A Null Model of Speciation by Reproductive Isolation

Mechanisms of Reproductive Isolation Session

Flo(rence) Débarre

20 February 2017

Acknowledgements

Work done in collaboration with

François Bienvenu

Amaury Lambert

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Funding

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Charley Harper, “Tree of Life”

But what is a species?

de Quieroz (2007)

But what is a species?

Biological

Interbreeding

Isolation

Recognition

Cohesion

Phenotypic cohesion

Ecological

Same niche or adaptive zone

Phylogenetic

Hennigian

Segment btw nodes

Monophyletic

Monophyly

Genealogical

Exclusive coalescence of alleles

Diagnosable

Smallest appropriate unit

Evolutionary

Unit of evolution

Phenetic

Phenetic cluster

Genotypic cluster

Deficits of genetic intermediates

de Quieroz (2007)

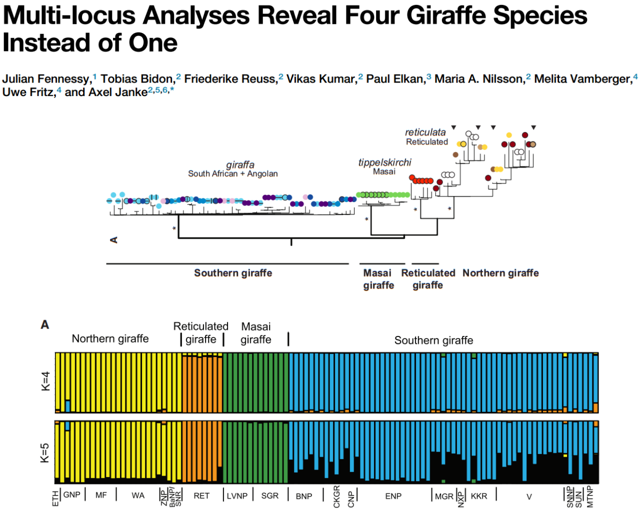
But what is a species?

"there is no unique relation which is privileged in that the species taxa it generates will answer to the needs of all biologists and will be applicable to all groups of organisms."

Kitcher (1984)

de Quieroz (2007)

Counting species

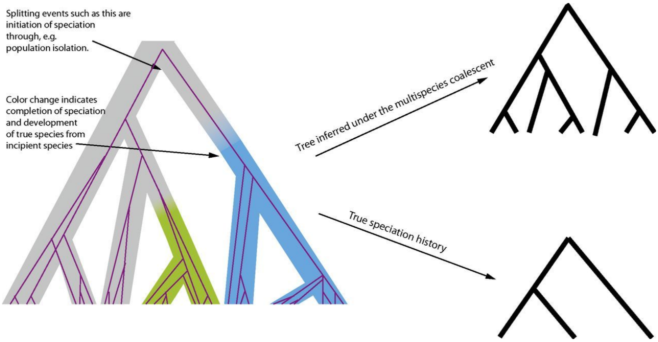


Fennessy et al. (2016)

Counting species (*continued*)

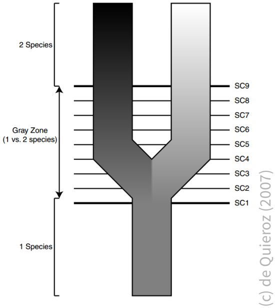
Multispecies coalescent delimits structure, not species

Jeet Sukumaran[a,1,2] and L. Lacey Knowles[a,1]



Sukumaran and Knowles (2017)

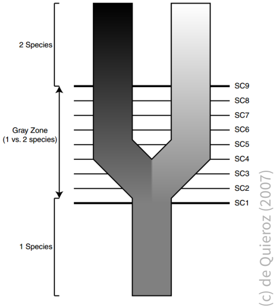
Counting species (*continued*)



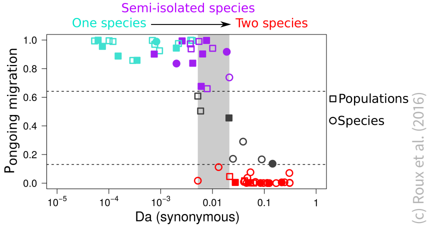
- Gre/ay zone of speciation

de Quieroz (2007)

Counting species (*continued*)

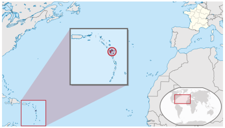


- Gre/ay zone of speciation
- Continuum of speciation



de Quieroz (2007)
Roux et al. (2016)

Other consequences of species definitions



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Helgen et al. (2008)

http://www.radiolab.org/story/stanger-paradise/

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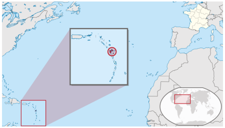

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Procyon minor

Protected

Helgen et al. (2008)
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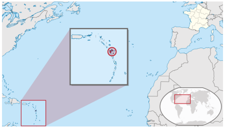
Other consequences of species definitions



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Procyon minor	*Procyon lotor*

Protected	Invasive!

