On Fisher's geometrical model

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Fisher's geometrical model considers evolution in a high-dimensional phenotypic space. Let us consider a situation in which fitness is a function of n quantitative traits, $\boldsymbol{x} = (x_1, \dots, x_n)$, where n is a large number. We assume that the optimal phenotype lies at a point O in the space of phenotypes, and that the fitness decreases as the Euclidean distance from the maximum increases. Without loss of generality, we can choose O as the origin of the coordinates. Then the surfaces of equal fitness are spheres centered in O, and the larger the radius of the sphere, the smaller the fitness value.

Let us now consider an organism whose phenotype is not optimal, and is described by a point P at some distance from O. We would like to evaluate the probability that a random mutation, that generates a phenotype at a distance r from P, produces a phenotype which is better adapted than P. Without loss of generality, we can choose the unit of length to be equal to twice the distance of P from O, so that P lies on a sphere Σ, centered in O, of radius equal to $\frac{1}{2}$. The mutated phenotype lies on a sphere S centered in P of radius r. Its fitness will be larger than that of P if it lies in the interior of Σ. We wish therefore to evaluate the fraction of the surface of S that lies in the interior of Σ (cf. Figure 1).

Let us first remind that the surface of a sphere of radius r in n dimensions is given by $S_{n-1}\, r^{n-1}$, where the constant S_{n-1} is given by

$$S_{n-1} = \frac{2\pi^{n/2}}{\Gamma(n/2)}, \tag{1}$$

where $\Gamma(z)$ is Euler's gamma function.

The condition that a point Q belonging to S lies in the interior of Σ is equivalent to the condition that its projection on the OP radius lies at a distance $\left(\frac{1}{2} - w\right)$ from O, where $w \geq u$, and u is the distance from P of the projection Q′ on OP of a point Q lying at the intersection of Σ and S. To evaluate u let us consider a point Q belonging to both Σ and S, and let us draw the plane containing O, P and Q (Figure 1), with the x-axis along OP and the y-axis normal to it. Let the coordinates of Q be $\left(\frac{1}{2} - u, y\right)$ We then have

$$u^2 + y^2 = r^2; \tag{2a}$$

$$\left(\frac{1}{2} - u\right)^2 + y^2 = \frac{1}{4}. \tag{2b}$$

This implies

$$u = r^2. \tag{3}$$

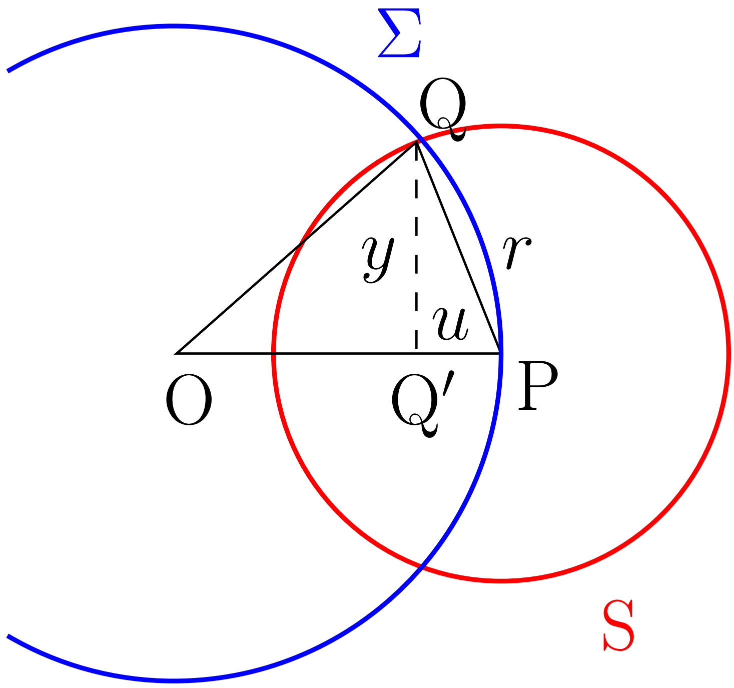

Figure 1: Fisher geometrical model. The sphere Σ is a sphere of radius $\frac{1}{2}$ in an n-dimensional space, with $n \gg 1$, centered in O. The sphere S is an analogous sphere of radius r, centered in P, where P belongs to Σ. One wishes to evaluate the fraction of the surface of S that lies in the interior of Σ. This corresponds to all points of S whose distance from P along the radius OP are larger than u, where u is the distance from P of the projection Q′ on OP of the points (like Q) that belong to both Σ and S.

We must now evaluate the surface of the spherical cap corresponding to $w > u$. This is given by the surface of S, divided by 2, minus the surface of the zone (region of the sphere between two parallels) determined by the condition $0 \le w \le u$. Let us consider a zone determined by the parallels w and $w + \mathrm{d}w$. The sum y^2 of all coordinates but the first one must satisfy

$$y^2 + w^2 = r^2. \tag{4}$$

Thus, for a given value of w, the region of space that satisfies this condition is a sphere in $(n-1)$ dimensions of radius $\sqrt{r^2 - w^2}$, which has a total area equal to $S_{n-1}(r^2 - w^2)^{n/2-1}$. On the other hand, the area of the zone intercepted by $\mathrm{d}w$ will be proportional to $\sqrt{\mathrm{d}w^2 + \mathrm{d}y^2}$, which is readily seen to be equal to $\mathrm{d}w\, r/\sqrt{r^2 - w^2}$. Thus the area of the zone we are interested in is given by

$$\mathcal{A} = r \int_0^{r^2} \mathrm{d}w\; S_{n-2}\,\left(r^2 - w^2\right)^{n/2-1}. \tag{5}$$

