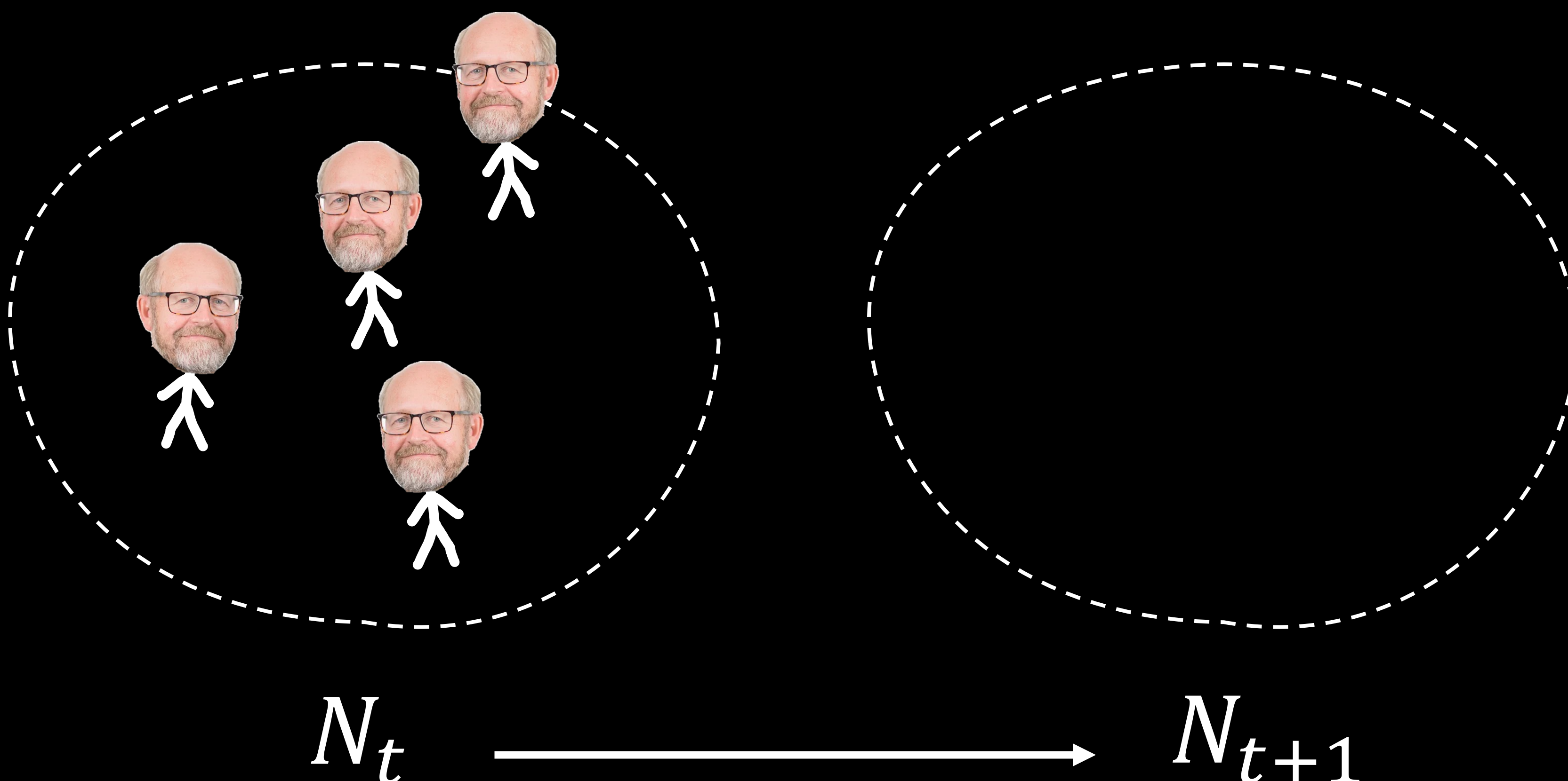
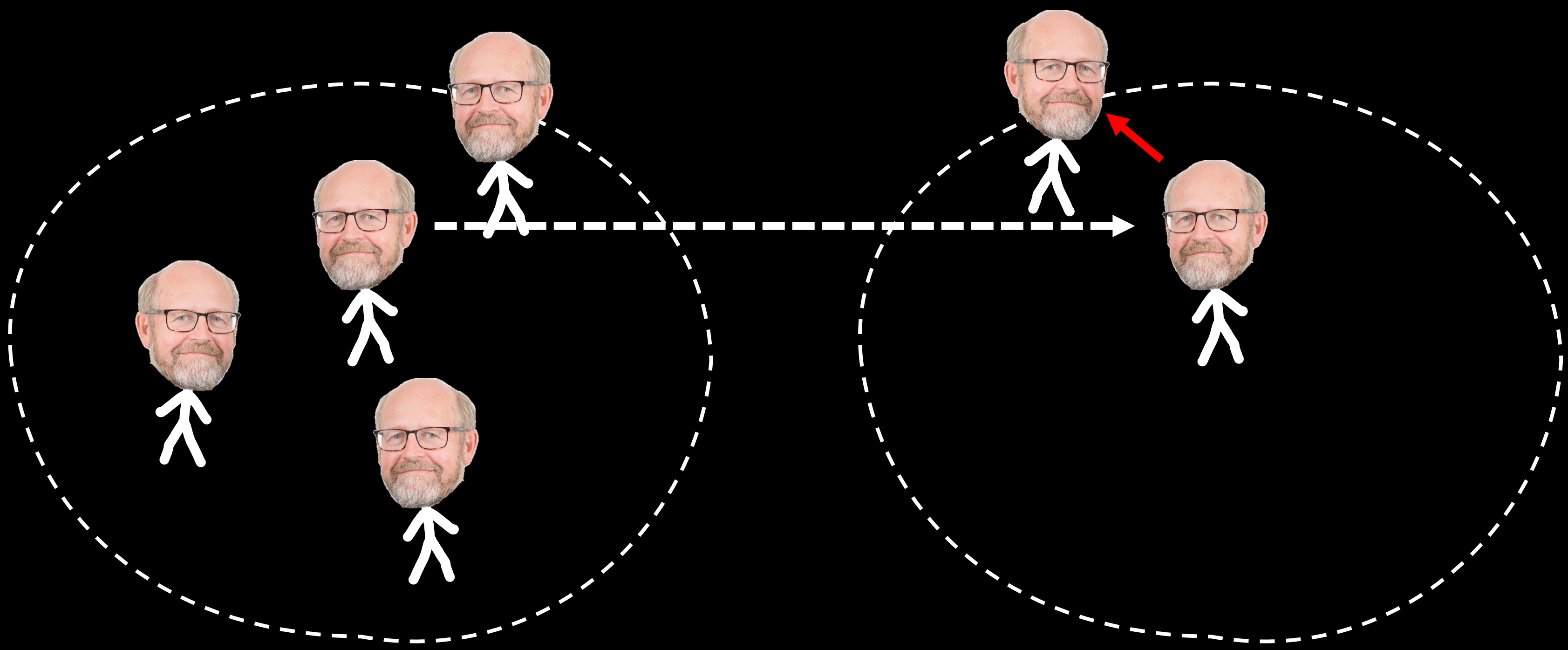
“In biological populations, ecological change is caused by the same processes of individual birth and death that cause evolutionary changes in allele frequencies and phenotypes.”