Helgen et al. (2008)

http://www.radiolab.org/story/stanger-paradise/

Reproductive isolation in the Biological Species Concept

Some limits

Rothfels et al. (2015)

Reproductive isolation in the Biological Species Concept

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- Asexuals

Rothfels et al. (2015)

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- Asexuals
- Horizontal gene transfer in Prokaryotes

Rothfels et al. (2015)

Reproductive isolation in the Biological Species Concept

Some limits

- Asexuals
- Horizontal gene transfer in Prokaryotes
- Hybrids

$\times$*Cystocarpium roskamianum*

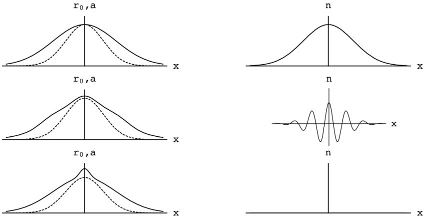
Rothfels et al. (2015)

From populations to species

Cluster formation

Models with competition/selection

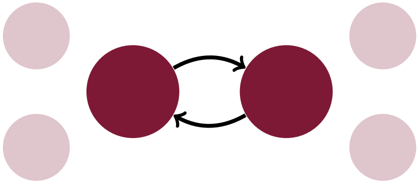
"the mathematical structure of the ecological coexistence problem itself dictates the discreteness of the species."



Gyllenberg and Meszéna (2005)

Neutral models of speciation

Evolution of reproductive isolation



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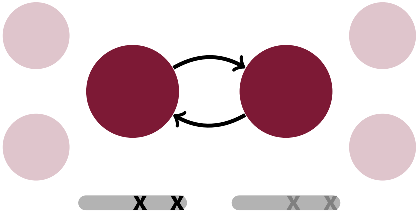

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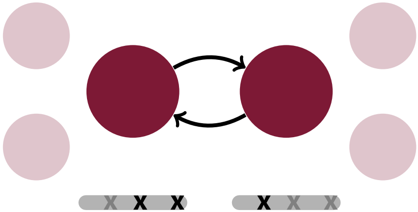

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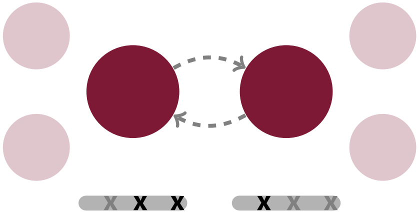

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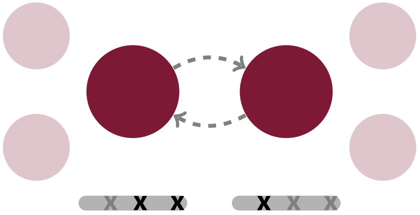

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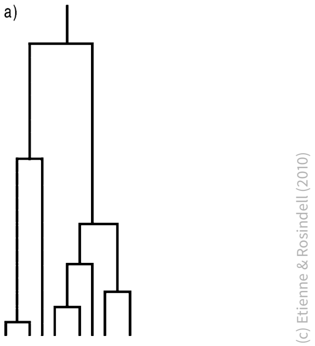
Macroevolutionary models



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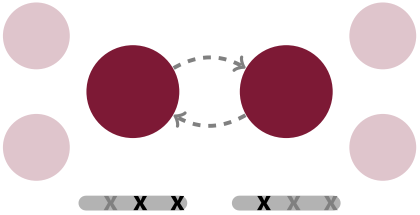

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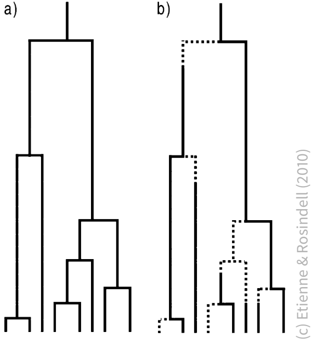

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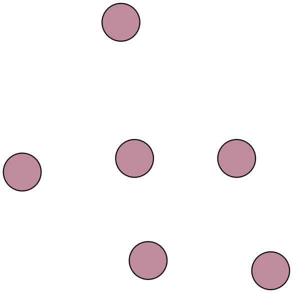

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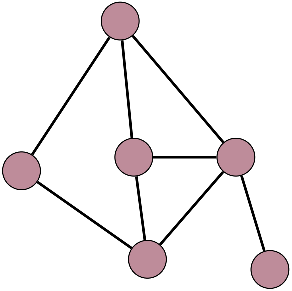

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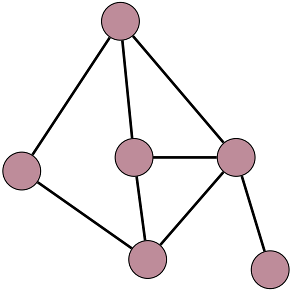

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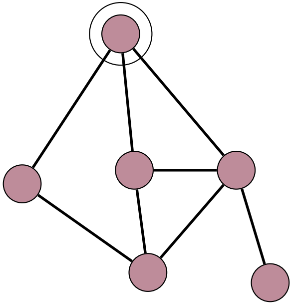

