Linking Population-Size-Dependent and Controlled Branching Processes

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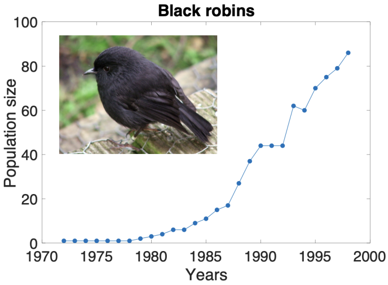
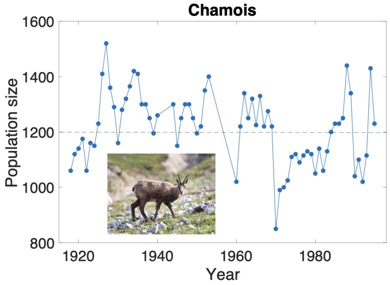
Overview

1. Motivation

- Many biological populations exhibit non-exponential growth :





- Which model of branching process is the most appropriate for populations with logistic growth and a carrying capacity ?
- Is the population size internally controlled (demographic stochasticity) or externally controlled (environmental stochasticity) ?

Two relevant classes of branching processes

The following two models see active use in modelling biological populations :

- A population-size-dependent branching process (PSDBP), $\{Z_n\}_{n\in\mathbb{N}_0}$, has recurrence relation

$$Z_n = \sum_{i=1}^{Z_{n-1}} \xi_{n,i}(Z_{n-1}), \quad n \geq 1.$$

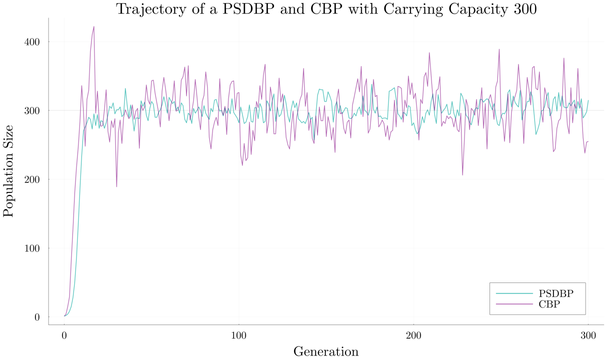
- A controlled branching process (CBP), $\{\tilde{Z}_n\}_{n\in\mathbb{N}_0}$, has recurrence relation

$$\tilde{Z}_n = \sum_{i=1}^{\tilde{\phi}(\tilde{Z}_{n-1})} \tilde{\xi}_{n,i}, \quad n \geq 1.$$

  where $\tilde{\phi}(\cdot)$ is a (possibly random) control function.

Both PSDBPs and CBPs can model logistic growth

- Useful to model populations that linger around a carrying capacity in habitats that exhibit resource scarcity.
- Trajectories of a PSDBP with $\xi(z) \stackrel{d}{=} \text{Bin}(2, Kz/(K+z))$, and a CBP with $\tilde{\phi}(z) \stackrel{d}{=} \text{Bin}(z+2, 2K^2/(3(K+2)(z+K)))$ and $\tilde{\xi} \stackrel{d}{=} \text{Poi}(3)$, for $K = 300$.



Comparing PSDBPs and CBPs

Population-size-dependent branching processes :

- Have flexibility in allowing the offspring distribution to vary in the current population size
- Have no built-in mechanism to model external random environment

Controlled branching processes :

- Do not have flexibility in allowing the offspring distribution to vary in the current population size
- Can model external conditions (random environment, migration,. . .)

Controlled Branching Processes

The entire class of CBPs is too flexible for statistical purposes.

Lemma 1

Any time-homogeneous Markov chain $\{X_n\}$ on $\mathbb{N}$ can be expressed as a CBP.

Indeed, let $\tilde{\phi}(z) \overset{d}{=} (X_n | X_{n-1} = z)$ and let $\tilde{\xi} = 1$ a.s.

The class of control functions is often restricted, popular choices being :

- $\tilde{\phi}(z) \sim \mathit{Poi}(\psi(z))$, *for* $\psi : \mathbb{N}_0 \to \mathbb{R}^+$, *or*
- $\tilde{\phi}(z) \sim \mathit{NB}(\psi(z), q)$, *for* $q \in [0, 1]$ *and* $\psi : \mathbb{N}_0 \to \mathbb{R}^+$, *or*
- $\tilde{\phi}(z) \sim \mathit{Bin}(\psi(z), p)$, *for* $p \in [0, 1]$ *and* $\psi : \mathbb{N}_0 \to \mathbb{N}_0$,

See for example the book "Controlled Branching Processes" by Miguel González Velasco, Inés M. del Puerto García, and George P. Yanev, page 129.

