Two Combinatorial Problems Arising from Phylogenetics

(joint with M. Drmota, E. Y. Jin, C.-H. Lee, Y.-W. Lee and A. R. Paningbatan)

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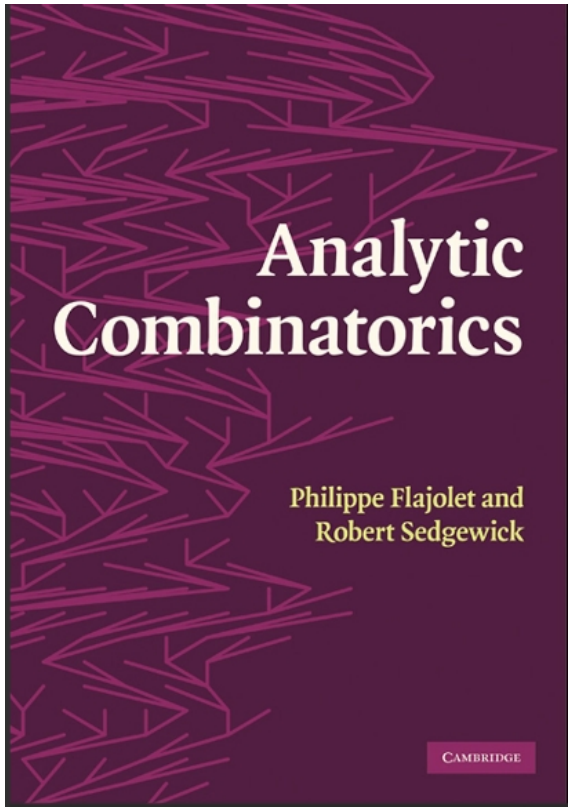
June 14th, 2019

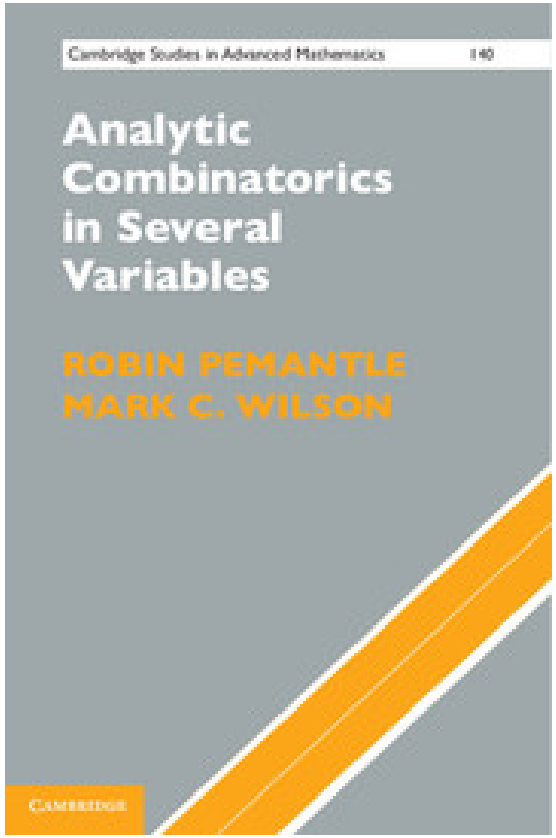
Analytic Combinatorics (i)

Combinatorialists use recurrence, generating functions, and such transformations as the Vandermonde convolution; others, to my horror, use contour integrals, differential equations, and other resources of mathematical analysis.

- John Riordan (1968).

Analytic Combinatorics (ii)





Outline of the Talk

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1. Introduction
2. Biodiversity Indices

F. and Jin (2015). Equality of Shapley value and fair proportion index in phylogenetic trees.

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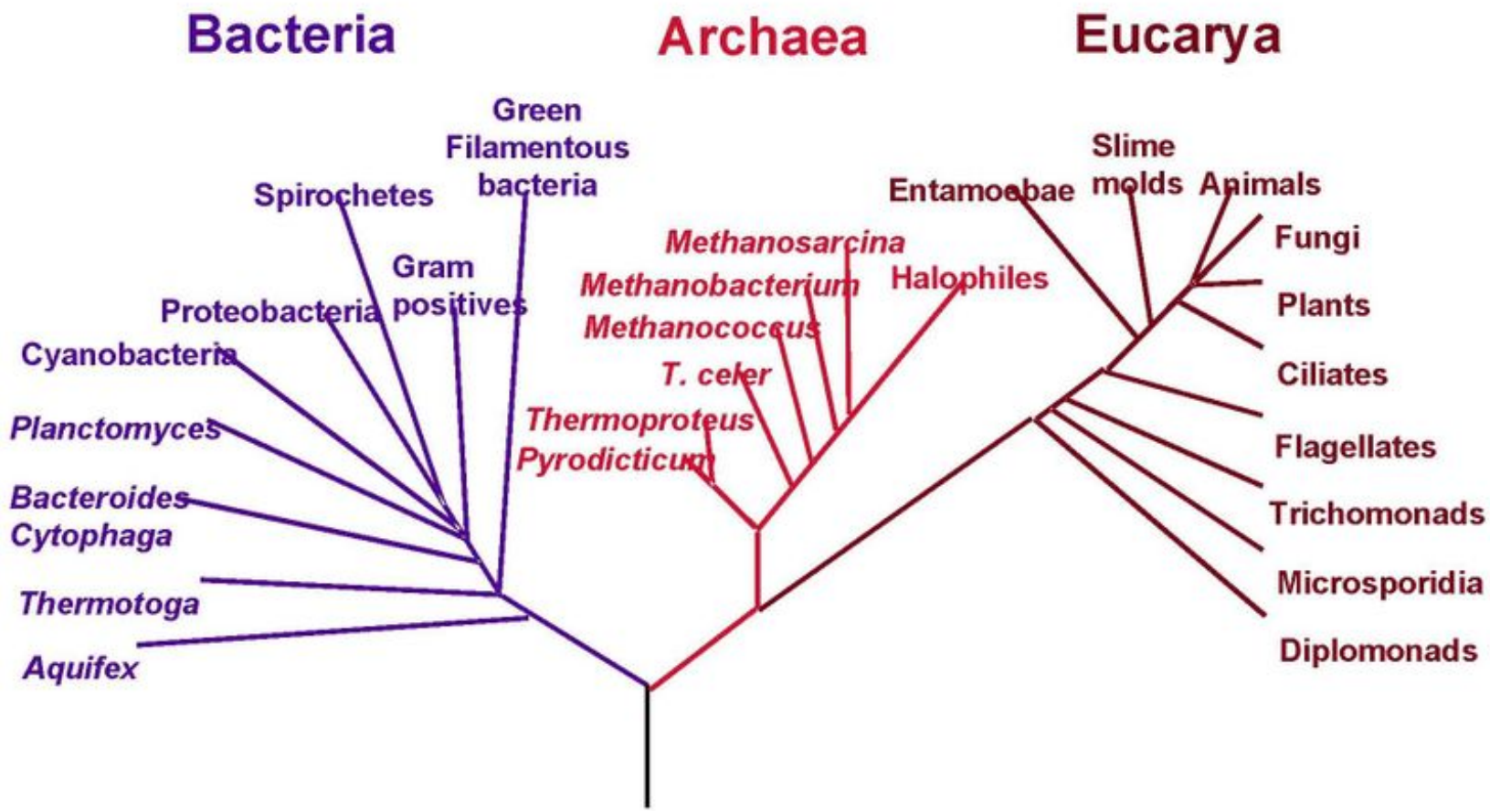
   F. and Paningbatan (2019+). Correlation between Shapley values of rooted phylogenetic trees under the beta-splitting model.