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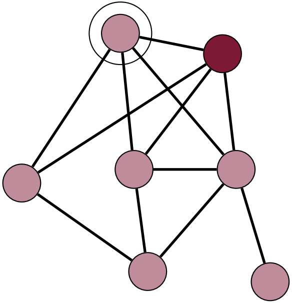

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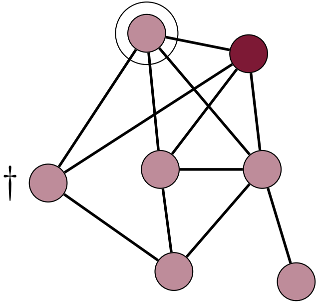

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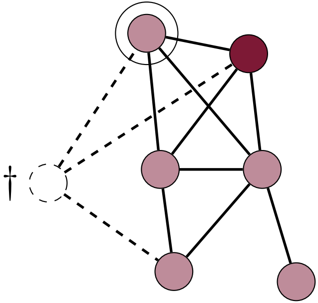

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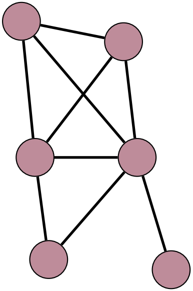

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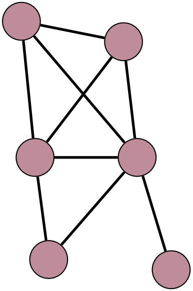

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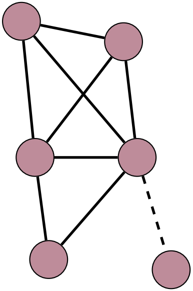

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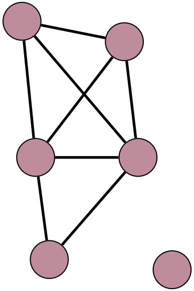

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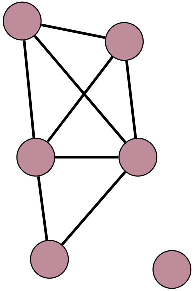

$\rightarrow$ Markov chain $(G_n(t))_{t\in\mathbb{R}_+}$ on all graphs of size n.

Questions and Aims

Question

- Is this simple, neutral model able to generate clusters of populations?

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Aims

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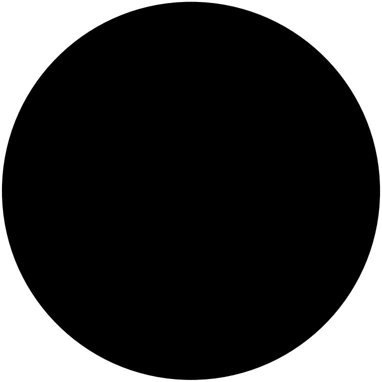
  - Degree distribution
  - Number of complete subgraphs (species?)
  - Number of connected components (species?)