Duthie & Luque (2025)

Ecological change

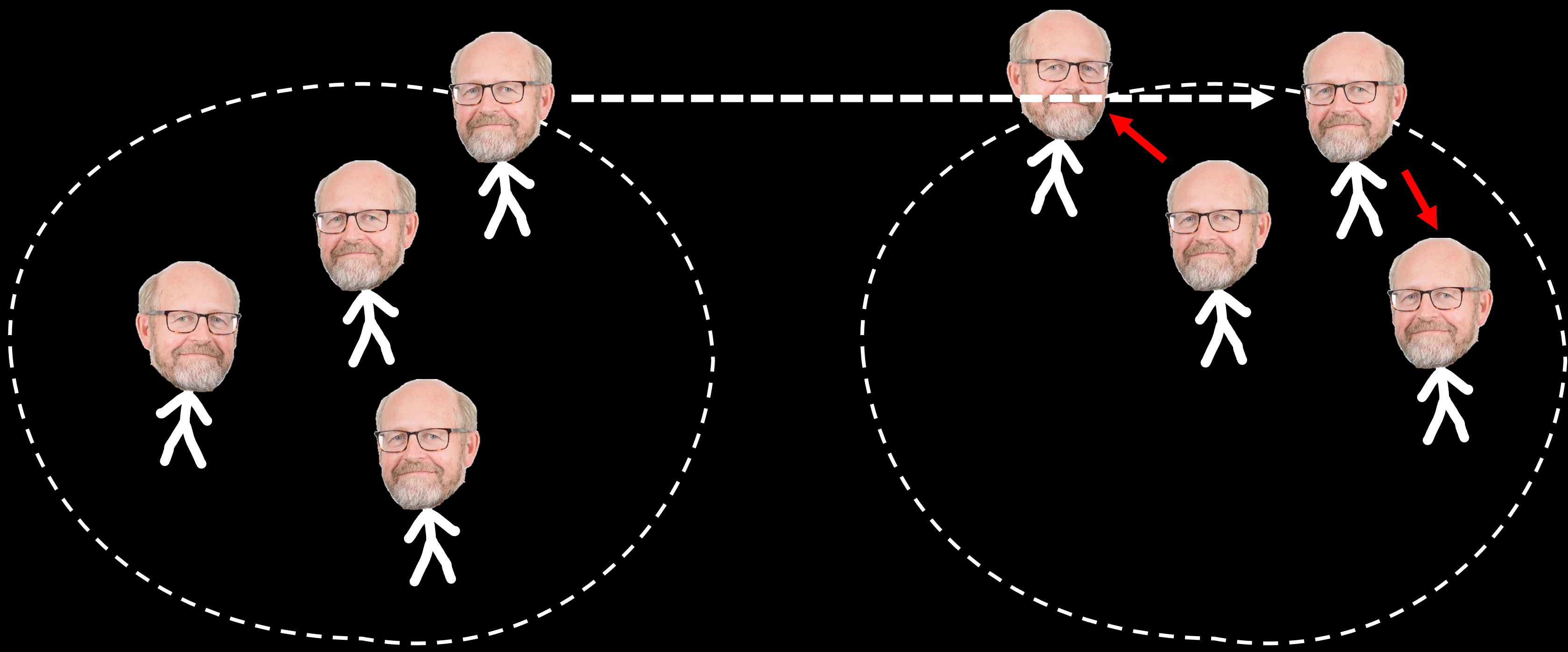


Ecological change



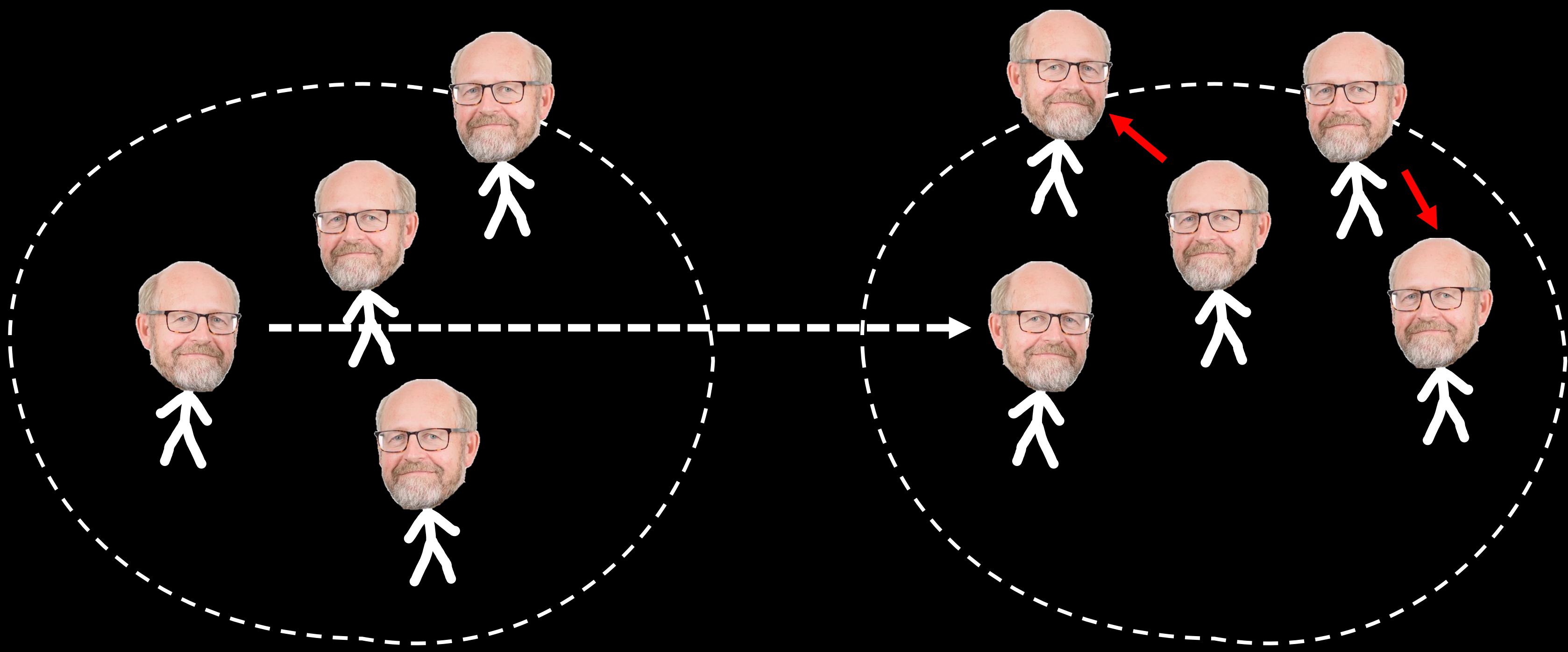
$N_t \longrightarrow N_{t+1}$

Ecological change