3. Group Pattern Formation of Social Animals

   Drmota, F., Y.-W. Lee (2016). Stochastic analysis of the extra clustering model for animal grouping.

   F., C.-H. Lee, Paningbatan (2019+). Distributional analysis of the extra clustering model with uniformly generated phylogenetic trees.

Evolutionary or Phylogenetic tree (=PT)



Phylogenetic tree of size n: rooted, plane, unlabelled binary tree with n external nodes (and consequently $n-1$ internal nodes).

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- Stop when a subinterval contains only one ball.

$\longrightarrow$ This gives a probability distribution on PTs of size n.

Aldous β-splitting Model (ii)

T ... random PT.

Choose a β-distribution ($\beta > -1$):

$$f(x) = \frac{\Gamma(2\beta+2)}{\Gamma^2(\beta+1)} x^\beta (1-x)^\beta, \qquad x \in [0,1].$$

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Let $\pi_{n,i}$ be the probability that left subtree has size i. Then,

$$\pi_{n,i} = \frac{1}{\pi_n(\beta)} \frac{\Gamma(\beta+i+1)\Gamma(\beta+n-i+1)}{i!(n-i)!}, \qquad 1 \le i \le n-1,$$

where $\pi_n(\beta)$ is a suitable constant.

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Note that the above expression makes also sense for $-2 < \beta \le -1$.

Special Cases

- $\beta = 0$: Yule-Harding model:

$$\pi_{n,i} = \frac{1}{n-1}, \qquad 1 \le i \le n-1.$$

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- $\beta = -3/2$: Uniform or PDA model:

$$\pi_{n,i} = \frac{C_{i-1}C_{n-i-1}}{C_{n-1}}, \qquad 1 \le i \le n-1,$$

where $C_n = \binom{2n}{n}/(n+1)$ are the Catalan numbers.

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- $\beta = -1$: with H_n the harmonic numbers:

$$\pi_{n,i} = \frac{n}{2H_{n-1}} \cdot \frac{1}{i(n-i)}, \qquad 1 \le i \le n-1.$$

This model seems to have the best match with real trees.

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Measure of importance of each player in a cooperative game

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$\longrightarrow$ recently used as prioritization tool of taxa in biodiversity

Shapley Value and Fair Proportion Index

Let T be a PT and a a taxon (=leaf) of T.

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Rooted Shapley Value $\mathrm{SV}_T^{[r]}(a)$:

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where $\mathrm{PD}(S)$ is the size of the ancestor tree of S.

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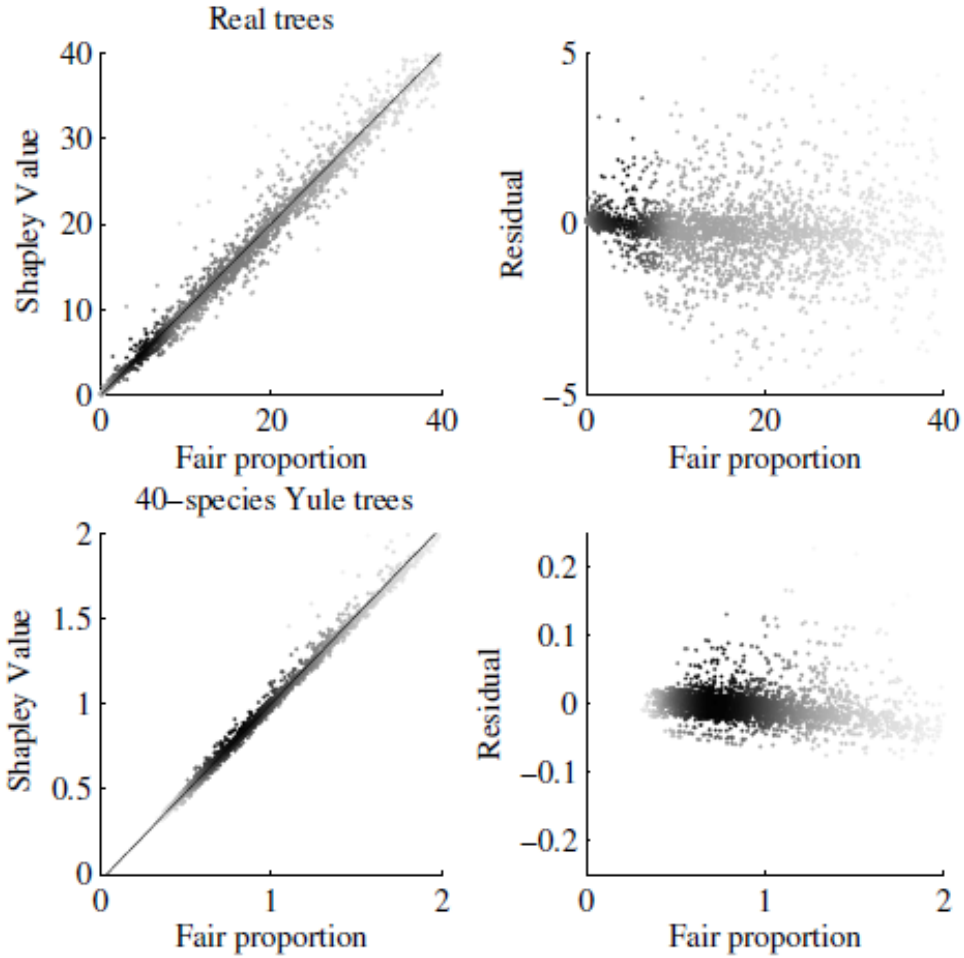
Used (somehow arbitrarily) for EDGE of Existence conservation program!