Which model to use ?

- When is it appropriate to model a population using a PSDBP ?
- When should we use a CBP instead ?
- *When does a PSDBP have an equivalent representation as a CBP ?*
- *When are PSDBPs and CBPs approximately equivalent ?*

2. PSDBP-CBP equivalence

- A PSDBP $\{Z_n\}_{n\geq 0}$ and a CBP $\{\tilde{Z}_n\}_{n\geq 0}$ with initial population size $Z_0 = \tilde{Z}_0 = z_0 \geq 1$ are equivalent if

$$(Z_n | Z_{n-1} = z) \stackrel{d}{=} (\tilde{Z}_n | \tilde{Z}_{n-1} = z)$$

for all $n \geq 1$ and $z \geq 0$.

- Recall that

$$(Z_n | Z_{n-1} = z) = \sum_{i=1}^{z} \xi_{n,i}(z), \quad (\tilde{Z}_n | \tilde{Z}_{n-1} = z) = \sum_{i=1}^{\tilde{\phi}(z)} \tilde{\xi}_{n,i}.$$

Lemma 2 (All PSDBPs are CBPs)

Every PSDBP can be expressed as a CBP.

- No CBP which allows immigration at zero can be expressed as a PSDBP.
- We now describe a class of CBPs which have an equivalent PSDBP.

Definition 1

A random variable X is said to be n-divisible if there exists a sequence of i.i.d. random variables $\{X_i^{(n)}\}_{i\leq n}$ such that $X \stackrel{d}{=} \sum_{i=1}^{n} X_i^{(n)}$. We say that X is infinitely divisible if X is n-divisible for all integers $n \geq 1$.

- Examples : Poisson, geometric, negative binomial r.v.'s are infinitely divisible ; a binomial r.v. is divisible but not infinitely divisible.
- We introduce another notion of divisibility, defined for processes rather than random variables :

Definition 2

A CBP $\{\tilde{Z}_n\}$ is said to have a $\tilde{Z}$-divisible control function $\tilde{\phi}$ if $\tilde{\phi}(0) = 0$ and $\tilde{\phi}(z)$ is z-divisible for all $z \geq 1$.

Theorem 1 (CBPs with $\tilde{Z}$-divisible $\tilde{\phi}$ have equivalent PSDBPs)

Let $\{\tilde{Z}_n\}$ be a CBP with a $\tilde{Z}$-divisible control function $\tilde{\phi}$. Then $\{\tilde{Z}_n\}$ can be expressed as a PSDBP.

Proof : For all attainable $z \geq 1$, we can write $\tilde{\phi}(z) = \sum_{j=1}^{z} \zeta_j(z)$, for some i.i.d random variables $\zeta_j(z)$. Then,

$$\sum_{i=1}^{\tilde{\phi}(z)} \tilde{\xi}_{n,i} = \sum_{j=1}^{z} \left(\sum_{i=1}^{\zeta_j(z)} \tilde{\xi}_{n,i} \right) = \sum_{j=1}^{z} \xi_{n,j}(z).$$

Corollary 1

If a CBP $\{\tilde{Z}_n\}$ has a control function such that $\tilde{\phi}(0) = 0$ and

- $\tilde{\phi}(z) \sim$ *Poi*$(\psi(z))$, *for* $\psi : \mathbb{N}_0 \to \mathbb{R}^+$, *or*
- $\tilde{\phi}(z) \sim$ *NB*$(\psi(z), q)$, *for* $q \in [0,1]$ *and* $\psi : \mathbb{N}_0 \to \mathbb{R}^+$, *or*
- $\tilde{\phi}(z) \sim$ *Bin*$(k \cdot z, p)$, *for* $p \in [0,1]$ *and* $k \in \mathbb{N}_0$,

then $\{\tilde{Z}_n\}$ can be expressed as a PDSBP.

- Is $\tilde{Z}$-divisibility of $\tilde{\phi}$ an 'if and only if' condition ?

  That is, is the $\tilde{Z}$-divisibility of the control function characterising the PSDBP-CBP equivalence ?

- In particular, in the binomial control case $\tilde{\phi}(z) \sim \text{Bin}(\psi(z), p)$, is the restriction $\psi(z) = k \cdot z$ necessary for equivalence ?