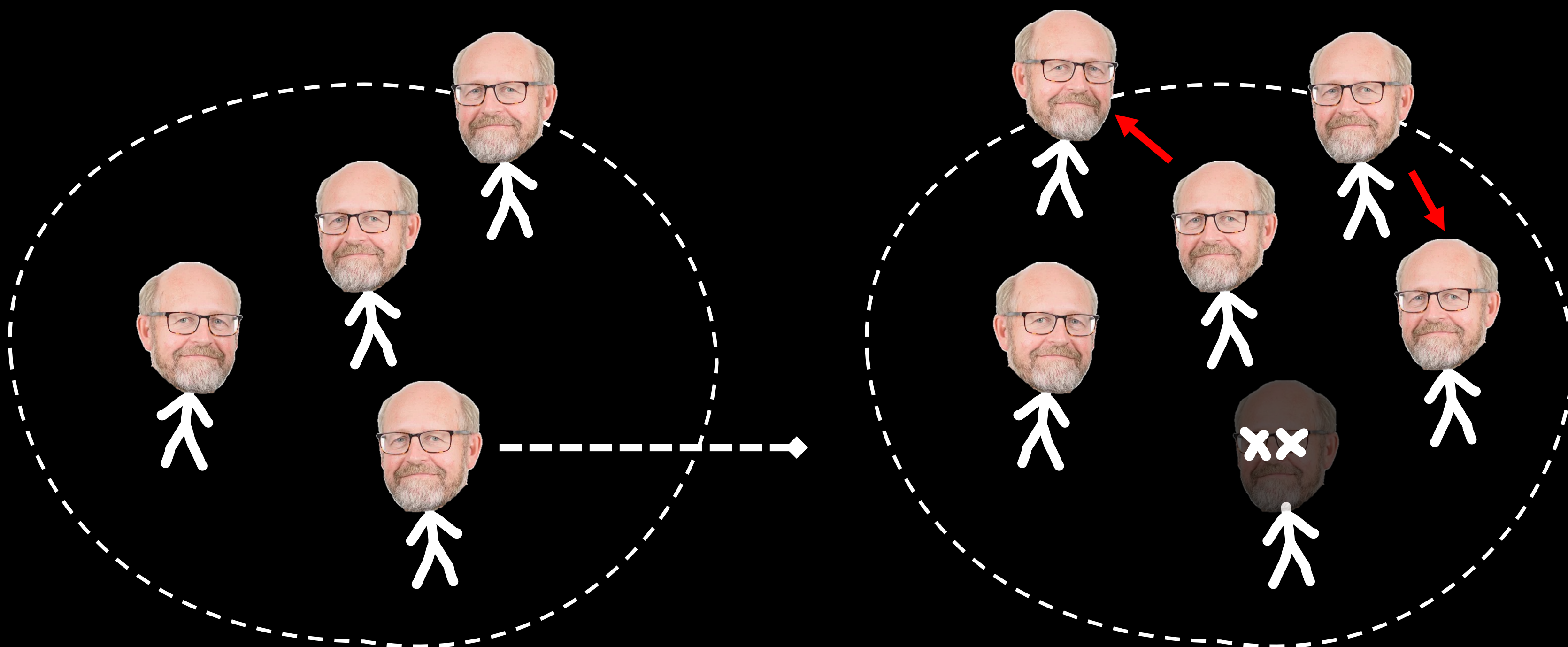
$N_t \longrightarrow N_{t+1}$

Ecological change



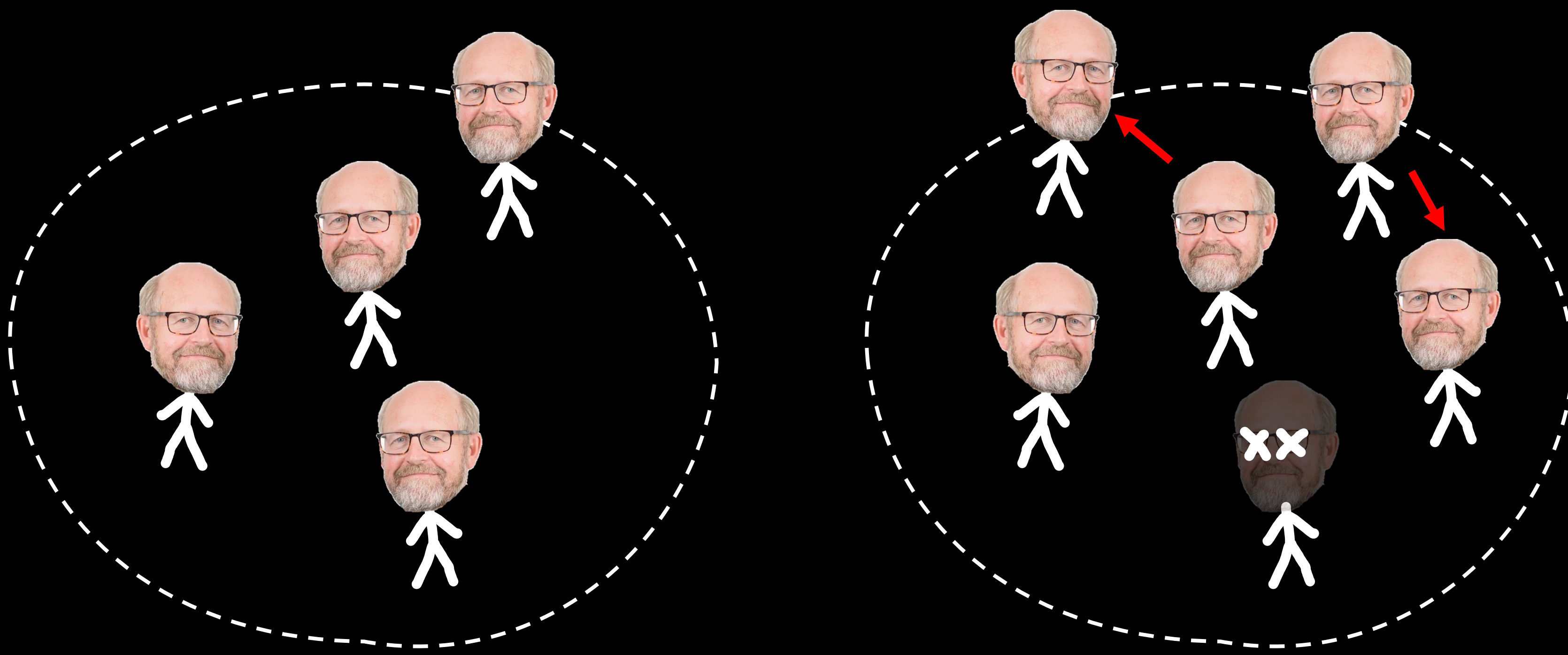
$N_t \longrightarrow N_{t+1}$

Ecological change