Correlation between $\mathrm{SV}^{[r]}$ and FP

Hartmann (2013):



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Theorem (F. and Jin; 2015)

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Theorem (F. and Jin; 2015)

Under the PDA model and the Yule-Harding model,

$$\lim_{n\to\infty} \rho(\widetilde{\mathrm{SV}}_n, \mathrm{FP}_n) = 1,$$

where ρ denotes the correlation coefficient.

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Theorem (F. and Paningbatan; 2019+)

Under the β-splitting model with $\beta > -1$,

$$\lim_{n \to \infty} \rho(\mathrm{SV}_n^{[u]}, \mathrm{FP}_n) = 1,$$

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- An expression for the difference:

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- Using the above two steps to bound the correlation coefficient with a bound which tends to 0.

Master Theorems

Let a_n satisfy the recurrence from the last slide with $\beta > -1$.

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Proposition

Assume that

$$b_n = \mathcal{O}(n^\gamma \log^\delta n)$$

for integers $\gamma, \delta \geq 0$. *Then,*

(i) *if* $\gamma = 1$, *then* $a_n = \mathcal{O}(n \log^{\delta+1} n)$;

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Proposition

If b_n *is non-negative and* $b_{n_0} > 0$ *for at least one* n_0, *then*

$$b_n = \Omega(n).$$

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Corollary

For $\beta > -1$, we have

$$\mathbb{E}(S_n) = \mathcal{O}(n \log n), \qquad \mathbb{E}(S_n^2) = \mathcal{O}(n^2 \log^2 n);$$
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For $\beta > -1$, we have

$$\mathrm{Var}(\mathrm{FP}_n) = \Omega(1).$$

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We have,

$$X_T^{[i]} = X_{T_\ell}^{[i]} + X_{T_r}^{[i]} + \binom{|T_\ell|}{i} + \binom{|T_r|}{i}$$

and

$$Y_T^{[i]}(a) = \begin{cases} Y_{T_\ell}^{[i]}(a) + X_{T_r}^{[i]} + \binom{|T_r|}{i}, & \text{if } a \in T_\ell; \\ Y_{T_r}^{[i]}(a) + X_{T_\ell}^{[i]} + \binom{|T_\ell|}{i}, & \text{if } a \in T_r. \end{cases}$$

Difference between $\mathrm{SV}^{[u]}$ and FP

Proposition

For $a \in T_\ell$, we have

$$\begin{aligned}\mathrm{SV}_T^{[u]}(a) - \mathrm{SV}_T^{[r]}(a) = &-\frac{1}{n} D_T(a) \\ &+ \frac{1}{n!} \sum_{i=1}^{|T_r|} i!(n-i-1)! \left(X_{T_r}^{[i]} + \binom{|T_r|}{i} \right) \\ &+ \frac{1}{n!} \sum_{i=1}^{|T_\ell|-1} i!(n-i-1)! Y_{T_\ell}^{[i]}(a).\end{aligned}$$