Simulation outcomes

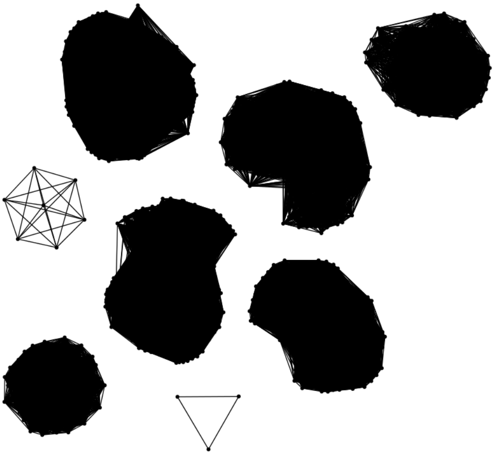
Simulation outcomes

$n = 1000,\ r = 0.1,\ \#CC = 1$



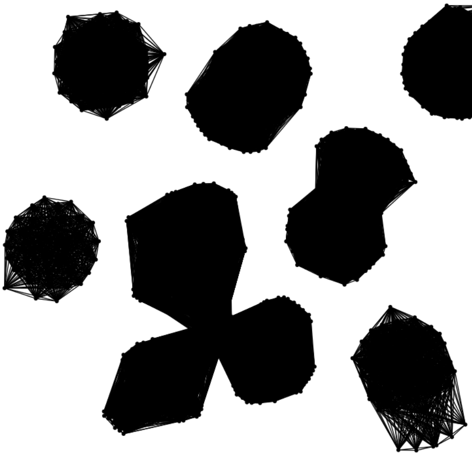
Simulation outcomes

$$n = 1000,\ r = 5,\ \#CC = 8$$



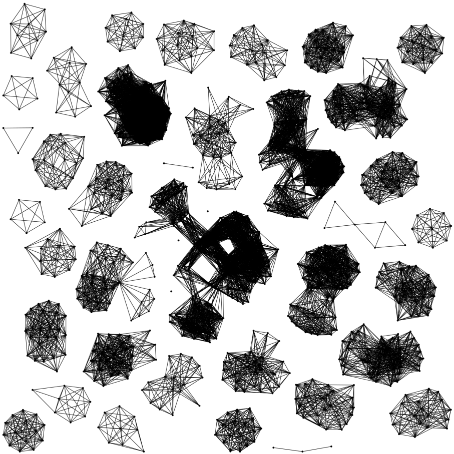
Simulation outcomes

$n = 1000$, $r = 7.5$, $\#CC = 7$



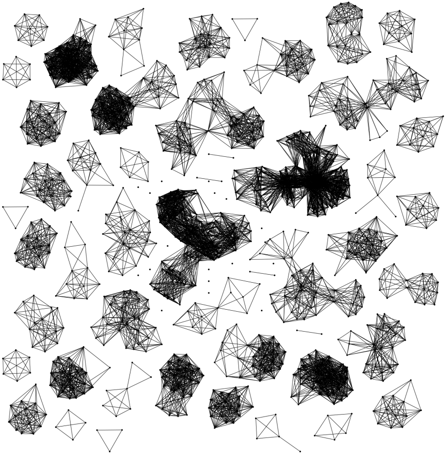
Simulation outcomes

$n = 1000$, $r = 38$, $\#CC = 40$



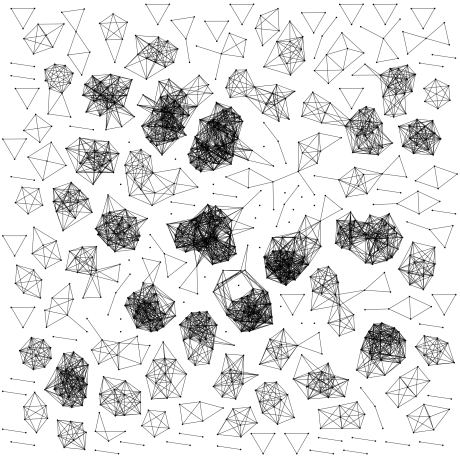
Simulation outcomes

$$n = 1000,\ r = 62,\ \#CC = 66$$



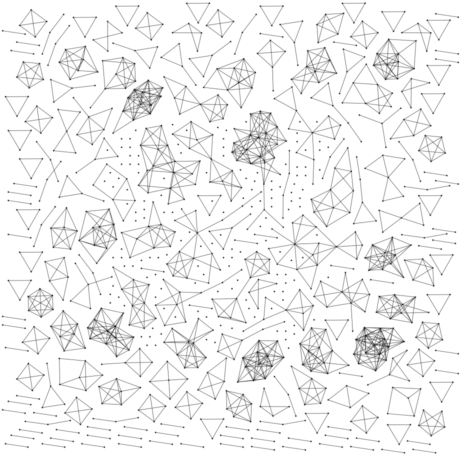
Simulation outcomes

$n = 1000,\ r = 107,\ \#CC = 141$



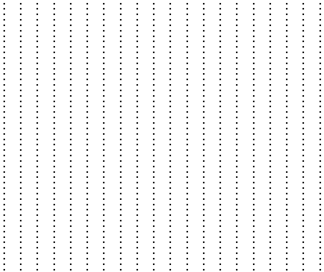
Simulation outcomes

$$n = 1000,\ r = 347,\ \#CC = 342$$



Simulation outcomes

$n = 1000,\ r = 1000,\ \#CC = 342$



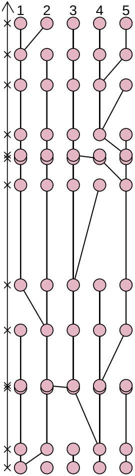
Analysis: Backward-forward approach

Vertex splitting

Edge removal

Analysis: Backward-forward approach

Vertex splitting



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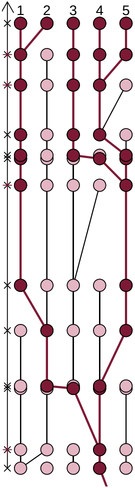

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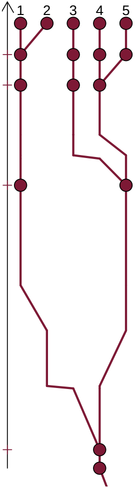

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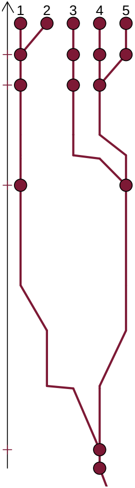

Kingman coalescent (rate 1)

Edge removal

Analysis: Backward-forward approach

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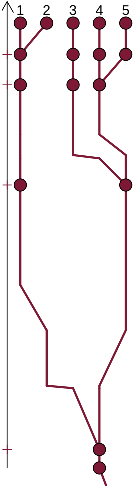

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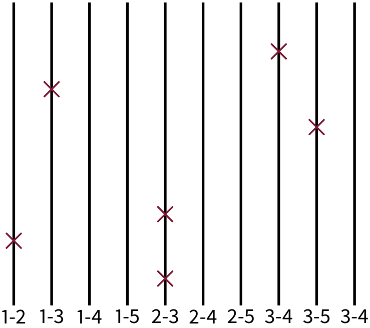
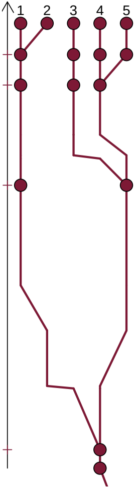


