

1 Coalescent process for epidemic models with superspreading

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# 1 Introduction

Superspreading in infectious disease epidemiology (Lloyd-Smith et al. 2005). For example SARS-CoV-2 superspreading (Wang et al. 2020; Lemieux et al. 2021; Gómez-Carballa et al. 2021). Coalescent model (Kingman 1982a,b). Work by Li and Fraser (Li et al. 2017; Fraser and Li 2017). Lambda-coalescent models (Pitman 1999; Sagitov 1999; Donnelly and Kurtz 1999). Beta-coalescent (Schweinsberg 2003) is a specific type of Lambda-coalescent. Was used in (Hoscheit and Pybus 2019) and (Menardo et al. 2021). David’s paper on inference of multiple mergers while dating a pathogen phylogeny (Helekal et al. 2024).

## 2 General case

Discrete time  $t$ . Non-overlapping generations of infected individuals. At time  $t$  there are  $N_t$  infected individuals. Each of them creates a number  $s_{t,i}$  of secondary infections at time  $t + 1$ , following the offspring distribution  $\alpha_t(s)$ . The mean of this distribution is the basic reproduction number  $R_t$  and the variance is  $V_t$ . We have:

$$N_{t+1} = \sum_{i=1}^{N_t} s_{t,i} \quad (1)$$

Let  $p_{k,t}$  be the probability that  $k$  individuals at time  $t + 1$  have the same infector at time  $t$ .

### 2.1 Inclusive coalescence probability

Inclusive coalescence probability  $p_{k,t}(N_t, N_{t+1})$  is the probability that a specific set of  $k$  individuals from generation  $t + 1$  find a common ancestor in generation  $t$ , conditional on population sizes  $N_t$  and  $N_{t+1}$ .

Given full information about offspring counts from individuals in generation  $t$   $\mathbf{s}_t = (s_{t,1}, \dots, s_{t,N_t})$ , we have

$$\begin{aligned} p_{k,t}(\mathbf{s}_t, N_t) &= \sum_{i=1}^{N_t} \frac{\binom{s_{t,i}}{k}}{\binom{N_{t+1}}{k}} \\ &= \sum_{i=1}^{N_t} \frac{\Gamma(s_{t,i} + 1) \Gamma(N_{t+1} - k + 1)}{\Gamma(s_{t,i} - k + 1) \Gamma(N_{t+1})}. \end{aligned} \quad (2)$$

Full information  $\{s_{t,i}\}$  yields the population size  $N_{t+1}$  but is not feasible to observe in practice. We can instead express the inclusive coalescence probability conditioning on the next population size  $N_{t+1}$

33 by summing over possible offspring counts  $\mathbf{s}_t = (s_{t,1}, \dots, s_{t,N_t})$  conditional on the total generation size.  
 34 Let  $S_t^{-(1)} = (S_{t,2}, \dots, S_{t,N_t})$ .

$$\begin{aligned}
 p_{k,t}(N_t, N_{t+1}) &= \sum_{\mathbf{s}_t \in \mathbb{N}_0^{N_t}} \mathbb{P} \left[ \mathbf{S}_t = \mathbf{s}_t \middle| \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right] p_{k,t}(\mathbf{s}_t, N_t) \\
 &= \sum_{\mathbf{s}_t \in \mathbb{N}_0^{N_t}} \mathbb{P} \left[ \mathbf{S}_t = \mathbf{s}_t \middle| \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right] \sum_{i=1}^{N_t} \frac{\binom{s_{t,i}}{k}}{\binom{N_{t+1}}{k}} \\
 &= \sum_{i=1}^{N_t} \sum_{\mathbf{s}_t \in \mathbb{N}_0^{N_t}} \frac{\binom{s_{t,i}}{k}}{\binom{N_{t+1}}{k}} \mathbb{P} \left[ S_{t,1} = s_{t,1}, \mathbf{S}_t^{-(1)} = \mathbf{s}_t^{-(1)} \middle| \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right] \\
 &= \frac{N_t}{\binom{N_{t+1}}{k}} \sum_{\mathbf{s}_t \in \mathbb{N}_0^{N_t}} \binom{s_{t,1}}{k} \mathbb{P} \left[ S_{t,1} = s_{t,1} \middle| \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right] \\
 &\quad \times \mathbb{P} \left[ \mathbf{S}_t^{-(1)} = \mathbf{s}_t^{-(1)} \middle| S_{t,1} = s_{t,1}, \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right] \\
 &= \frac{N_t}{\binom{N_{t+1}}{k}} \sum_{s_{t,1}=0}^{N_{t+1}} \binom{s_{t,1}}{k} \mathbb{P} \left[ S_{t,1} = s_{t,1} \middle| \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right] \\
 &\quad \times \underbrace{\sum_{\mathbf{s}_t^{-(1)} \in \mathbb{N}_0^{N_t-1}} \mathbb{P} \left[ \mathbf{S}_t^{-(1)} = \mathbf{s}_t^{-(1)} \middle| \sum_{i=2}^{N_t} S_{t,i} = N_{t+1} - s_{t,1} \right]}_{=1} \\
 &= \frac{N_t}{\binom{N_{t+1}}{k}} \mathbb{E} \left[ \binom{S_{t,1}}{k} \middle| \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right] \tag{3}
 \end{aligned}$$