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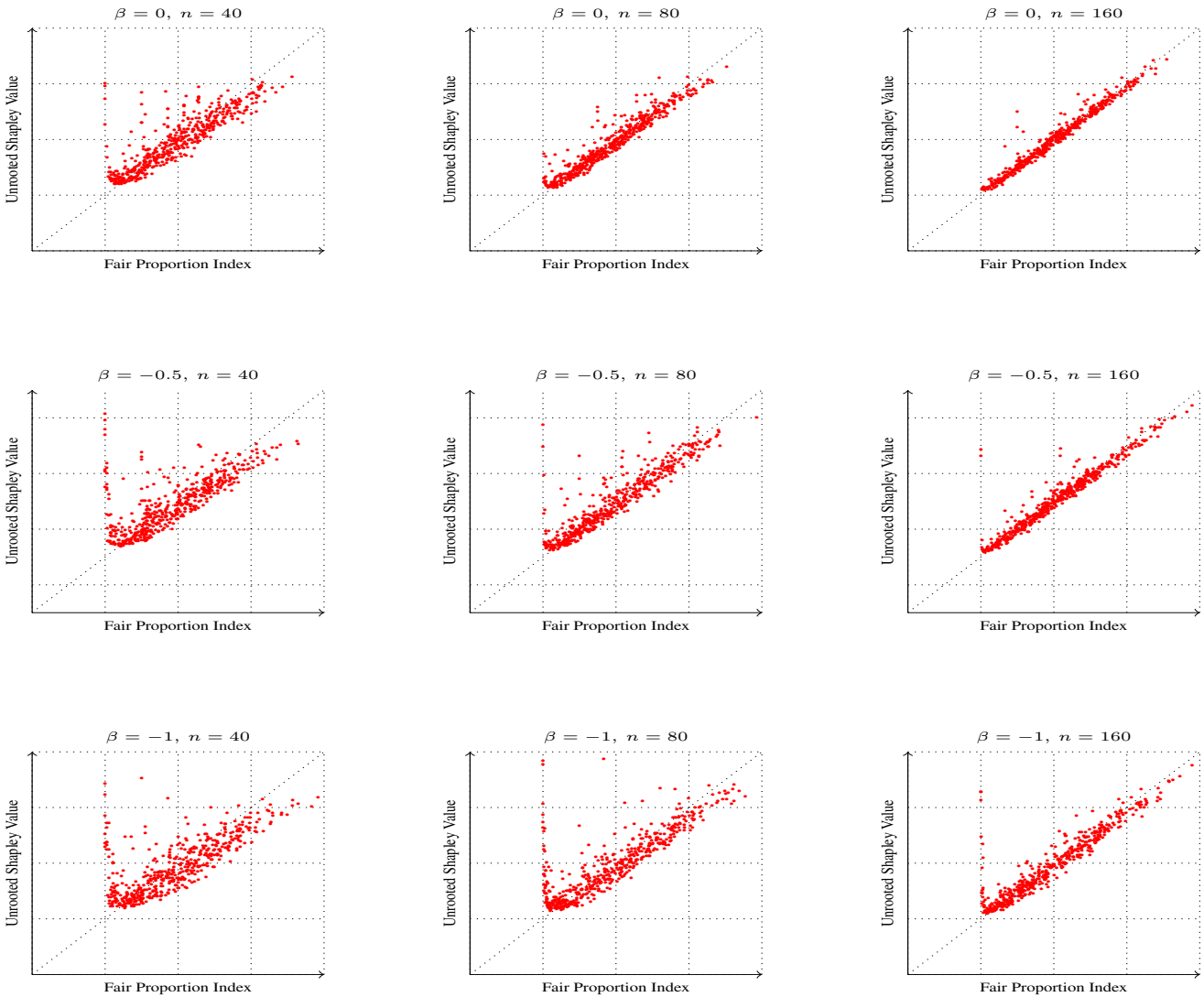
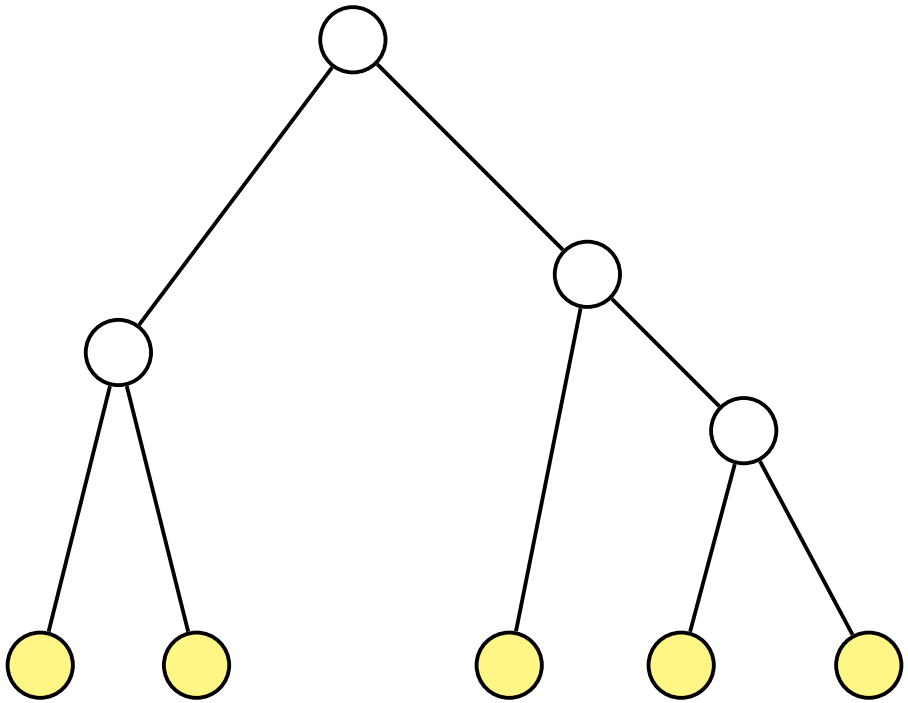
Since $\mathrm{FP}_T, D_T(a), X_T^{[i]}, Y_T^{[i]}(a)$ can all be computed recursively, $\mathrm{SV}_T^{[u]}$ can be computed efficiently.

Does our Theorem extend to $\beta = -1$ (and beyond)?



Phylogenetic Trees and Animal Grouping

Let the leaves represent social animals.



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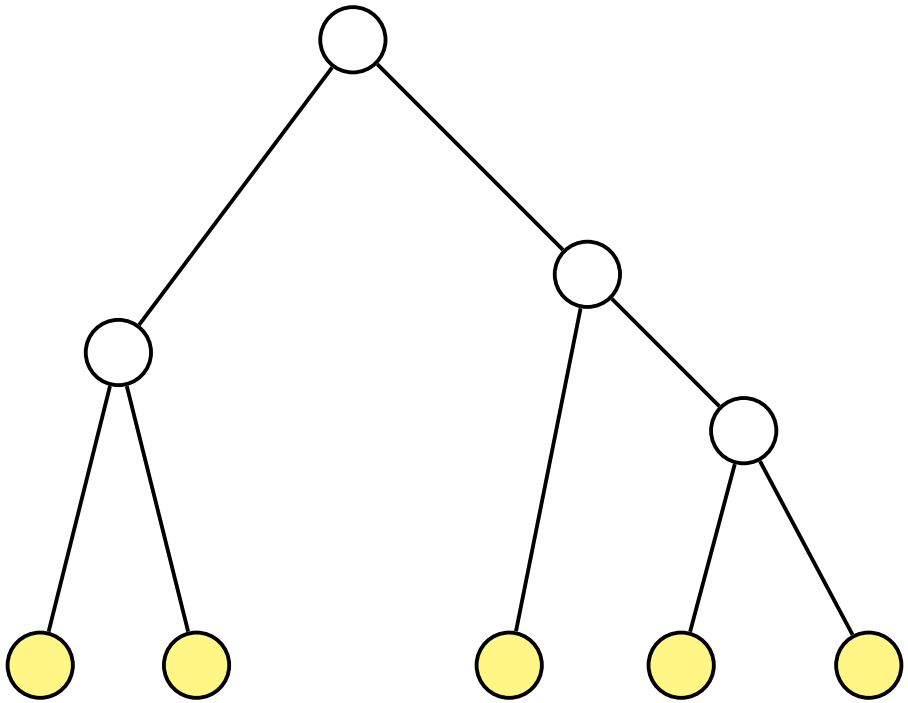

Describes the genetic relatedness of the animals.