$N_t \longrightarrow N_{t+1}$

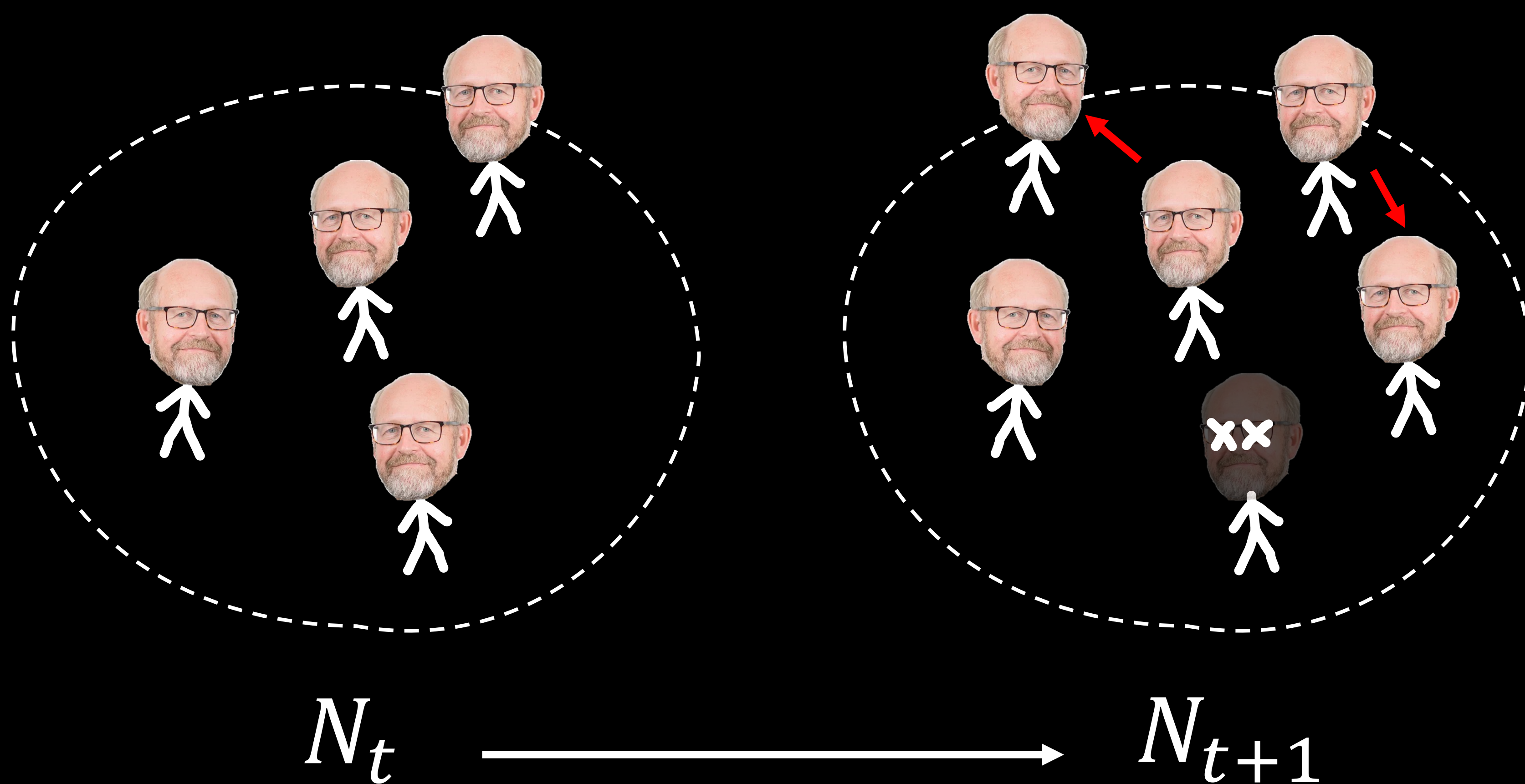
Ecological change



N_t ⟶ N_{t+1}

Ecological change

$$N_{t+1} = N_t + Births\ - Deaths$$



Ecological change