35 The falling factorial moments  $\mathbb{E} \left[ \frac{S_{t,1}!}{(S_{t,1}-k)!} \middle| \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right]$  in Equation (3) can be readily obtained  
 36 by differentiating the probability generating function of  $S_{t,1} | (\sum_{i=1}^{N_t} S_{t,i} = N_{t+1})$ .

## 37 2.2 Exclusive coalescence probability

38 Generally, we observe a sample of individuals from each generation rather than the entire population.  
 39 In this case, we are interested in the exclusive coalescence probability  $p_{n,k,t}(N_t, N_{t+1})$  that exactly  $k$   
 40 individuals from a sample of  $n$  arose from a common ancestor one generation in the past given knowledge  
 41 of the total population sizes  $N_t$  and  $N_{t+1}$ .

42 Given full information about offspring counts of the parents of sampled individuals at the present,

43  $\mathbf{x}_t = (x_{t,1}, \dots, x_{t,N_t})$ , we have

$$\begin{aligned} p_{n,k,t}(\mathbf{x}_t, N_t) &= \sum_{i=1}^{N_t} \frac{\binom{x_{t,i}}{k}}{\binom{n}{k}} \mathbb{I}\{x_{t,i} = k\} \\ &= \sum_{i=1}^{N_t} \frac{x_{t,i}!}{(x_{t,i} - k)!} \frac{(n - k)!}{n!} \mathbb{I}\{x_{t,i} = k\}. \end{aligned} \quad (4)$$

44 Similarly to the exclusive coalescence probability, we can use this to evaluate the exclusive probability  
45 given  $N_t$  and  $N_{t+1}$  by summing over possible parent offspring configurations (for  $k \leq n$ ),

$$\begin{aligned} p_{n,k,t}(N_t, N_{t+1}) &= \sum_{\mathbf{x}_t \in \mathbb{N}_0^{N_t}} \mathbb{P}\left[\mathbf{X}_t = \mathbf{x}_t \mid \sum_{i=1}^n X_{t,i} = n\right] p_{n,k,t}(\mathbf{x}_t, N_t) \\ &= \sum_{\mathbf{x}_t \in \mathbb{N}_0^{N_t}} \mathbb{P}\left[\mathbf{X}_t = \mathbf{x}_t \mid \sum_{i=1}^n X_{t,i} = n\right] \sum_{i=1}^{N_t} \frac{\binom{x_{t,i}}{k}}{\binom{n}{k}} \mathbb{I}\{x_{t,i} = k\} \\ &= \frac{N_t}{\binom{n}{k}} \sum_{\mathbf{x}_t \in \mathbb{N}_0^{N_t}} \binom{x_{t,1}}{k} \mathbb{P}\left[\mathbf{X}_t = \mathbf{x}_t \mid \sum_{i=1}^{N_t} X_{t,i} = n\right] \mathbb{I}\{x_{t,1} = k\} \\ &= \frac{N_t}{\binom{n}{k}} \sum_{\mathbf{x}_t^{-(1)} \in \mathbb{N}_0^{N_t-1}} \binom{k}{k} \mathbb{P}\left[X_{t,1} = k, \mathbf{X}_t^{-(1)} = \mathbf{x}_t^{-(1)} \mid \sum_{i=1}^{N_t} X_{t,i} = n\right] \\ &= \frac{N_t}{\binom{n}{k}} \mathbb{P}[X_{t,1} = k \mid \sum_{i=1}^{N_t} X_{t,i} = n] \underbrace{\sum_{\mathbf{x}_t^{-(1)} \in \mathbb{N}_0^{N_t-1}} \mathbb{P}\left[\mathbf{X}_t^{-(1)} = \mathbf{x}_t^{-(1)} \mid \sum_{i=1}^{N_t} X_{t,i} = n, X_{t,1} = k\right]}_{=1} \\ &= \frac{N_t}{\binom{n}{k}} \mathbb{P}\left[X_{t,1} = k \mid \sum_{i=1}^{N_t} X_{t,i} = n\right]. \end{aligned} \quad (5)$$