- We explore the general case $\tilde{\phi}(z) \sim \text{Bin}(\psi(z), p)$ with two different infinite divisible offspring distributions : Poisson and geometric.

Binomial control and Poisson offspring

- The following result suggests that $\tilde{Z}$-divisibility of $\tilde{\phi}$ might be a necessary and sufficient condition :

Proposition 1

Consider a CBP $\{\tilde{Z}_n\}$ with

$$\tilde{\phi}(z) \sim \textit{Bin}\big(\nu(z), p(z)\big) \quad \textit{and} \quad \tilde{\xi} \sim \textit{Poi}(\lambda), \qquad z \geq 0,$$

where $\nu : \mathbb{N}_0 \to \mathbb{N}_0$ is deterministic, and $p : \mathbb{N}_0 \to (0,1)$, and $\lambda > 0$. If $\tilde{\phi}(z)$ is not $\tilde{Z}$-divisible, and $\nu(z) \geq 1$ for all $z \geq 1$, then $\{\tilde{Z}_n\}$ cannot be expressed equivalently as a PSDBP.

Idea of the proof : Show that for a z^* s.t. that $\tilde{\phi}(z^*)$ is not z^*-divisible, $(\tilde{Z}_n | \tilde{Z}_{n-1} = z^*)$ is not z^*-divisible, i.e., $\sqrt[z^*]{G(t)}$ is not a valid pgf, where $G(t) = \big(p(z^*) + (1 - p(z^*))e^{\lambda(t-1)}\big)^{\nu(z^*)}$.

Binomial control and geometric offspring

- Changing the offspring distribution leads to a contrasting result :

Proposition 2

Consider a CBP $\{\tilde{Z}_n\}$ with

$$\tilde{\phi}(z) \sim \mathit{Bin}(\nu(z), p(z)) \quad \text{and} \quad \tilde{\xi} \sim \mathit{Geom}(q),$$

for $z \in \mathbb{N}_0$, deterministic functions $\nu : \mathbb{N}_0 \to \mathbb{N}_0$, $p : \mathbb{N}_0 \to (0,1)$, and $q \in (0,1)$.

Then as long as $\nu(0) = 0$, $\{\tilde{Z}_n\}$ can be expressed equivalently as a PSDBP.

- We believe the tail of the offspring distribution $\tilde{\xi}$ impacts the overall divisibility of $(\tilde{Z}_n | \tilde{Z}_{n-1} = z)$.
- **Open Question :** *What are necessary and sufficient conditions for PSDBP-CBP equivalence ?*

3. PSDBP-DCBP equivalence

Definition 3

A deterministically-controlled branching process (DCBP) $\{\tilde{Z}_n\}$ is a CBP with a deterministic control function $\phi(\cdot)$.

- For a PSDBP and a DCBP to be equivalent, we require that

$$(Z_n | Z_{n-1} = z) = \sum_{i=1}^{z} \xi_{n,i}(z), \qquad (\tilde{Z}_n | \tilde{Z}_{n-1} = z) = \sum_{i=1}^{\phi(z)} \tilde{\xi}_{n,i}.$$

  share the same distribution for all $n \geq 1$ and all $z \geq 0$.

- Neither the set of PSDBPs nor the set of DCBPs encompasses the other, but a DCBP has an equivalent representation as a PSDBP when it has a $\tilde{Z}$-divisible control function.

- There exists an equivalent PSDBP to a DCBP if and only if $\tilde{\xi}$ is divisible by all the prime factors of z that $\phi(z)$ is not, for all $z \geq 0$.

Definition 4

We say that a DCBP $\{\tilde{Z}_n\}$ is $\tilde{Z}$-divisible if $\phi(0) = 0$ and, for all values

$$y \in \mathcal{Y}_{\tilde{Z}} := \left\{ \frac{z}{\mathit{gcd}[\phi(z), z]} : z \neq 0 \text{ attainable} \right\},$$

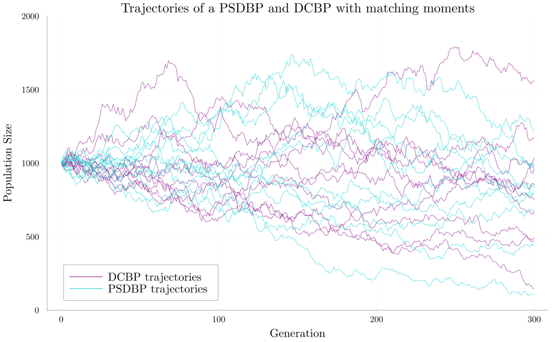
$\tilde{\xi}$ is y-divisible.