$$N_{t+1} = N_t(1 + b - d)$$

$$\lambda = (1 + b - d)$$

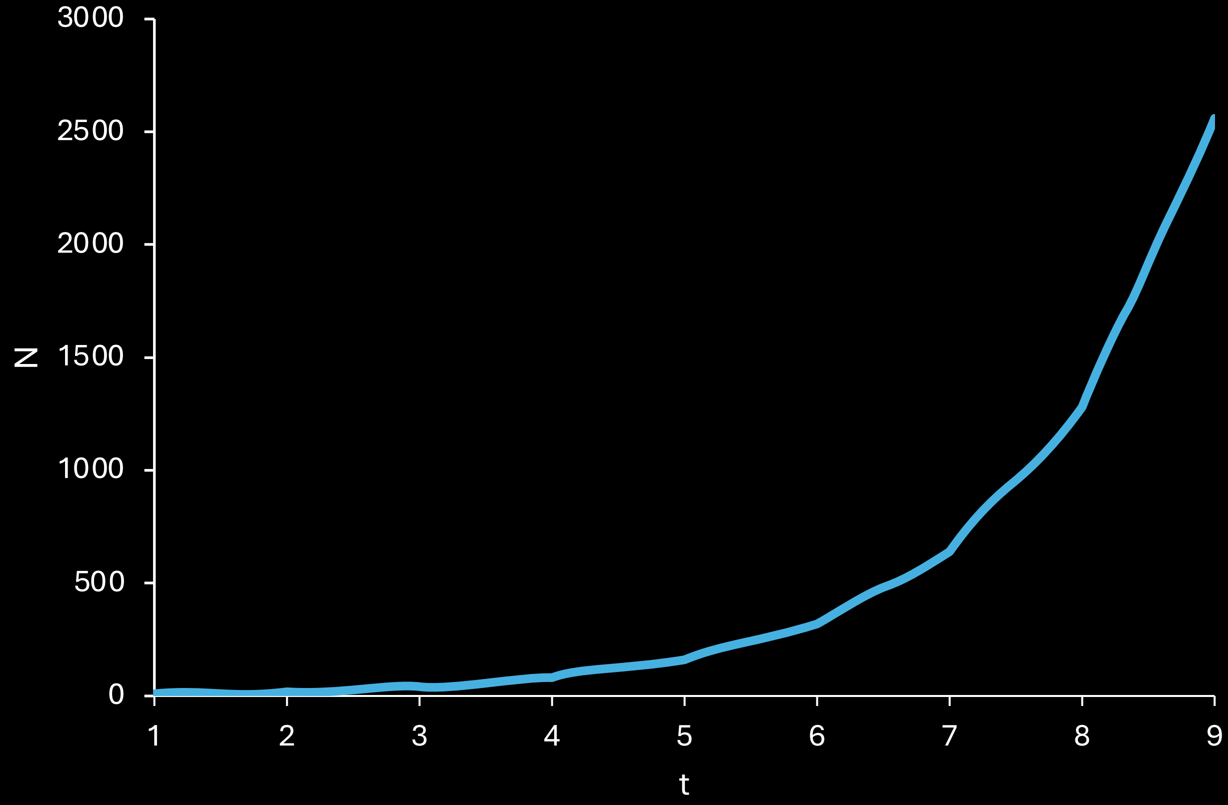
$$N_{t+1} = N_t\lambda$$

$$b = birth\, rate$$

$$d = death\, rate$$

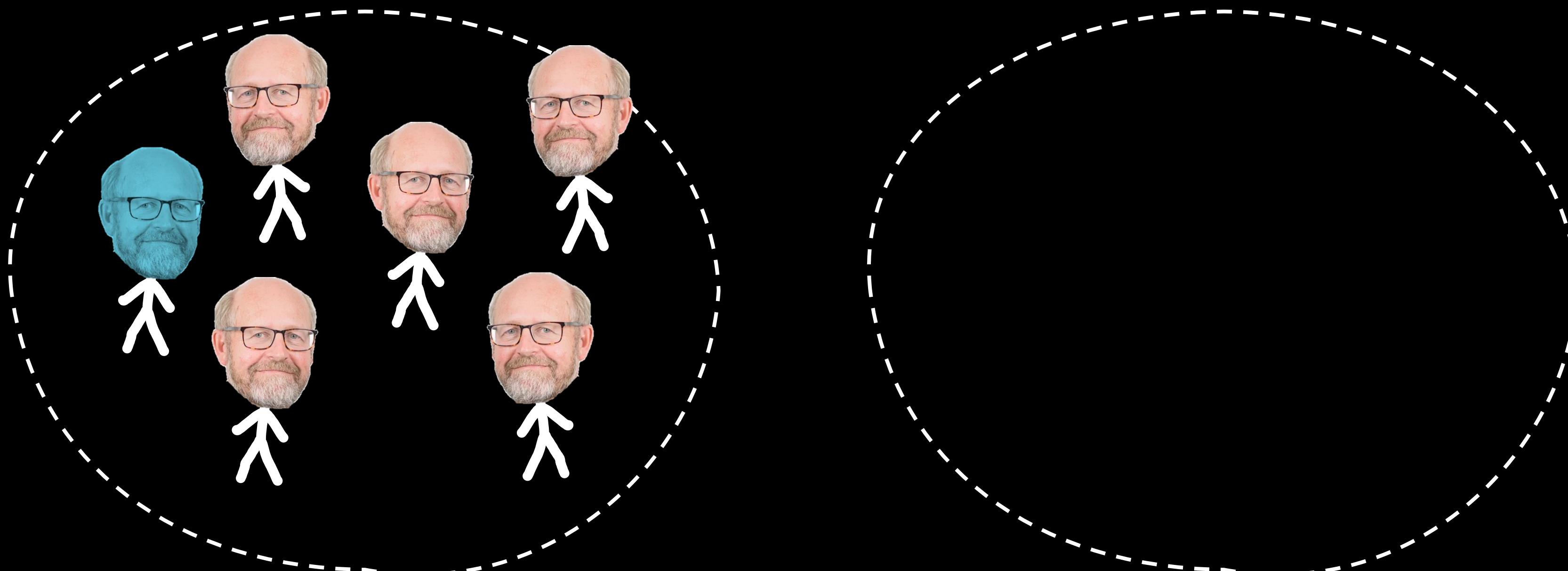