46 Note that  $X_{t,i}$  does not follow the same offspring distribution as  $S_{t,i}$ .  $(X_{t,1}, \dots, X_{t,N_t})$  consists of  $n$   
47 individuals sampled from generation  $t+1$  without replacement - there is no guarantee that all offspring  
48 from any given parent are included in the sample.

## 49 2.3 Complementarity of exclusive coalescence probabilities

50 If we consider one of the lines observed amongst a set of  $n$ , it can either remain uncoalesced (with  
51 probability  $p_{n,1,t}$ ) or coalesce in an event of size  $k$  (with probability  $p_{n,k,t}$ ) with any set of  $k-1$  lines  
52 among the  $n-1$  other lines, leading to the following complementarity equation:

$$\sum_{k=1}^n \binom{n-1}{k-1} p_{n,k,t} = 1 \quad (6)$$

53 We can show that it is indeed satisfied by the formula in Equation (5):

$$\begin{aligned}
\sum_{k=1}^n \binom{n-1}{k-1} p_{n,k,t} &= \sum_{k=1}^n \binom{n-1}{k-1} \frac{N_t}{\binom{n}{k}} \mathbb{P} \left[ X_1 = k \mid \sum_{i=1}^{N_t} X_i = n \right] \\
&= \sum_{k=1}^n N_t \frac{k}{n} \mathbb{P} \left[ X_1 = k \mid \sum_{i=1}^{N_t} X_i = n \right] \\
&= \frac{N_t}{n} \sum_{k=0}^n k \mathbb{P} \left[ X_1 = k \mid \sum_{i=1}^{N_t} X_i = n \right] \\
&= \frac{N_t}{n} \mathbb{E} \left[ X_1 \mid \sum_{i=1}^{N_t} X_i = n \right] \\
&= \frac{1}{n} \sum_{i=1}^{N_t} \mathbb{E} \left[ X_i \mid \sum_{i=1}^{N_t} X_i = n \right] \\
&= \frac{1}{n} \mathbb{E} \left[ \sum_{i=1}^{N_t} X_i \mid \sum_{i=1}^{N_t} X_i = n \right] \\
&= 1
\end{aligned} \tag{7}$$

### 54 3 Poisson case

55 Here the offspring distribution is  $\alpha_t = \text{Poisson}(R_t)$ . In this case, we have

$$\sum_{i=1}^{N_t} S_{t,i} \sim \text{Poisson}(N_t R_t), \tag{8}$$

56 and conditional distribution

$$\begin{aligned}
\mathbb{P} \left[ S_{t,1} = s \mid \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right] &= \frac{\mathbb{P} \left[ S_{t,1} = s, \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right]}{\mathbb{P} \left[ \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right]} \\
&= \frac{\alpha_t(s) \mathbb{P} \left[ \sum_{i=2}^{N_t} S_{t,i} = N_{t+1} - s \right]}{\mathbb{P} \left[ \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right]} \\
&= \frac{\frac{R_t^s e^{-R_t}}{s!} \cdot \frac{((N_t - 1)R_t)^{N_{t+1} - s}}{(N_{t+1} - s)!}}{\frac{(N_t R_t)^{N_{t+1}} e^{-N_t R_t}}{N_{t+1}!}} \\
&= \binom{N_{t+1}}{s} \left( \frac{1}{N_t} \right)^s \left( 1 - \frac{1}{N_t} \right)^{N_{t+1} - s},
\end{aligned} \tag{9}$$

57 that is

$$S_{t,1} \left| \left( \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right) \sim \text{Binomial} \left( N_{t+1}, \frac{1}{N_t} \right). \quad (10)$$

