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Tree-free PCM

Tree-free phylogenetic comparative methods: macroevolutionary dynamics on a branching process

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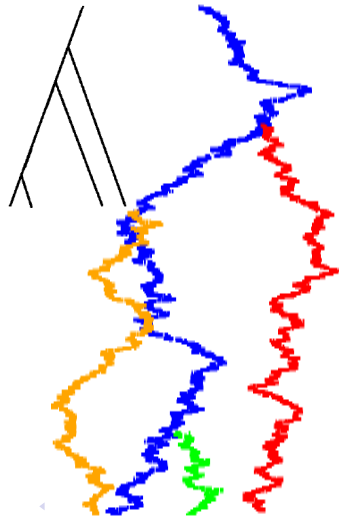
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joint work with Serik Sagitov
Mathematical Sciences
CTH, GU



Phylogenetic comparative methods

Introduction:

Euplectes spp. (subfam. Ploceinae = weaverbirds)





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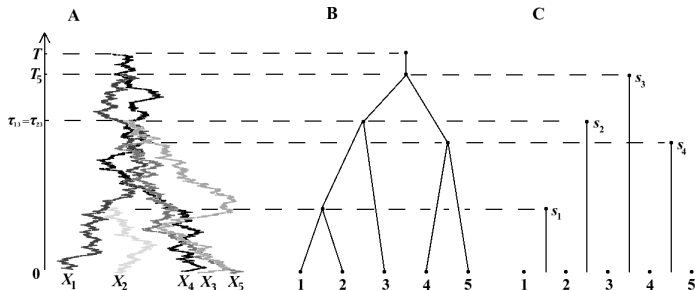
Tree-free PCM

“Tree-free” methods

But what if we do not
observe the tree ?



Conditioned branching processes





Gernhard (2008), Sagitov and KB (2012)

- ▶ Conditional on T all $n - 1$ s_i s are independent.



$$q_n(T|n) = n\lambda^n(\lambda - \mu)^2 \frac{(1 - e^{-(\lambda-\mu)T})^{n-1} e^{-(\lambda-\mu)T}}{(\lambda - \mu e^{-(\lambda-\mu)T})^{n+1}}$$



$$F(s|T) = \frac{1 - \lambda e^{-(\lambda-\mu)s} - \mu e^{-(\lambda-\mu)T}}{(\lambda - \mu e^{-(\lambda-\mu)s})(1 - e^{-(\lambda-\mu)T})} \mathbf{1}(s \leq T)$$



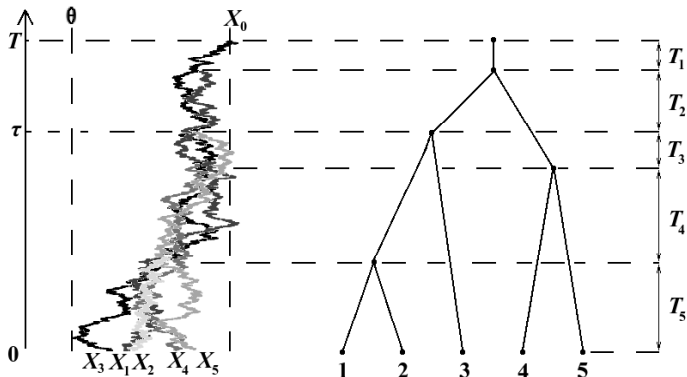
$$\begin{aligned} \mathbb{E}[T - \tau] &= \mathbb{E} \left[T - \int_0^T 1 - F^\kappa(s|T) ds \right] \\ &= \sum_{k=1}^{n-1} \frac{n-k}{\binom{n}{2}} \int_0^T \left(\int_0^T F^k(s|T) ds \right) q_n(T) dT \end{aligned}$$





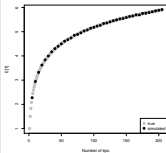
Conditioned Yule tree

$$T_i \sim \exp(\lambda i)$$

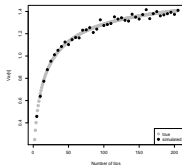
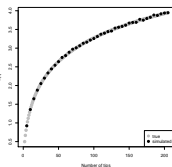