Ecological change

$$N_{t+1} = N_t \lambda$$



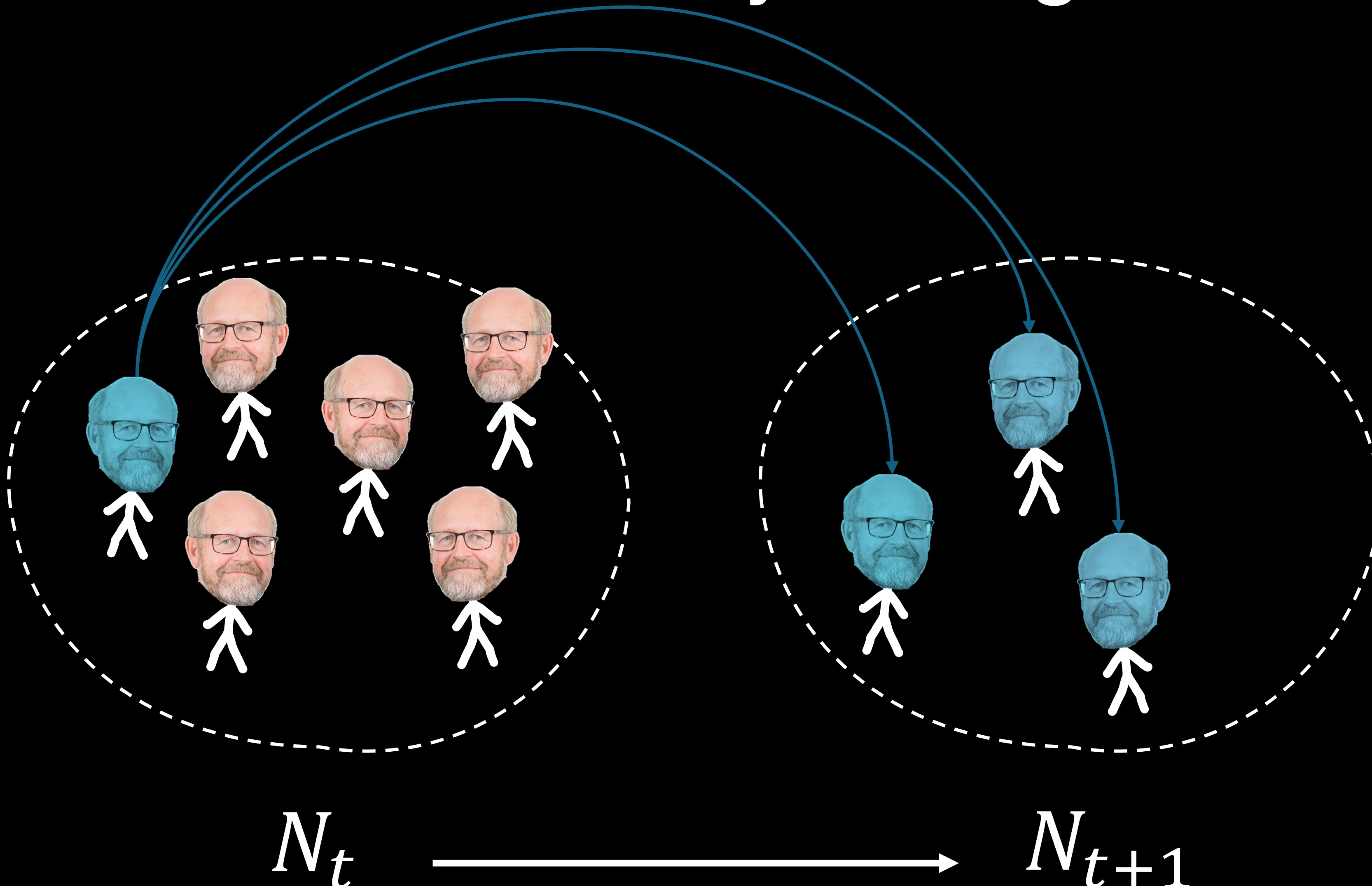
Turchin, P. 2001. “Does Population Ecology Have General Laws?” Oikos 94: 17–26.