58 The inclusive probability of coalescence for  $k$  lines is given by Equation (3) by injecting the falling  
59 factorial moments of a Binomial distribution (Potts 1953), resulting in:

$$\mathbb{E} \left[ \binom{S_{t,1}}{k} \left| \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right. \right] = \frac{1}{k!} \mathbb{E} \left[ \frac{S_{t,1}!}{(S_{t,1} - k)!} \left| \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right. \right] = \frac{1}{k!} \frac{N_{t+1}!}{(N_{t+1} - k)!} \left( \frac{1}{N_t} \right)^k. \quad (11)$$

60 Consequently, the inclusive probability of coalescence for  $k$  lines is

$$p_{k,t} = \frac{1}{N_t^{k-1}}. \quad (12)$$

61 By injecting the probability mass function of a binomial distribution in Equation (5) we deduce that  
62 the exclusive probability of coalescence for  $k$  lines from a sample of  $n$  ( $n \geq k$ ) is

$$p_{n,k,t} = \frac{(N_t - 1)^{n-k}}{N_t^{n-1}}. \quad (13)$$

63 It is interesting to note that neither the inclusive nor the exclusive coalescence probability depend on  
64 the mean  $R_t$  of the Poisson offspring distribution or the size  $N_{t+1}$  of the population at time  $t+1$ . The  
65 inclusive coalescent probability in Equation (12) can also be obtained conceptually by considering that  
66 among the  $k$  lines, the first one has an ancestor with probability one, and the remaining  $k-1$  need  
67 to have the same ancestor among a set of  $N_t$  from which they choose uniformly at random so that  
68 the probability of picking the same ancestor is  $1/N_t$ . The exclusive coalescent probability in Equation  
69 (13) can be derived likewise by considering that in addition to the above, each of the  $n-k$  other lines  
70 need to choose a different ancestor, which happens with probability  $(N_t - 1)/N_t$ .

## 71 4 Negative-Binomial case

72 Here the offspring distribution is  $\alpha_t = \text{Negative-Binomial}(r, p)$  with parameters  $(r, p)$  set my moment-  
73 matching mean  $R_t$  and variance  $V_t$ . The resulting parameters for this distribution are  $r = R_t^2/(V_t - R_t)$   
74 and  $p = R_t/V_t$ . In this case, we have

$$\sum_{i=1}^{N_t} S_{t,i} \sim \text{Negative-Binomial}(N_t r, p), \quad (14)$$

75 and similarly to the  $\text{Poisson}(\lambda)$  offspring distribution identify the conditional distribution of  
76  $S_{t,1} | \sum_{i=1}^{N_t} S_{t,i}$  as follows,

$$\mathbb{P} \left[ S_{t,1} = s \left| \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right. \right] = \frac{\alpha_t(s) \cdot \mathbb{P} \left[ \sum_{i=2}^{N_t} S_{t,i} = N_{t+1} - s \right]}{\mathbb{P} \left[ \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right]} \quad (15)$$

$$= \frac{\frac{\Gamma(r+s)}{s!\Gamma(r)}(1-p)^s p^r \cdot \frac{\Gamma((N_t-1)r + (N_{t+1}-s))}{(N_{t+1}-s)!\Gamma((N_t-1)r)}(1-p)^{N_{t+1}-s} p^{(N_t-1)r}}{\frac{\Gamma(N_t r + N_{t+1})}{N_{t+1}!\Gamma(N_t r)}(1-p)^{N_{t+1}} p^{N_t r}} \quad (16)$$

$$= \frac{N_{t+1}!}{s!(N_{t+1}-s)!} \frac{\Gamma(r+s)\Gamma((N_t-1)r + (N_{t+1}-s))}{\Gamma(N_t r + N_{t+1})} \frac{\Gamma(N_t r)}{\Gamma(r)\Gamma((N_t-1)r)} \quad (17)$$

$$= \binom{N_{t+1}}{s} \frac{B(s+r, N_{t+1}-s + (N_t-1)r)}{B(r, (N_t-1)r)}, \quad (18)$$

that is  $S_{t,1} \left| \left( \sum_{i=1}^{N_t} S_{t,i} = N_{t+1} \right) \right. \sim \text{Beta-Binomial}(r, (N_t-1)r).$