Animal Groups

Durand, Blum and François (2007):

Groups contain more likely animals which are genetically related.

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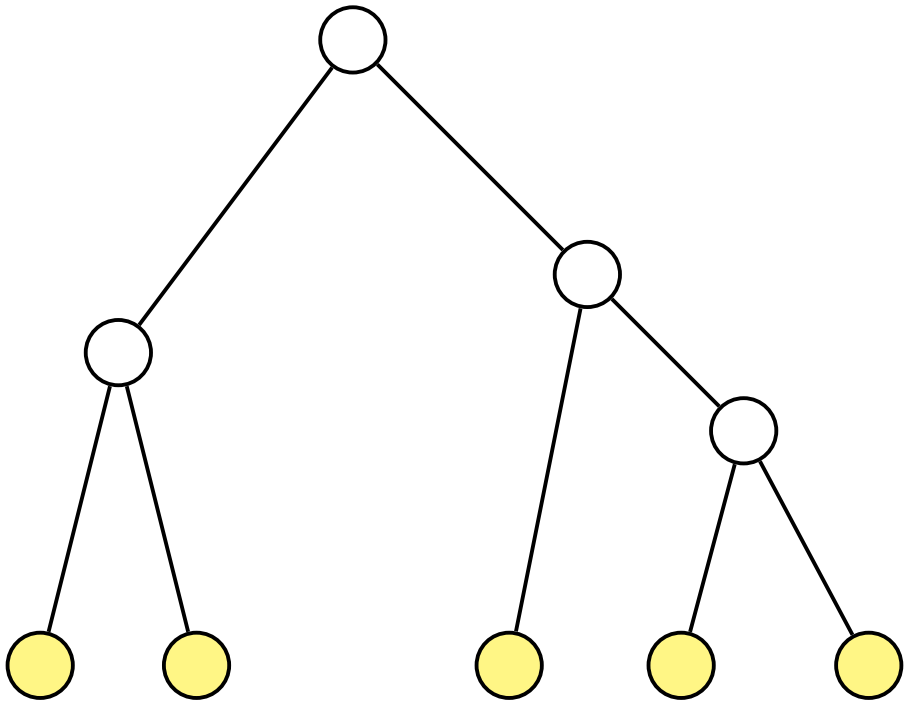

Clade of a leaf:

All leaves of the tree rooted at the parent.

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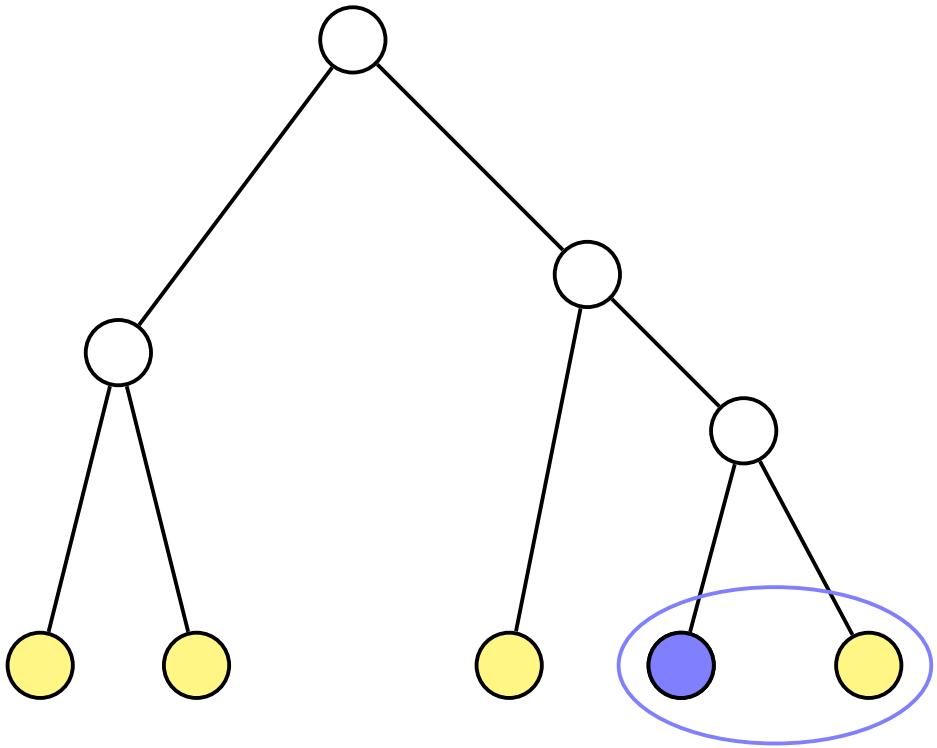

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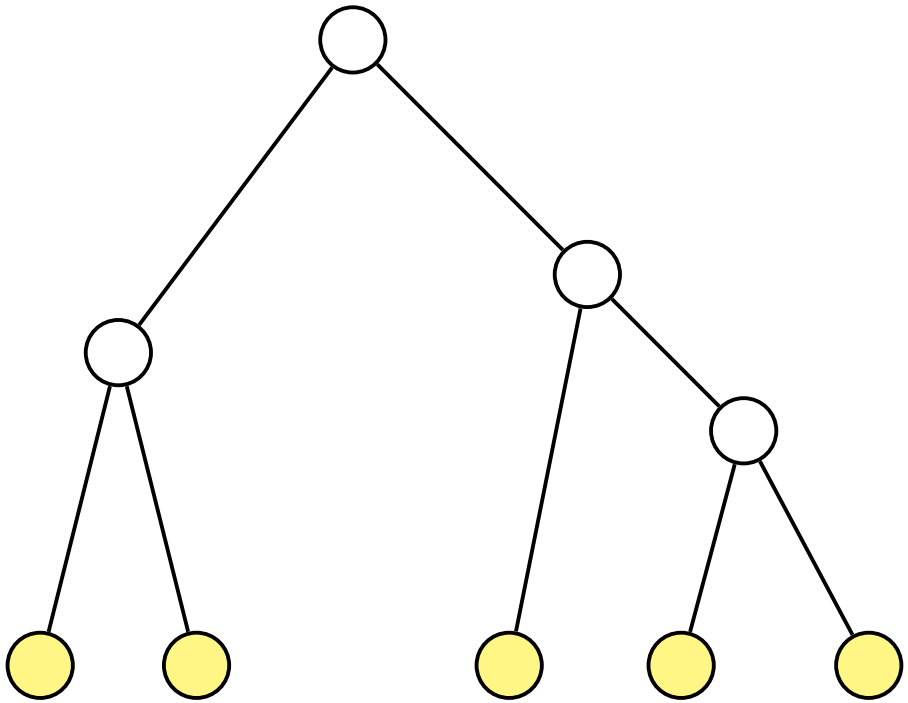