Theorem 2 (NSC for PSDBP-DCBP equivalence)

A DCBP $\{\tilde{Z}_n\}$ can be expressed as a PSDBP if and only if $\{\tilde{Z}_n\}$ is $\tilde{Z}$-divisible.

4. Approximate equivalence when moments are matching

- **Question :** *Do non-equivalent PSDBPs and DCBPs, with the same mean and variance, become 'close' in distribution if the initial population size is large ?*



- $\sum_{i=1}^{z} \xi_{n,i}(z)$ and $\sum_{i=1}^{\tilde{\phi}(z)} \tilde{\xi}_{n,i}$ are just sums of i.i.d. random variables
  $\rightarrow$ we may expect a central limit theorem-like result to hold.

Total variation distance

- The total variation distance (TVD) measures the 'closeness' between two probability distributions, or two random processes :

Definition 1

For random variables X and Y defined on a countable space $\mathcal{X}$, the TVD between each of their distributions is defined as

$$||\mathcal{L}_X - \mathcal{L}_Y||_{TV} := \sup_{A \subseteq \mathcal{X}} |\mathbb{P}(X \in A) - \mathbb{P}(Y \in A)|.$$

Interpretation : H_0 : data generated from X ; H_1 : generated from Y.
Type I-error : reject H_0 if actually true ; Type II-error : fail to reject H_0 if actually false.

$$\mathbb{P}(\text{Type I-error}) + \mathbb{P}(\text{Type II-error}) \geq 1 - ||\mathcal{L}_X - \mathcal{L}_Y||_{TV}$$

So if TVD approaches 0, it is impossible to detect from which distribution the data come from.

A one-step upper bound on the TVD

Lemma 2

For a PSDBP $\{Z_n\}$ *and a DCBP* $\{\tilde{Z}_n\}$*, with matching mean and variance and satisfying certain conditions, there exists* $b \in \mathbb{R}^+$ *such that, for any* $z \geq 1$*,*

$$||\mathcal{L}_{Z_1|Z_0=z} - \mathcal{L}_{\tilde{Z}_1|\tilde{Z}_0=z}||_{TV} \leq \frac{b}{\sqrt{z}}.$$

Idea of the proof : We use the triangle inequality to bound the overall TVD as the sum of TVDs between each one-step distribution and the discretised normal distribution.

A k-step upper bound on the TVD

Theorem 3

Under the same conditions as in Lemma 2, and for any $z, k \geq 1$,

$$||\mathcal{L}_{(Z_1,\ldots,Z_k)|Z_0=z} - \mathcal{L}_{(\tilde{Z}_1,\ldots,\tilde{Z}_k)|\tilde{Z}_0=z}||_{TV} \leq \frac{c_1(\gamma)\left|1-\gamma^{-\frac{k}{2}}\right|}{\sqrt{z}} + \frac{c_2(\gamma)\left|1-\gamma^{-k+1}\right|}{z},$$

where γ *is a criticality parameter that is* > 1 *if the processes grow on average, and* < 1 *if they shrink on average, and* $c_1(\gamma), c_2(\gamma) \in \mathbb{R}^+$.

- *In the proof*, we used an inductive argument to find explicit expressions for the constants in the upper bound.
- When $\gamma > 1$, in the limit as z increases to infinity the CBP and the PSDBP are indistinguishable over their *entire* paths.

Necessary and sufficient conditions for moment matching

- Let $m(z)$ and $\sigma^2(z)$ be the offspring mean and variance of a PSDBP
- Let $\tilde{m}$ and $\tilde{\sigma}^2$ the offspring mean and variance of a DCBP
- A PSDBP and a DCBP have matching mean and variance if

$$z \cdot m(z) = \tilde{m} \cdot \phi(z) \quad \text{and} \quad z \cdot \sigma^2(z) = \tilde{\sigma}^2 \cdot \phi(z) \qquad \text{for all } z \in \mathbb{N}_0.$$

Theorem 3 (NSC to match a PSDBP to a DCBP)

A PSDBP $\{Z_n\}$ can be found to match the mean and variance of a DCBP $\{\tilde{Z}_n\}$ if and only if $\{\tilde{Z}_n\}$ satisfies

$$\frac{\tilde{\sigma}^2 \cdot \phi(z)}{z} \geq d(z)(1 - d(z)), \qquad \textit{for all } z \in \mathbb{N}_1,$$

where $d(z) := \frac{\tilde{m}\cdot\phi(z)}{z} - \left\lfloor \frac{\tilde{m}\cdot\phi(z)}{z} \right\rfloor$.