Pairwise Poisson processes (rate r)

Analysis: Backward-forward approach

Vertex splitting



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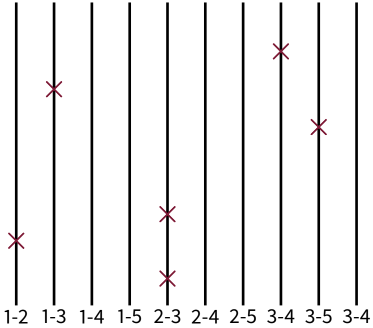
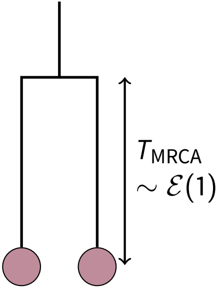


Pairwise Poisson processes (rate *r*)

Degree

Focus on two populations (2 nodes of $G_{n,r}$):

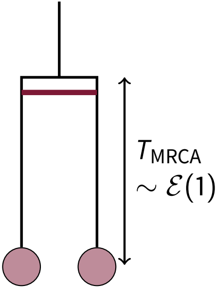
Degree



Focus on two populations (2 nodes of $G_{n,r}$):

- The time to their MRCA is exp(1) (because Kingman),

Degree



Focus on two populations (2 nodes of $G_{n,r}$):

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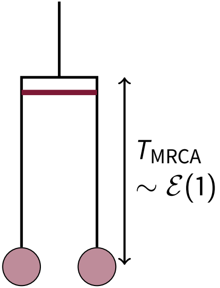

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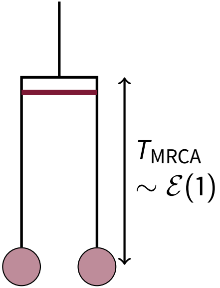

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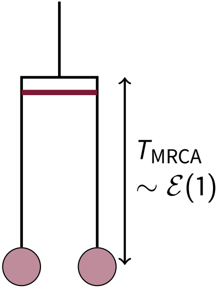

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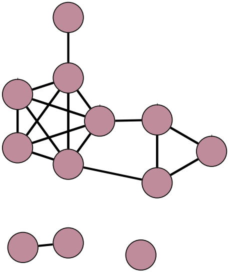
Degree of a fixed node $=: D(n, r)$

$$\mathbb{E}[D] = \frac{n-1}{1+r}, \qquad \mathrm{Var}[D] = \frac{r\,(n-1)\,(n+2r+1)}{(1+r)^2\,(3+2r)}$$

Cliques



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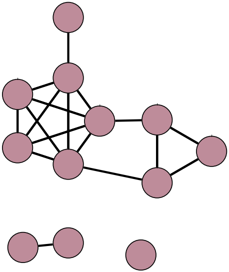
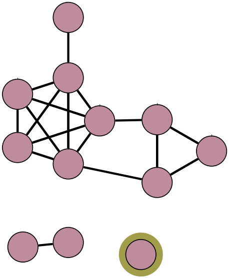


k-clique: complete subgraph of order *k*

Cliques



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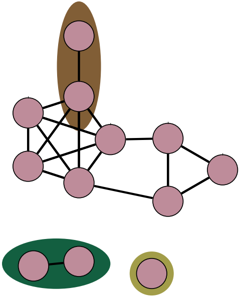

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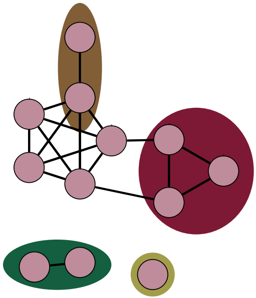

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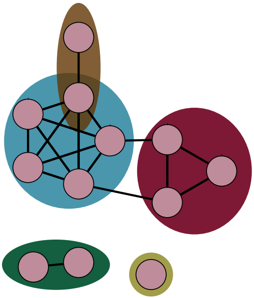

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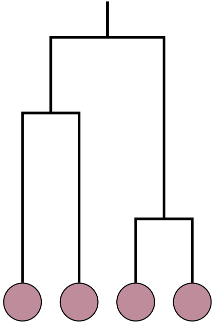
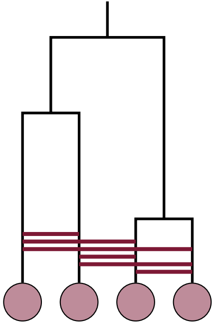
Cliques (*continued*)



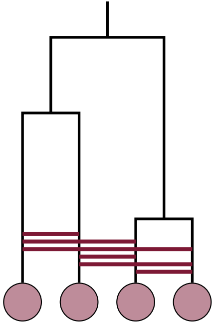
- Consider *k* populations;

Cliques (*continued*)



- Consider k populations;
  there are $\binom{j}{2} = \frac{k(k-1)}{2}$ potential interfecundity links.

