

# Rough calculation for the rate of hybridization from diploids

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Assume diploids follow a constant rate birth-death process with birth rate  $\lambda$  and death rate  $\mu$  in units of  $\text{My}^{-1}$ . Suppose that hybridization occurs at a rate  $\beta\lambda$  between any pair of diploids as long as the mrca of the diploids is no more than  $t$ .

If there are  $n$  diploids at time 0, then at a time  $x$  in the past, there will have been about  $ne^{(\mu-\lambda)x}$  diploids. The rate of hybridization at time 0 is  $\beta\lambda$  multiplied by the number of pairs of diploids whose mrca is after  $t$ , and is therefore the number of pairs within the approximately  $ne^{(\lambda-\mu)t}$  subtrees which have grown from the diploids that were present at time  $t$ . Any pairs from different subtrees will have an mrca which is too old; any pairs within a single tree have an mrca which is recent enough.

So the rate of hybridization at time 0 is approximately

$$H = nE\beta\lambda \sum_{i \geq 2} \binom{i}{2} p_i(t)$$

where  $E = e^{(\mu-\lambda)t}$  and  $p_i(t)$  is the probability of the birth-death process producing  $i$  species from one at time  $t$ . The formula for  $p_i(t)$  seems to be well-known, but I don't have a reference. It is

$$p_i(t) = p(t)r(t)^{i-1}$$

where

$$p(t) = \frac{(\lambda - \mu)^2 e^{(\mu-\lambda)t}}{(\lambda - \mu e^{(\mu-\lambda)t})^2} = \frac{(\lambda - \mu)^2 E}{(\lambda - \mu E)^2}$$

and

$$r(t) = \lambda \frac{(1 - e^{(\mu-\lambda)t})}{\lambda - \mu e^{(\mu-\lambda)t}} = \lambda \frac{1 - E}{\lambda - \mu E}.$$

So

$$H = nE\beta\lambda p(t) \sum_{i \geq 2} \binom{i}{2} r(t)^{i-1} = nE\beta\lambda p(t)r(t)(1 - r(t))^{-3}.$$

Now

$$1 - r(t) = \frac{\lambda - \mu E - \lambda + \lambda E}{\lambda - \mu E} = E \frac{\lambda - \mu}{\lambda - \mu E}$$

so

$$H = nE\beta\lambda \frac{(\lambda - \mu)^2 E}{(\lambda - \mu E)^2} \lambda \frac{1 - E}{\lambda - \mu E} E^{-3} \frac{(\lambda - \mu E)^3}{(\lambda - \mu)^3}$$

which simplifies to

$$H = nE\beta\lambda \frac{1 - E}{E^2} \frac{\lambda}{(\lambda - \mu)}$$

The rate of new diploid production is  $n\lambda$ . So the ratio of rates is approximately

$$R = \frac{H}{n\lambda} = \beta \frac{\lambda}{(\lambda - \mu)} \frac{1 - E}{E^3}$$

Suppose  $t = 36\text{My}$ . Suppose  $\lambda = 1/9$ , and  $\mu = 1/8$  (ie speciations happen once per 8My, extinctions once per 9My). Then  $E = e^{-t/72} = e^{-1/2}$

$$R = \beta \frac{1/9}{1/72} \frac{1 - e^{-1/2}}{e^{-3/2}} \approx 14\beta$$

Keep  $t = 36\text{My}$ . Suppose  $\lambda = 1/36$ , and  $\mu = 1/72$  (ie speciations happen once per 36My, extinctions once per 72My). Then  $E = e^{-t/72} = e^{-1/2}$

$$R = \beta \frac{1/36}{1/72} \frac{1 - e^{-1/2}}{e^{-3/2}} \approx 3.5\beta$$

The assumption that hybridization occurs at a constant rate and then suddenly stops is obviously too simple, but I think a decreasing rate with similar mean (18 My) will give similar results.  $\lambda - \mu = 1/72$  in both the examples above, which corresponds to the number of diploid species increasing by about 2.5 times in the last 65 My. The  $\lambda = 1/9$ , and  $\mu = 1/8$  is probably most realistic. The situation is complicated by the fact that phylogenetic analyses will mostly study groups which have been diversifying better than average.

I've used 'hybridization' above, since the calculations apply to any sort of hybridization. Now I shall take the calculations as applying to allopolyploidization only. In this case there should be a minimum on the time between mrca and allopolyploidization, but I don't think that will make a big difference.

[1], p327, has some estimates for polyploidy: in ferns about 7% of speciation events are due to polyploidy, in angiosperms about 2-4% of speciation events are due to polyploidy. Both probably underestimates. Discussion pp328-30 of frequency of auto- vs allopolyploidy does not give any clear numbers. Plant evolutionists used to think that allo- was the norm, but now less clear.

Nonetheless, it is possible to say something about a likely value for  $\beta$ . If  $\beta \geq 0.1$  far more allopolyploidization events will occur in the model than are observed. If  $\beta \leq 0.001$  too few allopolyploidization events will occur in the model. A prior for  $\beta$  could be an exponential with mean 0.02. This has about 5% probability mass below 0.001 and about 0.7% above 0.1.

## References

- [1] Coyne, J.A., Orr, H.A.: Speciation. Sinauer Associates (2004)