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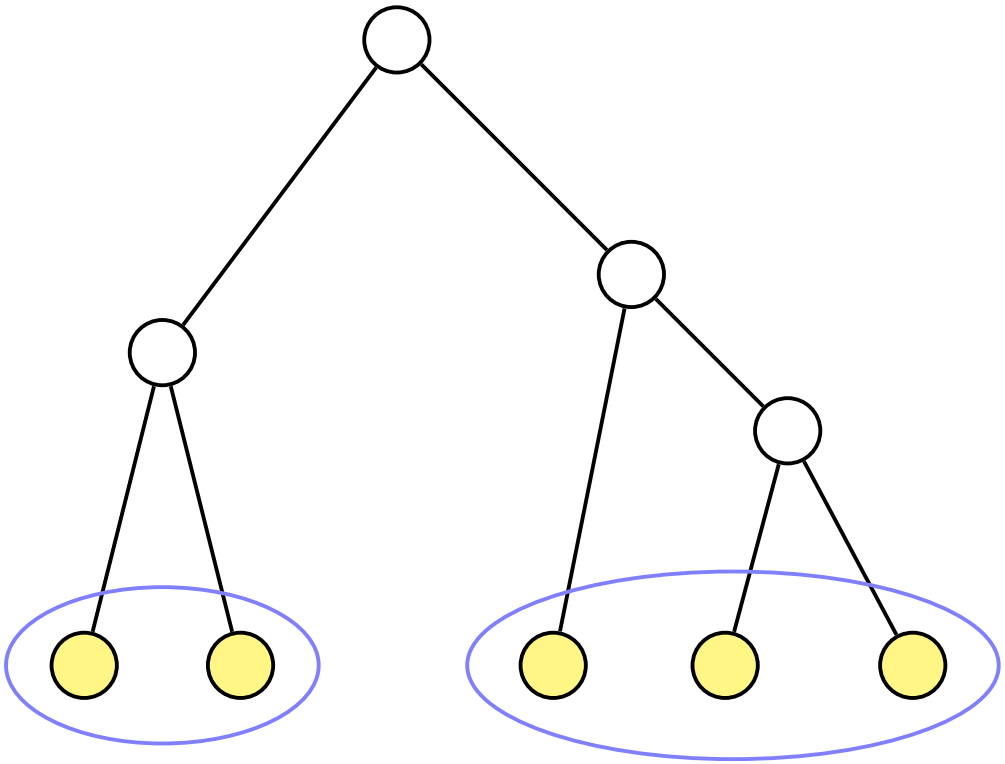

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$X_n = \#$ of groups

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$$X_n \stackrel{d}{=} \begin{cases} 1, & \text{if } I_n = 1 \text{ or } I_n = n-1, \\ X_{I_n} + X^*_{n-I_n}, & \text{otherwise,} \end{cases}$$

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For $p = 0$ this is the neutral model.

Expected Number of Groups – YH Model

Theorem (Durand and François; 2010)

We have,

$$\mathbb{E}(X_n) \sim \begin{cases} \dfrac{c(p)}{\Gamma(2(1-p))} n^{1-2p}, & \text{if } p < 1/2; \\ \dfrac{\log n}{2}, & \text{if } p = 1/2; \\ \dfrac{p}{2p-1}, & \text{if } p > 1/2, \end{cases}$$

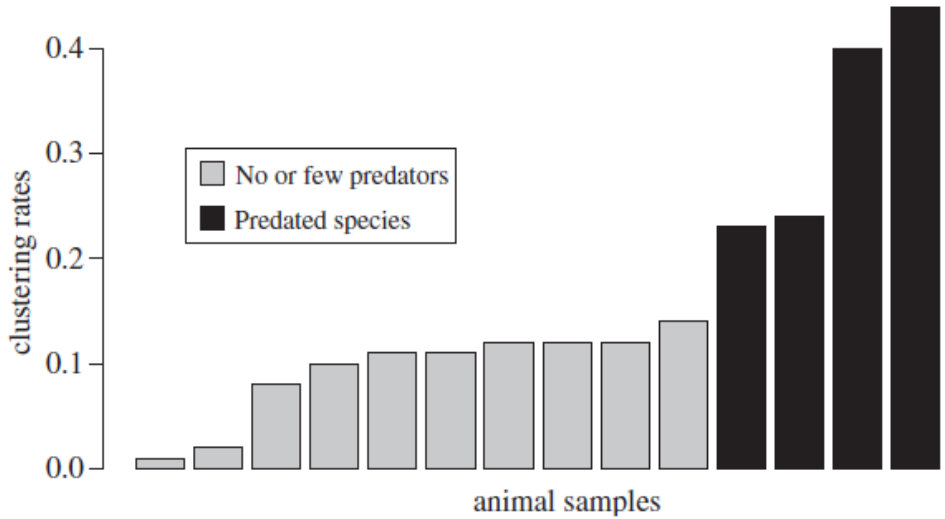
where

$$c(p) := \frac{1}{e^{2(1-p)}} \int_0^1 (1-t)^{-2p} e^{2(1-p)t} \left(1 - (1-p)t^2\right) \mathrm{d}t.$$

Testing for the Neutral Model

Durand, Blum and François (2007):