Cliques (*continued*)



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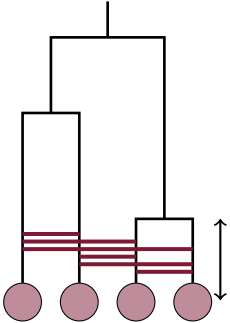

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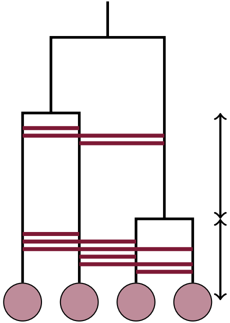

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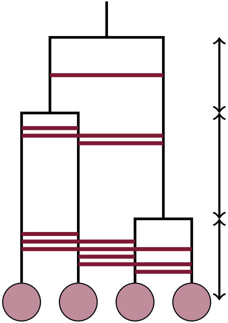

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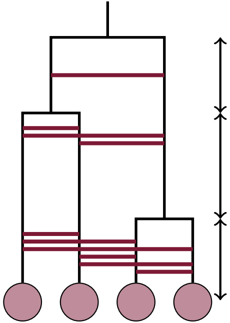

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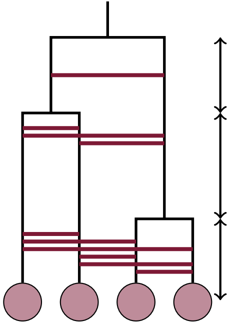
$$\prod_{j=2}^{k} \frac{\binom{j}{2}}{\binom{j}{2} + r\binom{j}{2}} = \left(\frac{1}{1+r}\right)^{k-1}.$$

Cliques (*continued*)



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$$\mathbb{E}(X_k) = \binom{n}{k} \left(\frac{1}{1+r}\right)^{k-1}.$$

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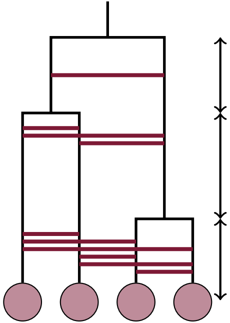

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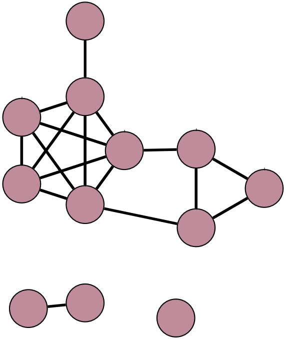
- Clique number $=: \omega(n,r)$

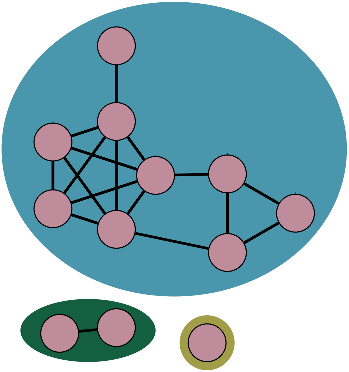
$$\mathbb{P}[\omega \geq k] = \mathbb{P}[X_k \geq 1] \leq \mathbb{E}[X_k].$$

Connected components



Subgraph in which any two nodes are connected to each other by paths, and which is connected to no additional nodes in the supergraph.

Connected components



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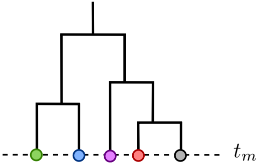
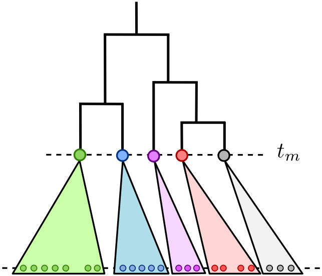


Connected components (*continued*)

Assume $1 \ll r_n \ll n$.
Let $t_k :=$ time when the coalescent tree has k lineages

Lower bound

Choose m such that the graph at time t_m is empty with high probability



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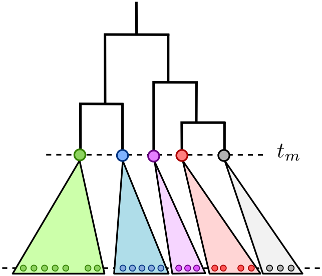
Result: $m \sim \dfrac{r_n}{2}$



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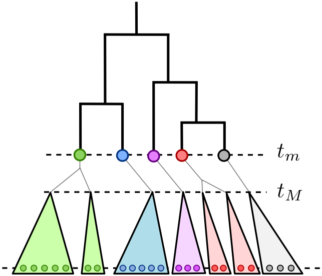
Choose M such that the descending subtrees of each of the M nodes of time t_M are connected with high probability



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Assume $1 \ll r_n \ll n$.
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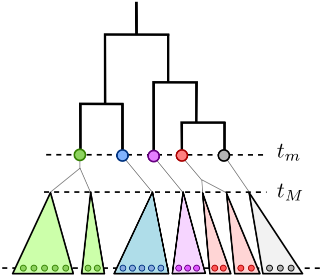
Result: $M \sim 2 r_n \log(n)$



