# Multiple birth-death model – conditioning probability

The idea is to keep track of the number of species $m_1$ and $m_2$ descending from each of the crown species. We construct the $Q$-equation for the components $Q_{m_1,m_2}$. Multiple-birth events can affect all species ($2+m_1+m_2$ in total). Their contribution to the $Q$-equation is

$$\begin{aligned}
\text{contrib} = \nu & \sum_{a_1=0}^{\lfloor\frac{1+m_1}{2}\rfloor} \sum_{a_2=0}^{\lfloor\frac{1+m_2}{2}\rfloor} \sum_{j_1=0}^{\min(1,a_1)} \sum_{j_2=0}^{\min(1,a_2)} 2^{j_1+j_2} \binom{1}{j_1}\binom{1}{j_2}\binom{m_1-a_1}{a_1-j_1}\binom{m_2-a_2}{a_2-j_2} \\
& \qquad q^{a_1+a_2}(1-q)^{2+m_1+m_2-2a_1-2a_2} Q_{m_1-a_1,m_2-a_2} \\
& - \nu\, Q_{m_1,m_2} \\
= \nu & \sum_{a_1=0}^{\lfloor\frac{1+m_1}{2}\rfloor} \sum_{a_2=0}^{\lfloor\frac{1+m_2}{2}\rfloor} \frac{m_1+1}{m_1-2a_1+1}\binom{m_1-a_1}{a_1} \frac{m_2+1}{m_2-2a_2+1}\binom{m_2-a_2}{a_2} \\
& \qquad q^{a_1+a_2}(1-q)^{2+m_1+m_2-2a_1-2a_2} Q_{m_1-a_1,m_2-a_2} \\
& - \nu\, Q_{m_1,m_2} \\
= \nu & \sum_{a_1=0}^{\lfloor\frac{1+m_1}{2}\rfloor} \sum_{a_2=0}^{\lfloor\frac{1+m_2}{2}\rfloor} \frac{(m_1+1)(m_1-a_1)!}{(m_1-2a_1+1)!\,a_1!} \frac{(m_2+1)(m_2-a_2)!}{(m_2-2a_2+1)!\,a_2!} \\
& \qquad q^{a_1+a_2}(1-q)^{2+m_1+m_2-2a_1-2a_2} Q_{m_1-a_1,m_2-a_2} \\
& - \nu\, Q_{m_1,m_2}
\end{aligned}$$

The full $Q$-equation is

$$\begin{aligned}
\frac{dQ_{m_1,m_2}}{dt} &= \lambda\big((m_1+1)Q_{m_1-1,m_2} + (m_2+1)Q_{m_1,m_2-1}\big) \\
&\quad + \mu\big((m_1+1)Q_{m_1+1,m_2} + (m_2+1)Q_{m_1,m_2+1}\big) \\
&\quad - (\lambda+\mu)(m_1+m_2+2)Q_{m_1,m_2} \\
&\quad + (\text{contribution of multiple-birth events})
\end{aligned}$$

The solution of the $Q$-equation has the following interpretation: the probability that the diversification process has $m_1+1$ descendant species of the first crown species and $m_2+1$ descendant species of the second crown species is given by

$$P^c_{m_1,m_2} = \frac{Q_{m_1,m_2}}{(m_1+1)(m_2+1)}$$

Hence, the conditional probability $P_c$ is given by

$$P^c = \sum_{m_1,m_2} P^c_{m_1,m_2} = \sum_{m_1,m_2} \frac{Q_{m_1,m_2}}{(m_1+1)(m_2+1)}$$

My claim is that

- in the model without multiple births ($\nu = 0$), the terms in this sum for fixed $m_1+m_2$ are equal, i.e., all combinations $(m_1, m_2)$ for fixed $m_1+m_2$ are equally probable. In the PRSB paper we took advantage of this property to efficiently compute the conditioning probability.
- in the model with multiple births ($\nu > 0$), this symmetry property does not hold. As a result, we have to compute the conditioning probability explicitly.

Here is a (quick – it can be improved) implementation of this approach for your example (this is Matlab code):

```
la=0.0204942104;
mu=0.0001333249;
nu=1.5728643216;
pq=0.0787076385;
tt=10; % time between crown age and present
lq=100; % maximal number of missing species

% construct auxiliary matrix
cc=probcond2_matr(pq,lq);

% integrate equations
[~,X4]=ode45(@(t,x) probcond2_rhs(x,la,mu,0,zeros(100),1),[0 tt],x0);
Q4=X4(end,:);
Q4=reshape(Q4,lq,lq);
% compute conditioning probability
m1=ones(lq,1)*(0:(lq-1));
m2=m1';
Pc4=Q4./((m1+1).*(m2+1));
sum(Pc4(:))
```

The code for the right-hand side of the differential equation:

```
function dq=probcond2_rhs(qq,la,mu,nu,cc,kk)

lq2=length(qq(:));
lq=sqrt(lq2);
qq=reshape(qq,lq,lq);
m1=ones(lq,1)*(0:(lq-1));
m2=m1';
dq1=la*(2*kk+m1-1).*[zeros(lq,1) qq(:,1:end-1)] ...
    +la*(2*kk+m2-1).*[zeros(1,lq); qq(1:end-1,:)] ...
    -la*(2*kk+m1+m2).*qq;
dq2=mu*(m1+1).*[qq(:,2:end) zeros(lq,1)] ...
    +mu*(m2+1).*[qq(2:end,:); zeros(1,lq)] ...
    -mu*(2*kk+m1+m2).*qq;
dq3=nu*cc*qq*cc'-nu*qq;
dq=dq1+dq2+dq3;
dq=reshape(dq,lq2,1);

end
```

And the code for the auxiliary matrix used in the differential equation:

```
function [cc,cp]=probcond2_matr(pq,lq)

cc=zeros(lq);
cp=zeros(lq);
for m1=0:(lq-1)
    for a1=0:floor((1+m1)/2)
        aux=log(m1+1)+gammaln(m1-a1+1)-gammaln(m1-2*a1+2)-gammaln(a1+1);
        aux=exp(aux);
        cp(m1+1,m1-a1+1)=aux;
        aux=aux*pq^a1*(1-pq)^(m1+1-2*a1);
        cc(m1+1,m1-a1+1)=aux;
    end
end

end
```

The conditioning probability I obtain is `0.9985889671`, smaller than one as it should be. I checked that the symmetry property is verified for $\nu = 0$ and that it is not verified for $\nu > 0$. I also checked that for $\nu = 0$ I get the same conditioning probability as previously.