	Sample size	Number of herds	Rate $\hat{p}$
(A)			
Springboks (browsers)	149	6	0.40
Springboks (graze)	1064	40	0.24
Fallow deers	349	22	0.23
Grant's gazelles	221	6	0.44
Wild camels	227	27	0.14
Kangaroos	348	41	0.12
African savannah elephants	304	45	0.08
	Sample size	Number of packs/prides	Rate $\hat{p}$
(B)			
Yellowstone Wolves 2002	90	14	0.11
Yellowstone Wolves 2004	112	16	0.12
Alaska Wolves	151	30	0.02
Scandinavian wolf	76	12	0.11
Zambia Kafue lions	95	14	0.12
Selous Game lions	51	13	0.00
Serengeti lions	100	16	0.10



$p = 0$ – YH Model

Theorem (Lee; 2012)

We have,

$$\mathrm{Var}(X_n) \sim \frac{(1-e^{-2})^2}{4} n \log n$$

and for $k \geq 3$,

$$\mathbb{E}(X_n - \mathbb{E}(X_n))^k \sim (-1)^k \frac{2k}{k-2} \left(\frac{1-e^{-2}}{4}\right)^k n^{k-1}.$$

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Theorem (Drmota, F., Lee; 2016)

We have,

$$\frac{X_n - \mathbb{E}(X_n)}{\sqrt{\mathrm{Var}(X_n)/2}} \xrightarrow{d} N(0,1).$$

$0 < p < 1/2$ – YH model

Theorem (Drmota, F., Lee; 2016)

We have,

$$\frac{X_n}{n^{1-2p}} \xrightarrow{d} X,$$

with convergence of all moments.

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Here, the law of X is the sum of a discrete law with mass $p/(1-p)$ at 0 and a continuous law on $[0,\infty)$ with density

$$f(x) = -\delta(p)\frac{1-2p}{1-p}\sum_{k\geq 0}\frac{\delta(p)^k}{k!\Gamma(2(k+1)p-k)}x^k,$$

where

$$\delta(p) = \frac{(1-2p)^2 W_{p,(1-2p)/p}\left(-2(1-p)\right)}{e^{2\pi i p}4^{p-1}(1-p)^{2p}M_{p,(1-2p)/p}\left(-2(1-p)\right)}.$$

$1/2 \leq p < 1$ – YH Model

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We have,

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Theorem (Drmota, F., Lee; 2016)

For $p = 1/2$, *we have*

$$\mathbb{E}(X_n^k) \sim \frac{k! J_{2k-1}}{(2k-1)! 2^{2k-1}} \log^{2k-1} n, \qquad J_{2k-1} = (2k-1)! [z^{2k-1}] \tan(z).$$

A Decomposition

Every PT can be decomposed as:

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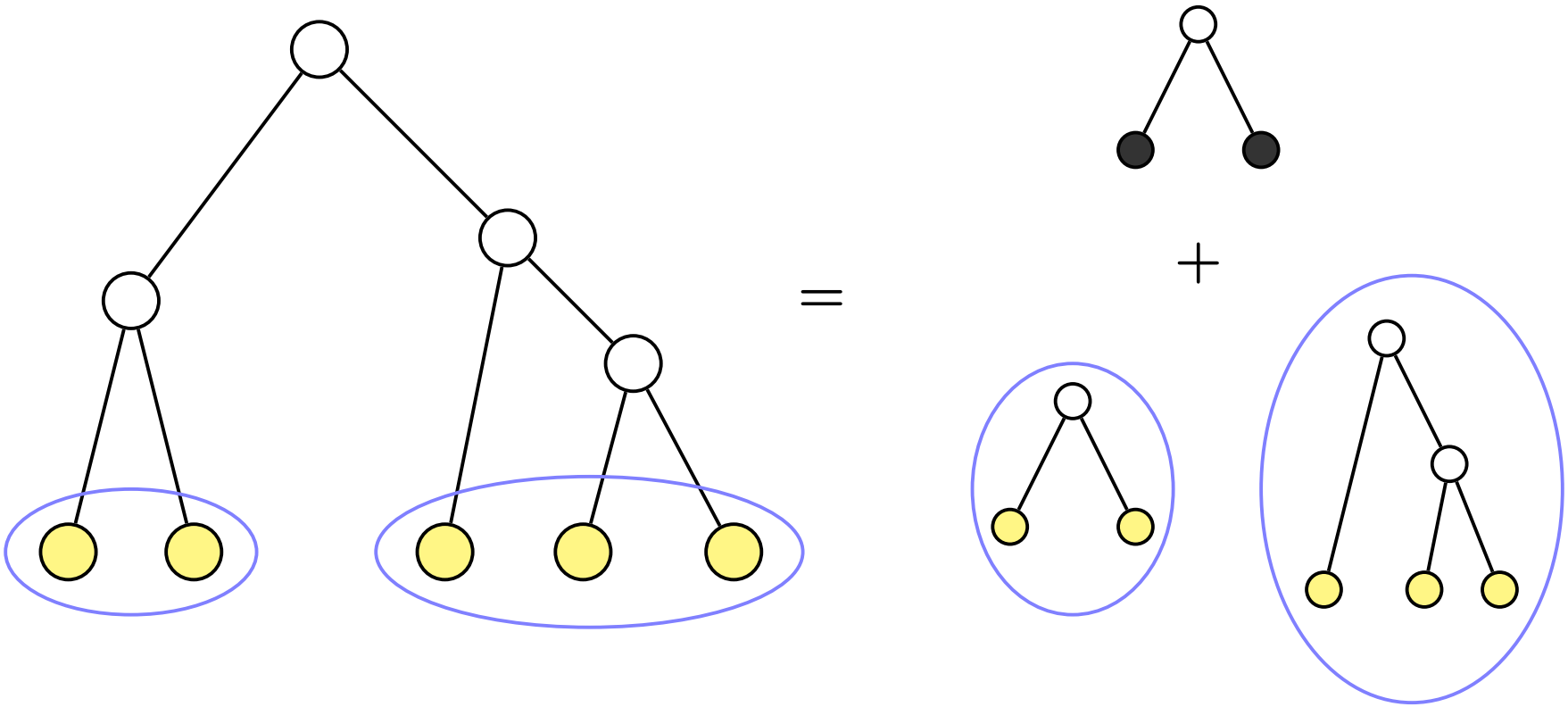