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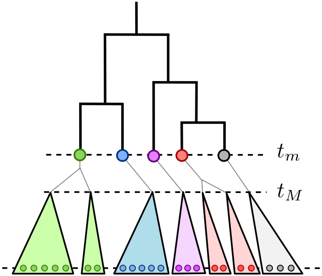


Assume that as $n \to \infty$, $r_n \to \infty$ and $r_n / n \to 0$. Then

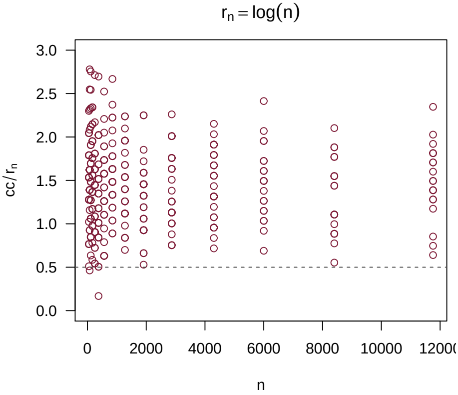
$$\lim_{n \to \infty} \mathbb{P}\left[\frac{r_n}{2} \leq \#CC(G_{n,r_n}) \leq 2 r_n \log(n)\right] = 1.$$

Connected components (*continued*)

Number of species?

$$\lim_{n\to\infty} \mathbb{P}\left[\frac{r_n}{2} \leq \#CC(G_{n,r_n}) \leq 2r_n \log(n)\right] = 1.$$

$$\#CC/r_n \text{ vs } n$$



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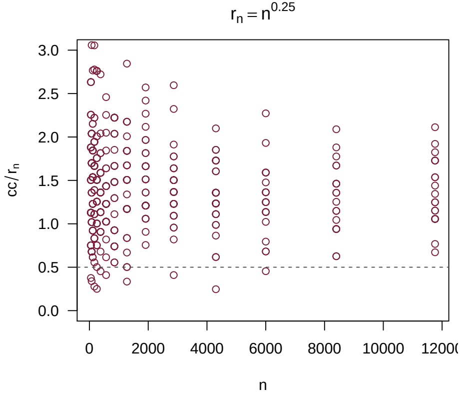

Connected components (*continued*)

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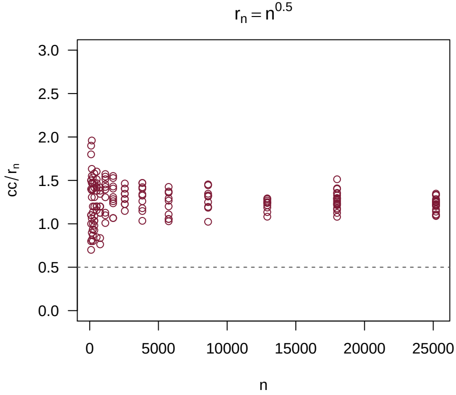

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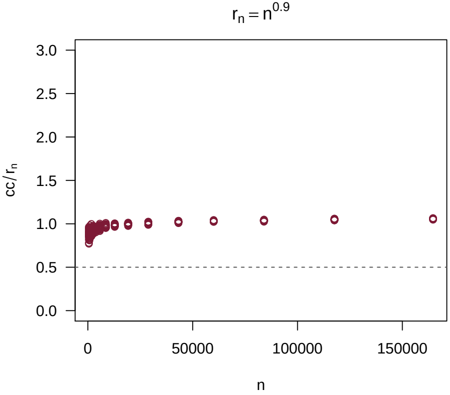

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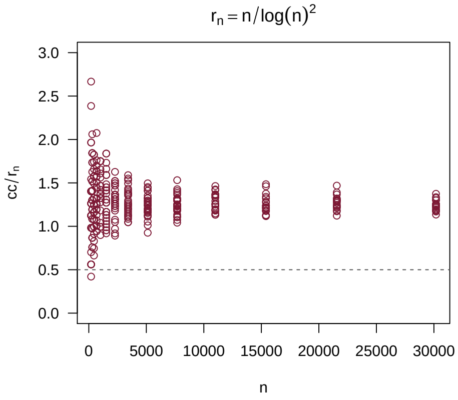

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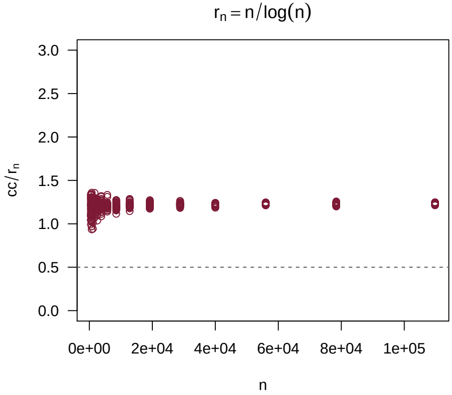

Species Abundance Distributions (SAD)

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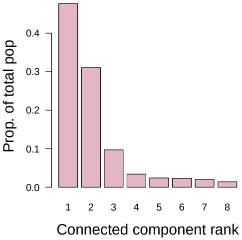
$n = 1000$