Evolutionary change

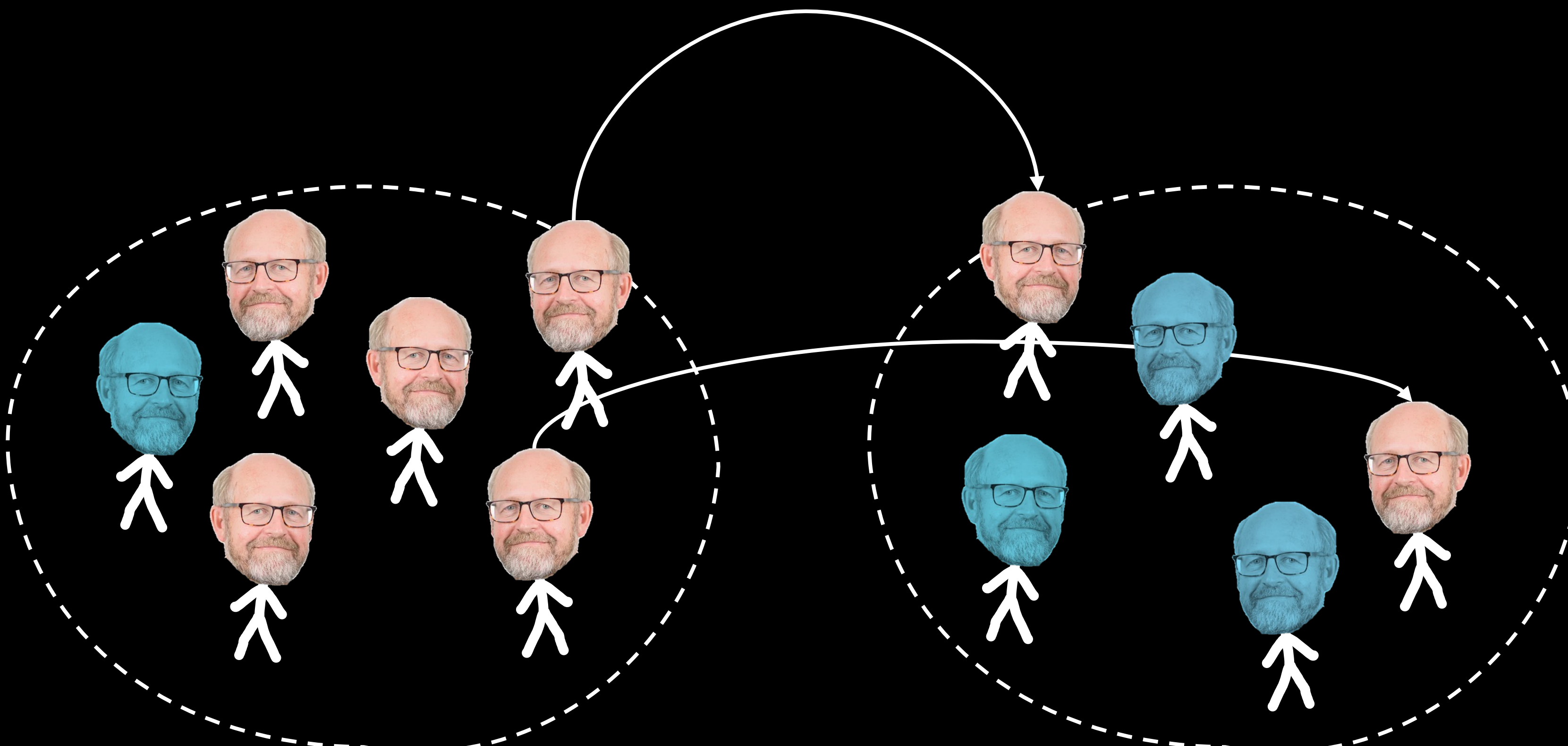


$N_t \longrightarrow N_{t+1}$

Evolutionary change

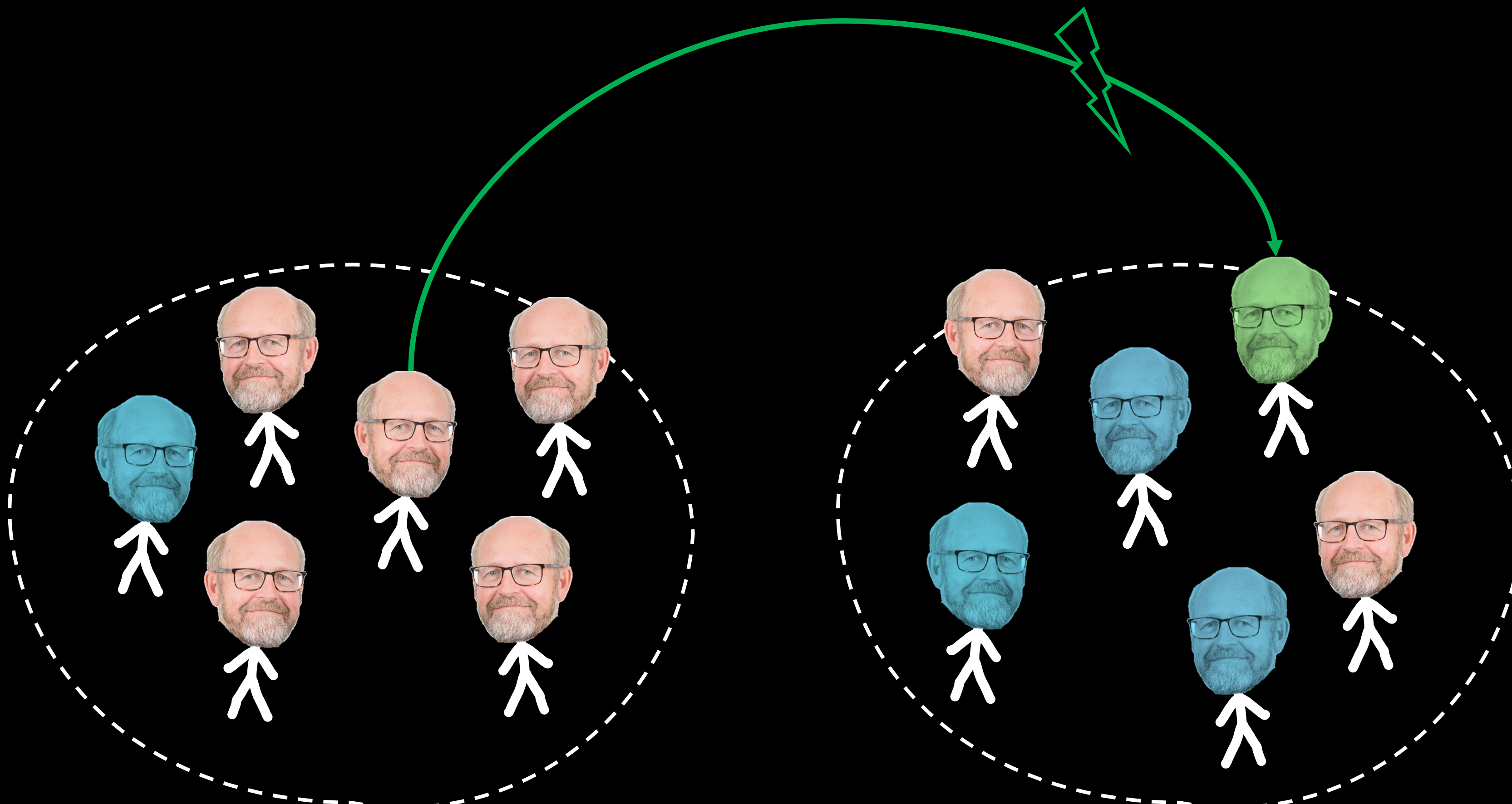


Evolutionary change