The falling factorial moments of  $X \sim \text{Beta-Binomial}(\alpha, \beta)$  are (Tripathi et al. 1994):

$$\mathbb{E} \left[ \frac{X!}{(X-r)!} \right] = \binom{n}{r} \frac{B(\alpha+r, \beta)r!}{B(\alpha, \beta)} \quad (19)$$

where  $B(x, y)$  denotes the Beta function defined as  $B(x, y) = \Gamma(x)\Gamma(y)/\Gamma(x+y)$ , and injecting this formula into Equation (3), we deduce that the inclusive probability of coalescence for  $k$  lines is:

$$p_{k,t} = \frac{B(N_t r + 1, r + k)}{B(r + 1, N_t r + k)} \quad (20)$$

By injecting the probability mass function of a beta-binomial distribution in Equation (5) we deduce that the exclusive probability of coalescence for  $k$  lines is:

$$p_{n,k,t} = \frac{N_t B(k+r, n-k + N_t r - r)}{B(r, N_t r - r)} \quad (21)$$

It is interesting to note that as for the Poisson case, the inclusive and exclusive coalescence probabilities do not depend on the size  $N_{t+1}$  of the population at time  $t+1$ . They both depend on the Negative-Binomial offspring distribution only through the dispersion parameter  $r$ .

## 5 Example

Let the offspring distribution have a mean of  $R_t = 2$ . In the Poisson case the offspring distribution is Poisson(2). We consider NegBin cases with the same mean and varying dispersion parameters  $r$ . When  $r = 1$  the NegBin reduces to a Geometric distribution. When  $r$  is high the dispersion is low and the NegBin behaves almost like a Poisson. See Figure 1.