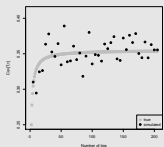
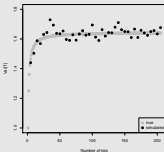
Conditioned Yule tree



$$H_{n,k} = \sum_{i=1}^n \frac{1}{i^k} \quad b_{n,x} = \prod_{i=1}^n \frac{i}{i+x}$$



- ▶ $E[T] = H_{n,1}/\lambda \sim \ln n/\lambda$
- ▶ $\text{Var}[T] = H_{n,2}/\lambda^2 \rightarrow \frac{\pi^2}{6\lambda^2}$
- ▶ $E[\tau] = \frac{n+1}{\lambda(n-1)}H_{n,1} - \frac{2n}{\lambda(n-1)} \sim \ln n/\lambda$
- ▶ $\text{Var}[\tau] = \frac{(n^2-1)H_{n,2} - 2(n+1)H_{n,1}^2 + 4(n+1)H_{n,1} - 4n}{\lambda^2(n-1)^2} \rightarrow \frac{\pi^2}{6\lambda^2}$
- ▶ $\text{Cov}[T, \tau] = \frac{1}{\lambda^2(n-1)}(2n - (n+1)H_{n,2}) \rightarrow \frac{1}{\lambda^2}(2 - \frac{\pi^2}{6})$
- ▶ $E[e^{-\gamma T}] = b_{n,\gamma}, \quad E[e^{-\gamma \tau}] = \frac{2 - (n+1)(\gamma+1)b_{n,\gamma}}{(n-1)(\gamma-1)}$





Application: Interspecies correlation ($\lambda = 1$)

How similar do we expect two random species to be?

$$\rho_n = \frac{\text{Cov}[X_1, X_2]}{\text{Var}[X]}$$

Brownian motion

$$dX(t) = \sigma dB(t) \quad X(0) = X_0$$

$$E[X(t)] = X_0 \quad \text{Var}[X(t)] = \sigma^2 t$$

$$\rho_n \sim 2(\ln n)^{-1}$$

Ornstein–Uhlenbeck process

$$dX(t) = -\alpha(X(t) - \theta)dt + \sigma dB(t) \quad X(0) = X_0$$

$$E[X(t)] = e^{-\alpha t} X_0 + (1 - e^{-\alpha t})\theta \quad \text{Var}[X(t)] = \frac{\sigma^2}{2\alpha}(1 - e^{-2\alpha t})$$

$$\rho_n \sim \begin{cases} Cn^{-2\alpha} & 0 < \alpha < 0.5 \\ 2n^{-1} \ln n & \alpha = 0.5 \\ Cn^{-1} & \alpha > 0.5 \end{cases}$$



Application: Classical estimators ($\lambda = 1$)

Tree-free PCM

$$\bar{X}_n := \frac{1}{n} \sum_{i=1}^n X_i$$

$$S_n^2 := \frac{1}{n-1} \sum_{i=1}^n (X_i - \bar{X}_n)^2$$

	$E[\bar{X}_n]$	$\text{Var}[\bar{X}_n]$	$E[S_n^2]$	$\text{Var}[S_n^2]$
$\alpha = 0$	X_0	$2\sigma^2$	$\sigma^2 \ln n + O(1)$	$(\frac{\pi^2}{6} + 1)\sigma^4$
$\alpha \in (0, \frac{1}{2})$	$\theta + O(n^{-\alpha})$	$c_\alpha n^{-2\alpha}$	$\frac{\sigma^2}{2\alpha} + O(n^{-2\alpha})$	$O(n^{-2\alpha})$
$\alpha = \frac{1}{2}$	$\theta + O(n^{-\alpha})$	$2\frac{\ln n}{n}$	$\frac{\sigma^2}{2\alpha} + O(\frac{\ln n}{n})$	$O(\frac{\ln n}{n})$
$\alpha > \frac{1}{2}$	$\theta + O(n^{-\alpha})$	$c_\alpha n^{-1}$	$\frac{\sigma^2}{2\alpha} + O(n^{-2\alpha})$	$O(n^{-1})$