Theorem 4 (NSC to match a DCBP to a PSDBP)

A DCBP $\{\tilde{Z}_n\}$ *can be found to match the mean and variance of a PSDBP* $\{Z_n\}$ *if and only if the following requirements on* $\{Z_n\}$ *hold for all* $z \in \mathbb{N}_1$ *such that* $m(z) \neq 0$ *:*

(i) *there exists a constant* $k \in \mathbb{R}^+$ *such that* $m(z) = k \cdot \sigma^2(z)$,

(ii) *there exists a (necessarily non-unique) constant* $h \in \mathbb{R}^+$ *such that* $m(z) \in h \cdot \mathbb{N}_1$,

(iii) *For* $H := \{h \in \mathbb{R}_{>0} : m(z) \in h \cdot \mathbb{N}_1 \ \ \forall z \in \mathbb{N}_1\}$, *there exists* $h' \geq \sup_{h<1}\{h \in H\}$ *such that* $\frac{h'}{k} \geq (h' - \lfloor h' \rfloor)\,(1 - h' + \lfloor h' \rfloor)$.

A k-step upper bound on the TVD : Extensions

- Moments do not need to match exactly ! Our results extend to the case where the absolute difference of the means goes to 0 and the relative difference of the variance goes to 0.
- We can generalise our results to find the upper bound on the TVD between a PSDBP and a hybrid DCBP-PSDBP :

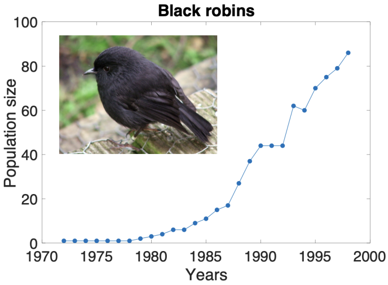
$$\tilde{Z}_n = \sum_{i=1}^{\phi(\tilde{Z}_{n-1})} \tilde{\xi}_{n,i}(\tilde{Z}_{n-1}), \quad n \geq 1.$$

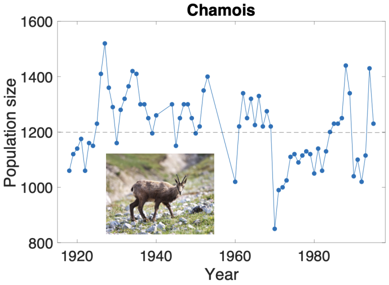
under additional assumption on $\tilde{\xi}(z)$.

This includes in particular, the binomial control case.

5. Numerical illustrations

- Coming back to our motivation : we are interested in populations exhibiting logistic growth with a carrying capacity.





- We have seen in our theoretical bound that the TVD between PSDBP and CBP paths decreases in $1/\sqrt{z}$.

  We introduce a practical example which goes slightly beyond the setting of the theorem but which exhibits similar decaying behaviour.

A Beverton-Holt model with immigration

For $\lambda \geq 2$, $M, K \in \mathbb{N}_1$, $M < K$, consider the CBP $\{\tilde{Z}_n\}_{n\in\mathbb{N}_0}$ with

$$\tilde{\phi}(z) \sim \text{Bin}\left((z+M)\mathbb{1}_{\{z>0\}}, \ \frac{2K^2}{\lambda(K+M)(z+K)}\right) \quad \text{and} \quad \tilde{\xi} \sim \text{Poi}\,(\lambda)\,,$$

and the PSDBP $\{Z_n\}_{n\in\mathbb{N}_0}$ with

$$\xi(z) \sim \text{NB}\left(\frac{2K^2(z+M)}{z(\lambda(K+M)z+\lambda KM+(\lambda-2)K^2)}, \ \frac{(z+K)(K+M)}{(1+\lambda)(K+M)(K+z)-2K^2}\right).$$

Both processes have matching moments, and a carrying capacity at K.

Letting $\nu(z) := (z+M)\mathbb{1}_{\{z>0\}}$ and $\zeta(z) \sim \text{ZIP}\left(1-\frac{2K^2}{\lambda(K+M)(z+K)}, \ \lambda\right)$,

$$(\tilde{Z}_n|\tilde{Z}_{n-1}=z) = \sum_{i=1}^{\tilde{\phi}(z)} \tilde{\xi}_i = \sum_{i=1}^{\nu(z)} \zeta_i(z),$$

where $\nu(z)$ is a deterministic function (hybrid DCBP-PSDBP).