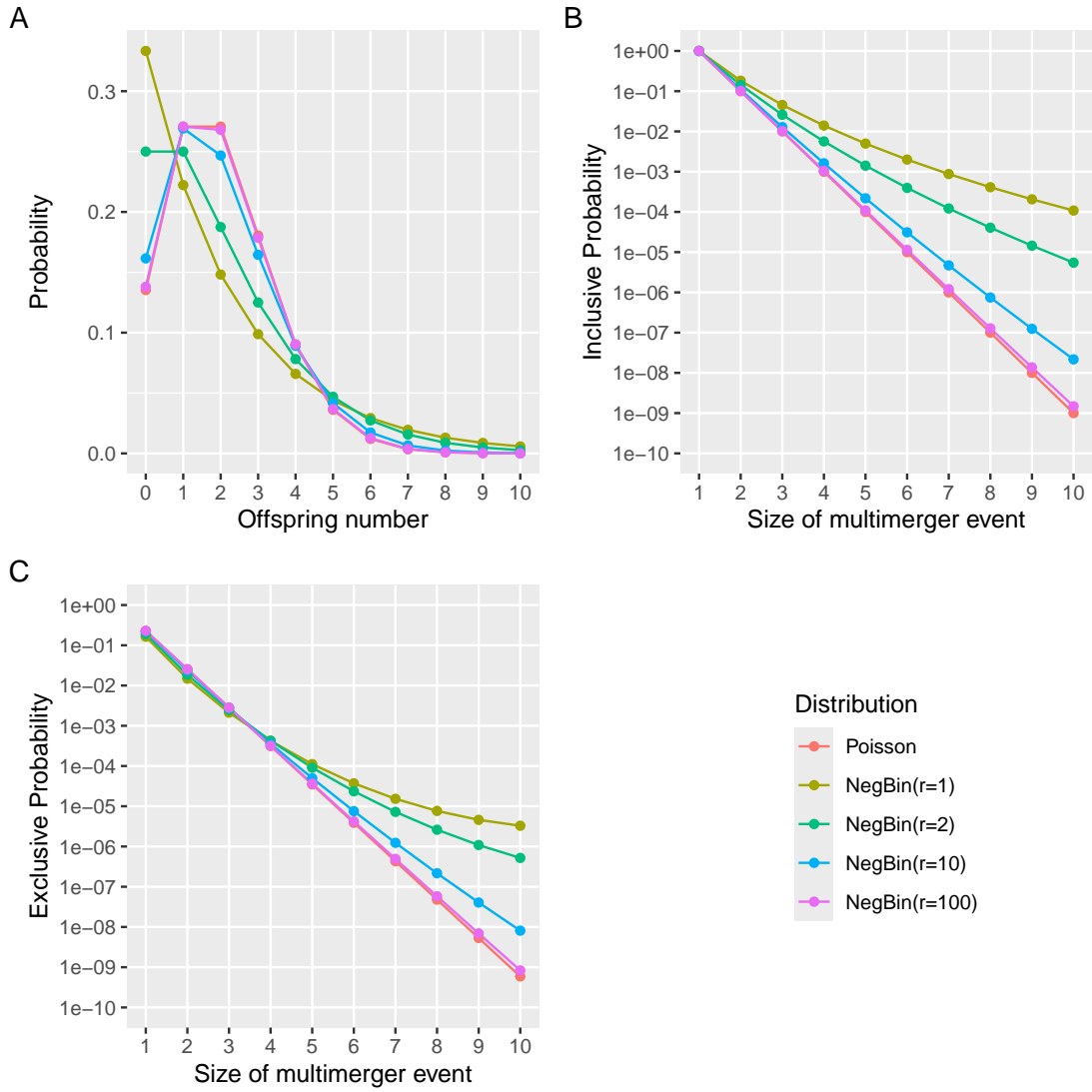


Figure 1: (A) Offspring distribution. (B) Inclusive probability of coalescence. (C) Exclusive probability of coalescence.

## 6 Limit when the population size is large

Consider that  $N_t$  is large.

Show that inclusive probabilities  $p_{k,t}$  for  $k > 2$  are small compared to  $p_{2,t}$ .

Show that exclusive probabilities  $p_{n,k,t}$  for  $k > 2$  is small compared to  $p_{n,2,t}$ , when  $n \ll N_t$ .

Show that inclusive and exclusive probabilities become equal, when  $n \ll N_t$  in exclusive probabilities.



96 For Poisson offspring distribution we have:

$$p_{2,t} = p_{n,2,t} = \frac{1}{N_t} \quad (22)$$

97 For Negative-Binomial offspring distribution we have:

$$p_{2,t} = p_{n,2,t} = \frac{r+1}{N_t r + 1} \approx \frac{r+1}{N_t r} \quad (23)$$

98 Then we can relate the inclusive coalescent probability for two lines  $p_{2,t}$  to previous results from (Volz  
99 2012), (Koelle and Rasmussen 2012) and (Li et al. 2017; Fraser and Li 2017).

100 (Fraser and Li 2017) have as their main result an estimate of the effective population size  $N_e(t)$  as a  
101 function of the actual population size  $N(t)$  and the mean and variance of the offspring distribution  $R$   
102 and  $\sigma^2$ :

$$N_e(t) = \frac{N(t)}{\sigma^2/R + R - 1} \quad (24)$$

103 In our notation, this is equivalent to:

$$p_{2,t} = \frac{V_t/R_t + R_t - 1}{N_t R_t} \quad (25)$$

104 In the Poisson case we have  $V_t = R_t$  so this reduces to  $p_{2,t} = 1/N_t$ .

105 For the Negative-Binomial case we have  $V_t/R_t = 1/p = (r + R_t)/r$  so that:

$$p_{2,t} = \frac{V_t/R_t + R_t - 1}{N_t R_t} = \frac{r + R_t + r R_t - r}{r N_t R_t} = \frac{r+1}{r N_t} \quad (26)$$

106 which is the same as in Equation (23).

## 107 7 Lambda-coalescent

108 A lambda-coalescent model is defined by a probability measure  $\Lambda(dx)$  on the interval  $[0, 1]$ , from which  
109 we can deduce the rate  $\lambda_{n,k}$  at which any subset of  $k$  lineages within a set of  $n$  observed lineages  
110 coalesce:

$$\lambda_{n,k} = \int_0^1 x^{k-2} (1-x)^{n-k} \Lambda(dx) \quad (27)$$

111 The Beta( $2 - \alpha, \alpha$ )-coalescent model (Schweinsberg 2003) has a single parameter  $\alpha \in [0, 2]$  and is  
 112 defined as:

$$\Lambda(dx) = \frac{x^{1-\alpha}(1-x)^{\alpha-1}}{B(2-\alpha, \alpha)}dx \quad (28)$$

113 from which we can deduce that:

$$\lambda_{n,k} = \frac{B(k-\alpha, n-k+\alpha)}{B(2-\alpha, \alpha)} \quad (29)$$

114 Special cases include  $\alpha = 2$  corresponding to the Kingman coalescent,  $\alpha = 1$  which is known as the  
 115 Bolthausen-Sznitman coalescent and  $\alpha = 0$  for which the phylogeny is always star-shaped.

## 116 8 Implementation

117 We implemented the analytical methods described in this paper in a new R package entitled *EpiLambda*  
 118 which is available at <https://github.com/xavierdidelot/EpiLambda> for R version 3.5 or later. All  
 119 code and data needed to replicate the results are included in the “run” directory of the *EpiLambda*  
 120 repository.

## 121 9 Discussion

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