One can check that

$$\int_{-r}^{r} \mathrm{d}w\; r S_{n-2}\,\left(r^2 - w^2\right)^{n/2-1} = r^{n-1} S_{n-2} \int_{-1}^{+1} \mathrm{d}u\;(1-u^2)^{n/2-1} = S_{n-1} r^{n-1}. \tag{6}$$

Let us now evaluate $\mathcal{A}$ for $n \gg 1$. We have

$$\begin{aligned}\mathcal{A} &= r\int_0^{r^2} \mathrm{d}w\ S_{n-2}\ \left(r^2 - w^2\right)^{n/2-1} \\ &= r^{n-1} S_{n-2}\int_0^{r} \mathrm{d}u\ \left(1 - u^2\right)^{n/2-1}.\end{aligned} \tag{7}$$

Assuming that $r \ll 1$ (whose consistency can be checked later) we can express the integrand as follows:

$$\left(1-u^2\right)^{n/2-1} \approx \mathrm{e}^{-nu^2/2}, \tag{8}$$

where we have also neglected $1/2$ with respect to n. Define the function

$$\phi(x) = \sqrt{\frac{2}{\pi}}\int_0^x \mathrm{d}t\ \mathrm{e}^{-t^2/2}. \tag{9}$$

This function vanishes for $x = 0$ and approaches 1 as $x \to \infty$. We then have

$$\mathcal{A} = r^{n-1} S_{n-2}\sqrt{\frac{\pi}{2n}}\,\phi\left(r\sqrt{n}\right). \tag{10}$$

The probability of being in the considered zone is given by $\mathcal{A}/(S_{n-1}r^{n-1})$, i.e.,

$$P_1 = \frac{S_{n-2}}{S_{n-1}}\sqrt{\frac{\pi}{2n}}\,\phi\left(r\sqrt{n}\right) \simeq \frac{1}{\sqrt{2}}\,\phi\left(r\sqrt{n}\right). \tag{11}$$

Now we have

$$\lim_{x\to\infty}\frac{\Gamma(x+3/2)}{\sqrt{x}\,\Gamma(x+1)} = 1, \tag{12}$$

as can be checked from Stirling's formula, and therefore

$$\lim_{n\to\infty}\frac{S_{n-2}}{S_{n-1}}\sqrt{\frac{\pi}{2n}} = \lim_{n\to\infty}\frac{\Gamma(n/2)}{\sqrt{\pi}\Gamma((n-1)/2)}\sqrt{\frac{\pi}{2n}} = \frac{1}{2}. \tag{13}$$

Thus the probability of being in the cap is given by

$$P = \frac{1}{2} - P_1 = \frac{1}{2}\left(1 - \phi\left(r\sqrt{n}\right)\right). \tag{14}$$

Since $\phi(u)$ approaches 1 rapidly when its argument grows beyond 1, the probability of being in the cap, i.e., that the mutation is beneficial, vanishes rapidly when $r \gtrsim 1/\sqrt{n}$, which, for large n, is a small number. Thus, Fisher concludes, the probability that a mutation is beneficial does not substantially vanish only when their phenotypic effect is very small. The behavior of this function is shown in Figure 2.

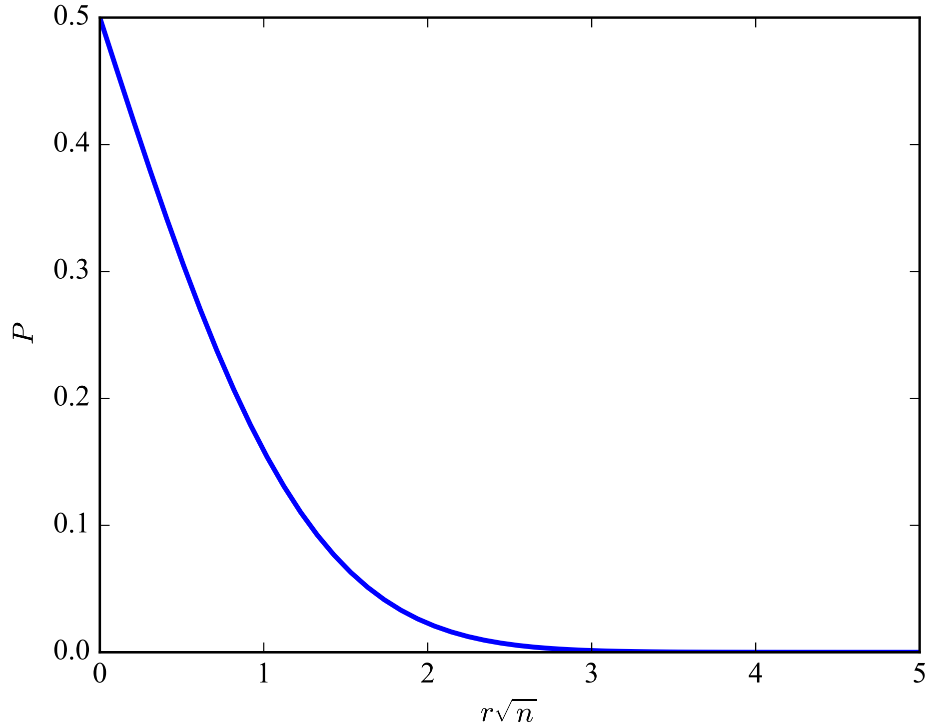

Figure 2: Probability of a beneficial mutation as a function of its size r, according to equation (14).