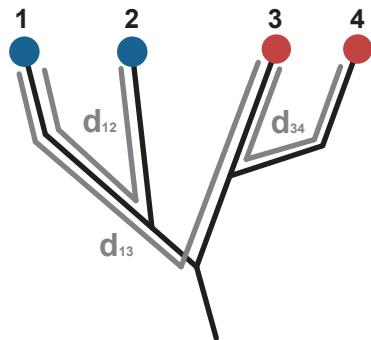


A

● population 1 ● population 2



$$\bar{d}_{within} = \frac{d_{12} + d_{34}}{2}$$

$$\bar{d}_{between} = \frac{(d_{13} + d_{14}) + (d_{23} + d_{24})}{4}$$

B

Elevation gradient

C

Urbanization gradient