Estimation of the TVD

- While the analytical bound on the TVD provides decay rates on the TVD in terms of the initial population size, this bound is not tight.
- To estimate the TVD between *any* PDSBP and CBP, we can use Monte-Carlo simulation and importance sampling :

Lemma 4 (An estimator for the TVD)

Let X and Y be two random variables defined on a countable space $\mathcal{X}$. For $n \geq 1$, let $X_1, \ldots, X_n$ be a random sample from the distribution of X, $\mathcal{L}_X$. Then

$$\hat{\theta}_n := \frac{1}{2n} \sum_{i=1}^{n} \frac{|\mathcal{L}_X(X_i) - \mathcal{L}_Y(X_i)|}{\mathcal{L}_X(X_i)}$$

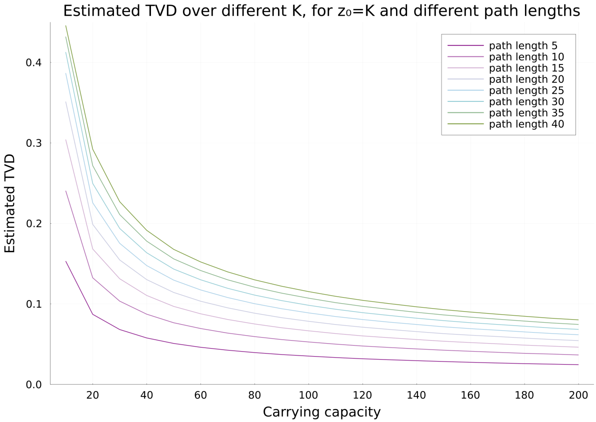
is an unbiased, consistent estimator for $||\mathcal{L}_X - \mathcal{L}_Y||_{TV}$.

Estimation of the TVD

Proof :

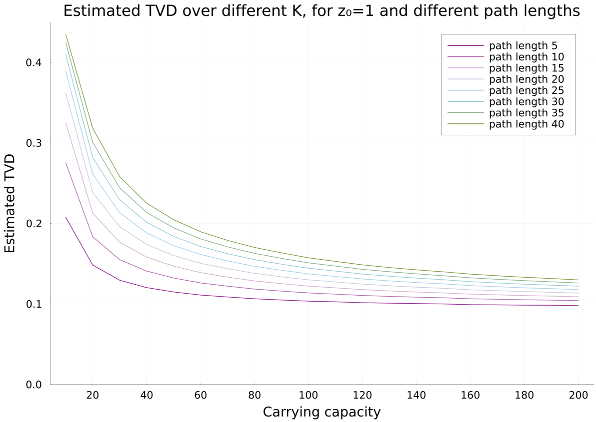
$$
\begin{aligned}
||\mathcal{L}_X - \mathcal{L}_Y||_{TV} &= \frac{1}{2} \sum_{n \in \mathcal{X}} |\mathbb{P}(X = n) - \mathbb{P}(Y = n)| \\
&= \frac{1}{2} \sum_{n \in \mathcal{X}} \frac{\big|\mathbb{P}(X = n) - \mathbb{P}(Y = n)\big|}{\mathbb{P}(X = n)} \cdot \mathbb{P}(X = n) \\
&= \frac{1}{2} \cdot \mathbb{E}_X \left(\frac{|\mathcal{L}_X(X) - \mathcal{L}_Y(X)|}{\mathcal{L}_X(X)} \right).
\end{aligned}
$$

Estimated TVD in our practical example



Estimated TVD between the processes $\{\tilde{Z}_n\}_{n\in\mathbb{N}_0}$ and $\{Z_n\}_{n\in\mathbb{N}_0}$ when $\lambda = 3$ and $M = 2$ based on 10^6 simulations.

Estimated TVD in our practical example



Estimated TVD between the processes $\{\tilde{Z}_n\}_{n\in\mathbb{N}_0}$ and $\{Z_n\}_{n\in\mathbb{N}_0}$ when $\lambda = 3$ and $M = 2$ based on 10^6 simulations.

6. Conclusions

- PSDBPS cannot incorporate external random factors.
- We have seen that many CBP models, including those with Poisson, negative binomial, and binomial control functions, can be expressed as PSDBPs, whether exactly, or approximately.
- Therefore, when we use these common control functions, we are not getting anything additional than if using PSDBPs.
- So which class of models should we look at ? How should we estimate their parameters ? Which parameters can be estimated consistently ? This is ongoing work.

Thank you for your attention !