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Features



Natural selection, maths and milk

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Let's recall the definitions:

F_X = observed frequency of the allele **X** (where **X** is one of **T**, **C**, **A** or **B**), regardless of which other allele it occurs with;

F_{XY} = observed frequency of **X** allele occurring with **Y** allele (where **X** is one of **T** or **C** and **Y** is one of **A** or **B**).

Each of the quantities above lie between zero and one, because they are *frequencies*: F_X is the number of times that the allele **X** was observed in our sample, divided by the total size of the sample.

Now, since in each individual case one of the **T** or **C** allele must always be observed, we have

$$F_T + F_C = 1.$$

Similarly,

$$F_A + F_B = 1.$$

We also have:

$$F_{TA} + F_{TB} = F_T;$$

$$F_{CA} + F_{CB} = F_C;$$

$$F_{TA} + F_{CA} = F_A;$$

$$F_{TB} + F_{CB} = F_B.$$

First we will show that

$$D = F_{TA} - F_T F_A = F_{CB} - F_C F_B.$$

This means that the value D can be calculated in two different ways and this will be useful later.

Clearly,

$$F_{TA} = F_T - F_{TB} = 1 - F_C - F_{TB}.$$

So

$$\begin{aligned} D &= F_{TA} - F_T F_A \\ &= 1 - F_C - F_{TB} - (1 - F_C)(1 - F_B) \\ &= F_B - F_{TB} - F_C F_B = F_{CB} - F_C F_B, \end{aligned}$$

which is what we wanted to show.

Now note that F_{TA} can take any value between 0 and F_T . If $F_{TA} = 0$, then this means that **T** was never observed with **A**, and if $F_{TA} = F_T$, then **T** was only ever observed with **A**.

Since $D = F_{TA} - F_T F_A$, we get

$$-F_T F_A \leq D \leq F_T - F_T F_A = F_T F_B.$$

Similarly, since D is also equal to $F_{CB} - F_C F_B$ and since $0 \leq F_{CB} \leq F_C$, we get

$$-F_C F_B \leq D \leq F_C - F_C F_B = F_C F_A.$$

For D^2 this means

$$0 \leq D^2 \leq F_T F_C F_A F_B.$$

Therefore, r^2 always lies between 0 and 1.

The last thing to notice is that D^2 can indeed take the value 1, but only when $F_{TA} = 0$ and $F_{CB} = 0$ (so that **T** only occurs with **B** and **C** only occurs with **A**), or when $F_{TA} = F_T$ and $F_{CB} = F_C$ (so that **T** only occurs with **A** and **C** only occurs with **B**).

In other words, $r^2 = 1$ precisely when there is complete association between alleles.

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