Application: weak convergence

Theorem

Let $\delta = \frac{X_0 - \theta}{\sqrt{\sigma_a^2/2\alpha}}$ be a normalized difference between the ancestral and optimal values. Consider the normalized sample mean $\bar{Y}_n = \frac{\bar{X}_n - \theta}{\sqrt{\sigma_a^2/2\alpha}}$ of the

Yule-Ornstein-Uhlenbeck process with $\bar{Y}_0 = \delta$. As $n \rightarrow \infty$ the process \bar{Y}_n has the following limit behaviour.

- (i) If $\alpha > 0.5$, then $\sqrt{n} \cdot \bar{Y}_n$ is asymptotically normally distributed with zero mean and variance $\frac{2\alpha+1}{2\alpha-1}$.
- (ii) If $\alpha = 0.5$, then $\sqrt{n/\ln n} \cdot \bar{Y}_n$ is asymptotically normally distributed with zero mean and variance 2.
- (iii) If $\alpha < 0.5$, then $n^\alpha \cdot \bar{Y}_n$ converges a.s. and in L^2 to a random variable $Y_{\alpha,\delta}$ with $E[Y_{\alpha,\delta}] = \delta\Gamma(1+\alpha)$ and $E[Y_{\alpha,\delta}^2] = \left(\delta^2 + \frac{4\alpha}{1-2\alpha}\right)\Gamma(1+2\alpha)$.



Application: confidence interval

$$E[S_n^2] \rightarrow \frac{\sigma_a^2}{2\alpha} \quad \text{Var}[S_n^2] \rightarrow 0$$

allows us to write confidence intervals

$$\text{for } \alpha > 0.5 \quad \bar{X}_n \pm z_{1-x/2} \cdot \sqrt{S_n^2} \cdot \frac{1}{\sqrt{n}} \cdot \sqrt{\frac{2\alpha + 1}{2\alpha - 1}},$$

$$\text{for } \alpha = 0.5 \quad \bar{X}_n \pm z_{1-x/2} \cdot \sqrt{S_n^2} \cdot \frac{\sqrt{2 \ln n}}{\sqrt{n}},$$

$$\text{for } \alpha < 0.5 \quad (\bar{X}_n - q_{x/2} \cdot \sqrt{S_n^2} \cdot n^{-\alpha}, \\ \bar{X}_n + q_{1-x/2} \cdot \sqrt{S_n^2} \cdot n^{-\alpha}).$$



Thank you !!!!

- ▶ S. Andersson, G. Jones, P. Mostad, B. Oxelman, S. Sagitov, M. Prager (GU, CTH)
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References

- ▶ K.B., J. Pienaar, P. Mostad, S. Andersson, T.F. Hansen. **A phylogenetic comparative method for studying multivariate adaptation.** *J. Theor. Biol.*, 314:204–215, 2012
- ▶ S.S., K.B. **Interspecies correlation for neutrally evolving traits.** *J. Theor. Biol.*, 309:11–19, 2012
- ▶ K.B., G. Jones, B. Oxelman, S.S. **Time to a single hybridization event in a group of species with unknown ancestral history.** *J. Theor. Biol.*, 322:1–6, 2013
- ▶ K.B., S.S. **Phylogenetic confidence intervals for the optimal trait value.** *J. Appl. Probab.*, 52, 2015
- ▶ K.B. **Quantifying the effects of anagenetic and cladogenetic evolution.** *Math. Biosc.*, 254:42–57, 2014
- ▶ K.B., S.S. **A consistent estimator of the evolutionary rate.** *J. Theor. Biol.*, 371:69–78, 2015