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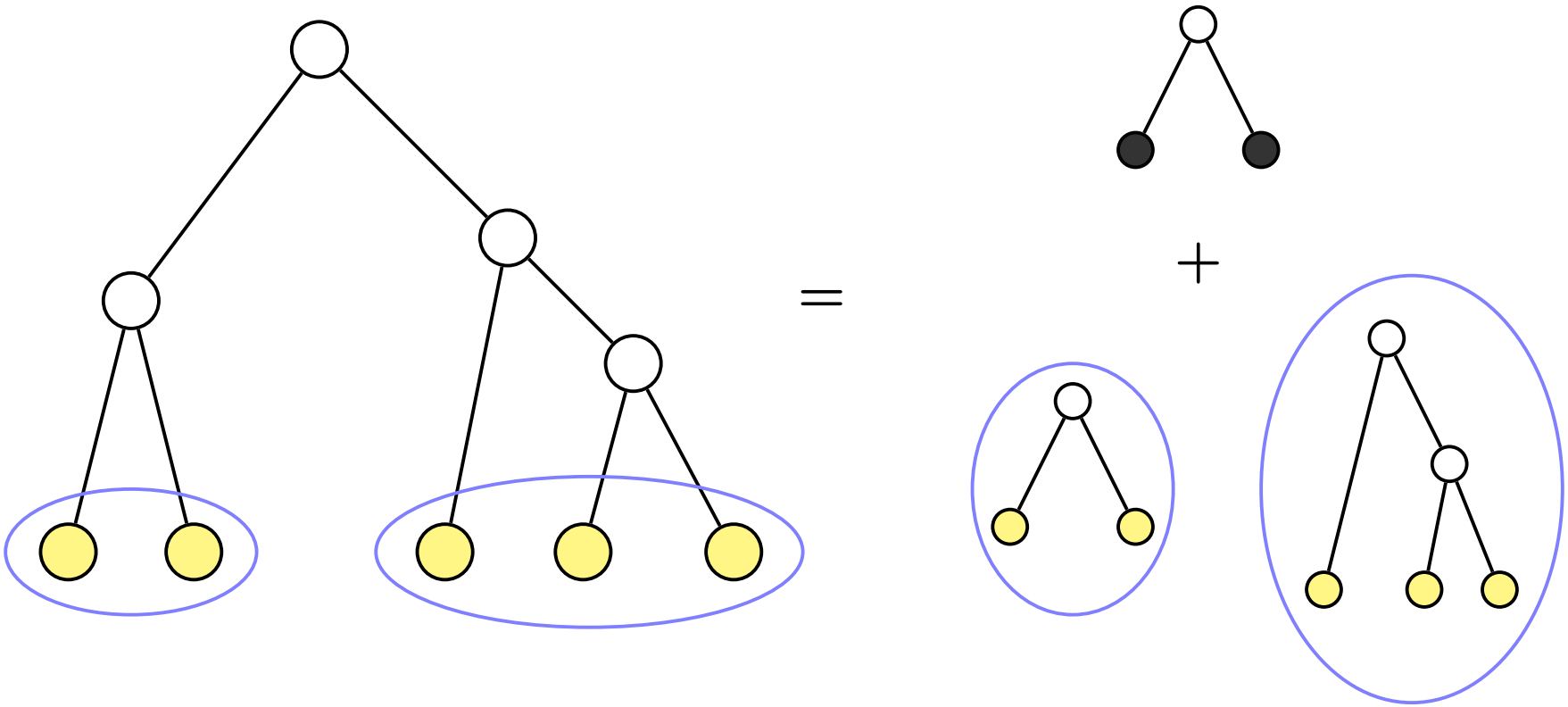

For the extra clustering model, one has to introduce weights!

Two Generating Functions

Weighted binary trees: internal nodes are weighted by $q := 1 - p$,

$$G(z) = \sum_{n \geq 1} q^{n-1} C_{n-1} z^n = zC(qz),$$

where $C(z) = (1 - \sqrt{1 - 4z})/(2z)$.

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Maximal clades:

$$\begin{aligned} H(z) &= z^2 + \sum_{n \geq 3} (pC_{n-1} + 2qC_{n-2}) z^n \\ &= z^2 + pz(C(z) - 1 - z) + 2qz^2(C(z) - 1). \end{aligned}$$

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Lemma

We have, $G(H(z)) = z(C(z) - 1)$

of Groups – PDA Model

We have,

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We have,

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Corollary

We have,

$$\mathbb{E}(X_n) \sim \frac{5+2p+p^2}{2+4p+2p^2}.$$

of Groups of Size m – PDA Model

With $a_m = pC_{m-1} + (2 - \delta_{2,m})qC_{m-2}$,

$$\mathbb{E}(X_n^{[m]} = k) = \frac{[u^k z^n] G(a_m(u-1)z^m + H(z))}{C_{n-1}}.$$

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Corollary

We have $\sum_{m \geq 2} \mathbb{E}(X^{[m]}) = \mathbb{E}(X) + 1$.

Largest Groups Size – PDA Model (i)

For the largest group size M_n, we have

$$\mathbb{P}(M_n = n-k) = \frac{[z^k]G'(H(z))[z^{n-k}]H(z)}{C_{n-1}},$$

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Theorem (F., Lee, Paningbatan; 2019+)

We have,

$$n - M_n \xrightarrow{d} M,$$

where M has probability generating function $(1+p)/(2F(u/4))$ with

$$F(u) = \sqrt{r(u) - 2p(p-2qu)\sqrt{1-4u}},$$

where $r(u) = 1 - 2p + 2p^2 - 4(1-2p)qu + 4q^2u^2$.

Largest Group Size – PDA Model (ii)

In the limit theorem for M_n, moments do not converge.

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and for $\ell \geq 2$,

$$\mathbb{E}((M_n - \mathbb{E}(M_n))^\ell) \sim (-1)^\ell d_\ell n^{\ell - 1/2},$$

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Proof uses singularity analysis and Euler-Maclaurin summation formula.

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  Mean for number of groups of fixed size was studied by Durand and François (2010). Refined results will appear in:

  A. Paningbatan (2020). Three Combinatorial Topics Arising from Phylogenetics, PhD thesis, in preparation.

謝謝聆聽!

谢谢聆听!