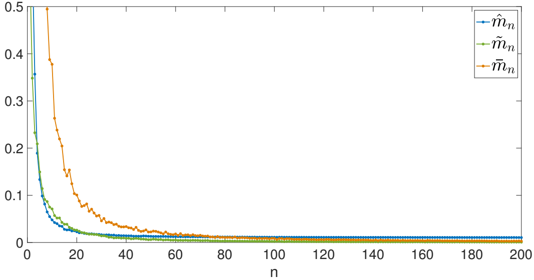


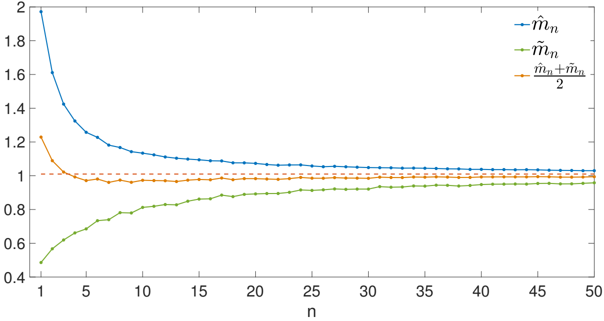
Geometric offspring distribution with mean $m = 0.9$, and $Z_0 = 1$

Supercritical Galton–Watson branching processes

- Mean offspring $m > 1$ (positive chance of survival)
- Conditional on $Z_n > 0$,

$$\hat{m}_n = \frac{\sum_{i=1}^{n} Z_i}{\sum_{i=1}^{n} Z_{i-1}} \longrightarrow m \qquad \text{as } n \to \infty \quad \text{(C-consistency)}$$

$$\tilde{m}_n = \frac{\sum_{i=1}^{n} (Z_i - b)}{\sum_{i=1}^{n} (Z_{i-1} + a)} \longrightarrow m \qquad \text{as } n \to \infty \quad \text{(C-consistency).}$$

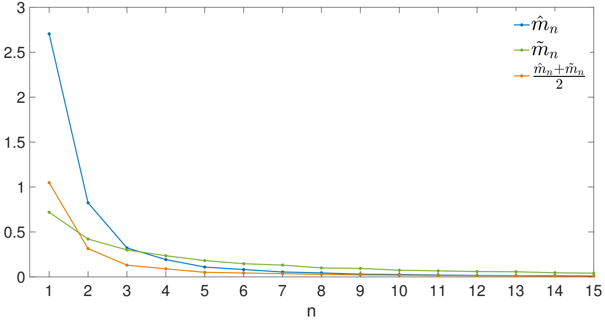


Geometric offspring distr. with mean $m = 1.01$, and $Z_0 = 1$

Supercritical Galton–Watson branching processes

Mean squared errors

$$\hat{m}_n = \frac{\sum_{i=1}^n Z_i}{\sum_{i=1}^n Z_{i-1}}, \qquad \tilde{m}_n = \frac{\sum_{i=1}^n (Z_i - b)}{\sum_{i=1}^n (Z_{i-1} + a)}$$



Geometric offspring distr. with mean $m = 1.01$, and $Z_0 = 1$

Conclusion

We studied the asymptotic properties of the estimator $\hat{m}_n(z)$ of the mean offspring at population size z in PSDBP

This lead us to

- the concept of 'Q-consistency' for estimators in branching processes which become extinct almost surely
- the construction of C-consistent estimators for subcritical GW processes

Ongoing work :

- How to use the estimators $\hat{m}_n(z)$ for $z \geq 1$ to estimate a single parameter θ ?
- How to construct C-consistent estimators for PSDBP ?

Main references

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Thank you for your attention

ACEMS