$r = 5.5$



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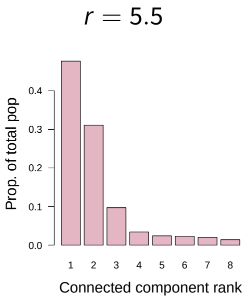

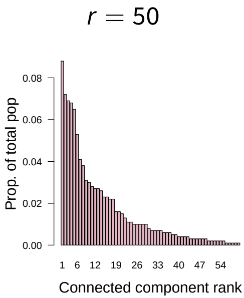

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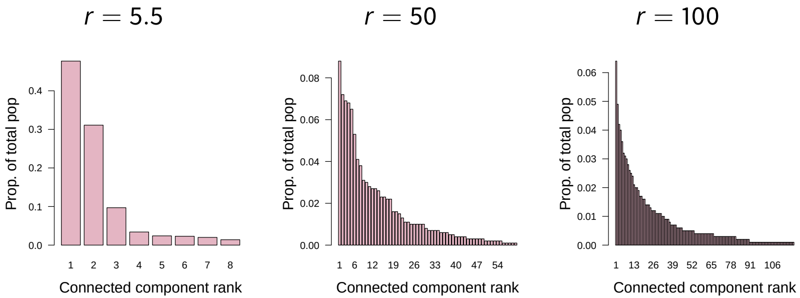

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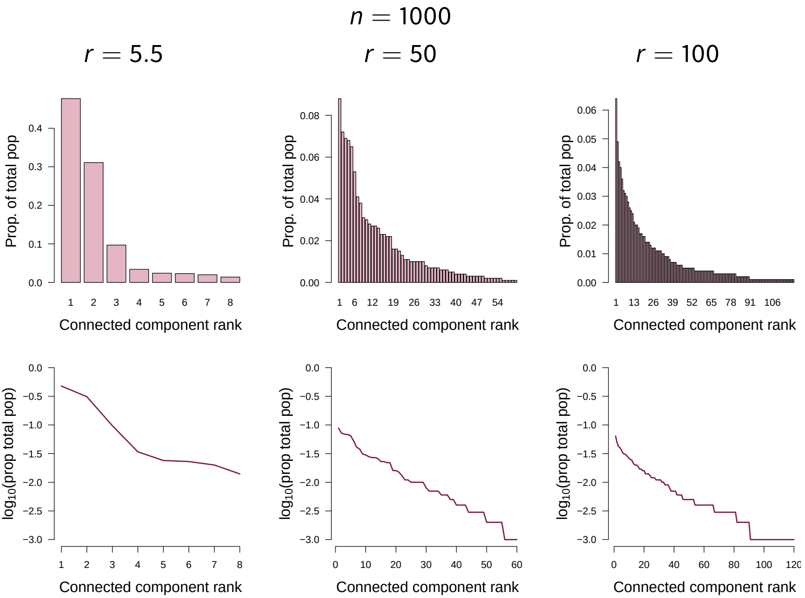
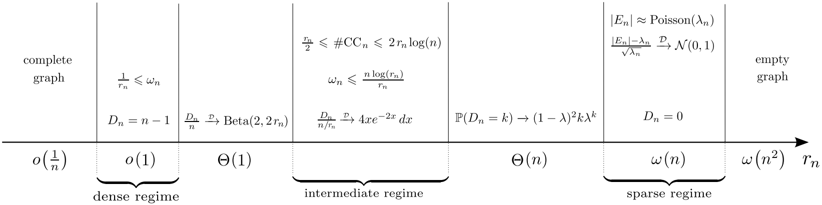
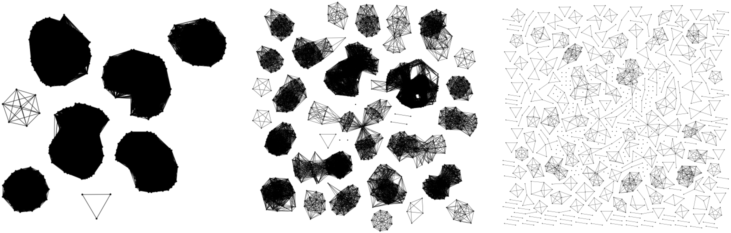


Summary of the mathematical results





$r = 5$ $\quad$ $r = 41$ $\quad$ $r = 347$

$n = 1000$

Take-home messages

The Split-and-Drift Random Graph

- A tractable neutral model for the evolution of reproductive isolation

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Perspectives

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Thanks for your attention!

Appendix

Degree Distribution

$$\mathbb{P}[D(n,r)=k] = \frac{2r(2r+1)}{(n+2r)(n-1+2r)}(k+1)\prod_{i=1}^{k}\frac{n-i}{n-i+2r-1}.$$

- As $r_n \to r$, $\dfrac{D(n,r_n)}{n}$ converges to a $Beta(2,2r)$ random variable
- If $1 \ll r_n \ll n$, $\dfrac{D(n,r_n)}{n/r_n}$ converges to a size-biased $Exp(2)$.
- If $r_n \sim \rho\, n/2$, $D(n,r_n)$ converges to a size-biased geometric random variable with parameter $1/(1+\rho)$.