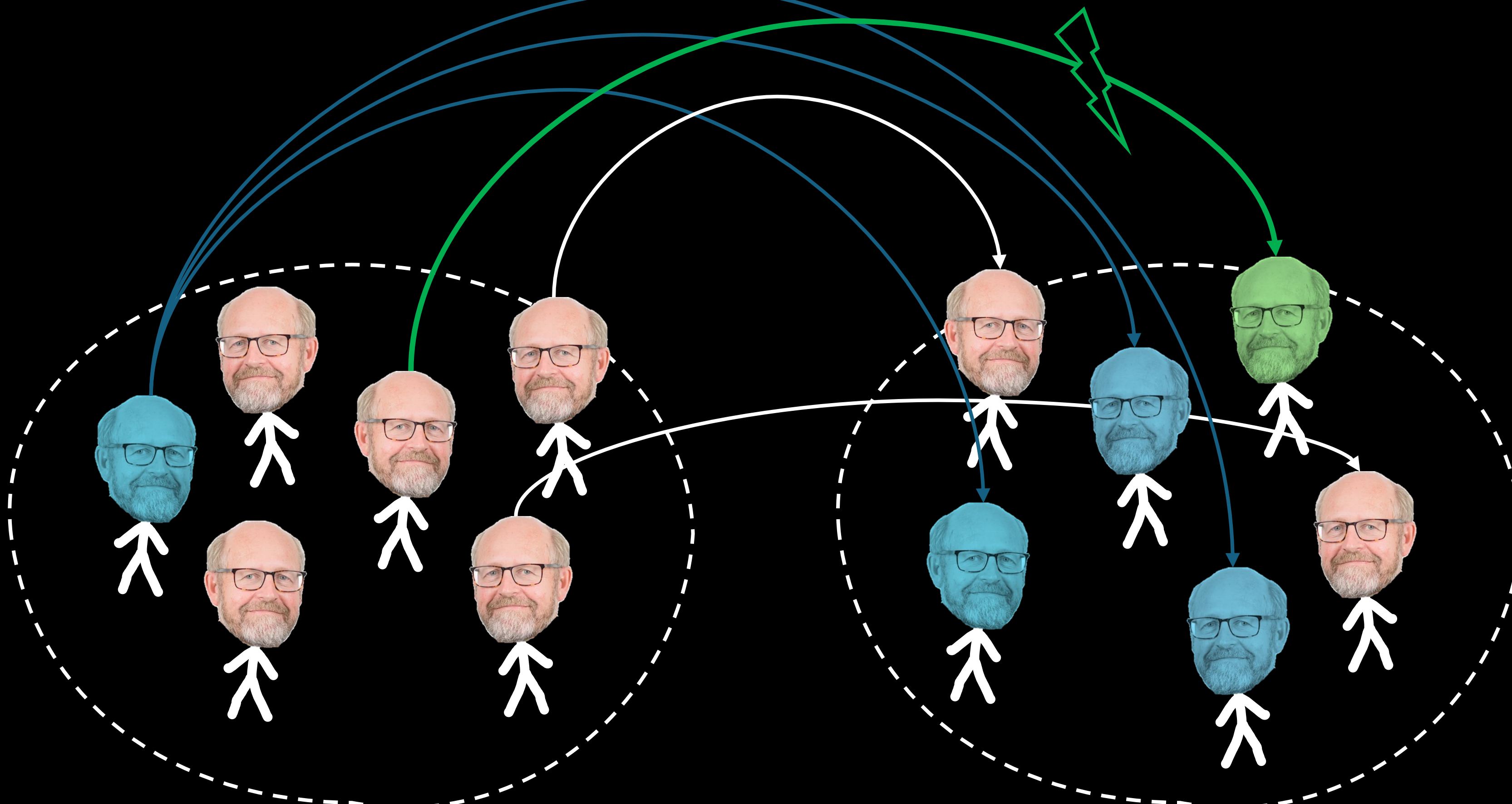
$$N_t \longrightarrow N_{t+1}$$

Evolutionary change



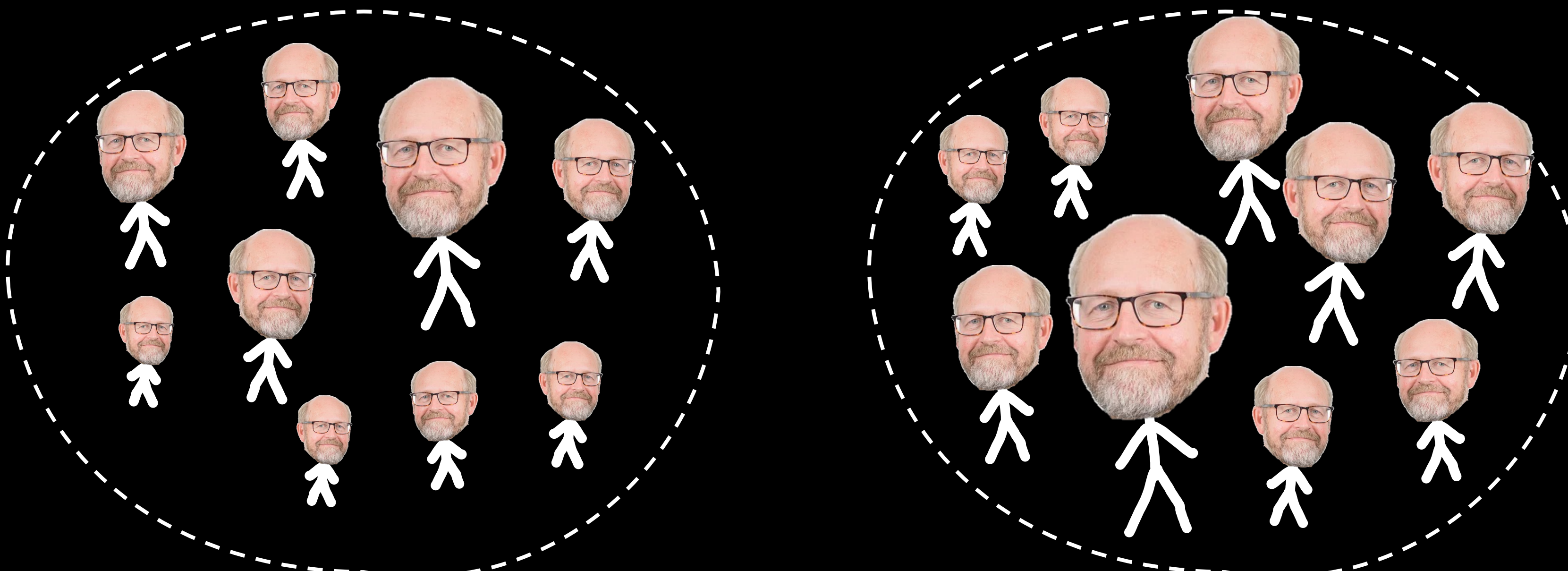
$N_t \longrightarrow N_{t+1}$

Evolutionary change



$N_t \longrightarrow N_{t+1}$

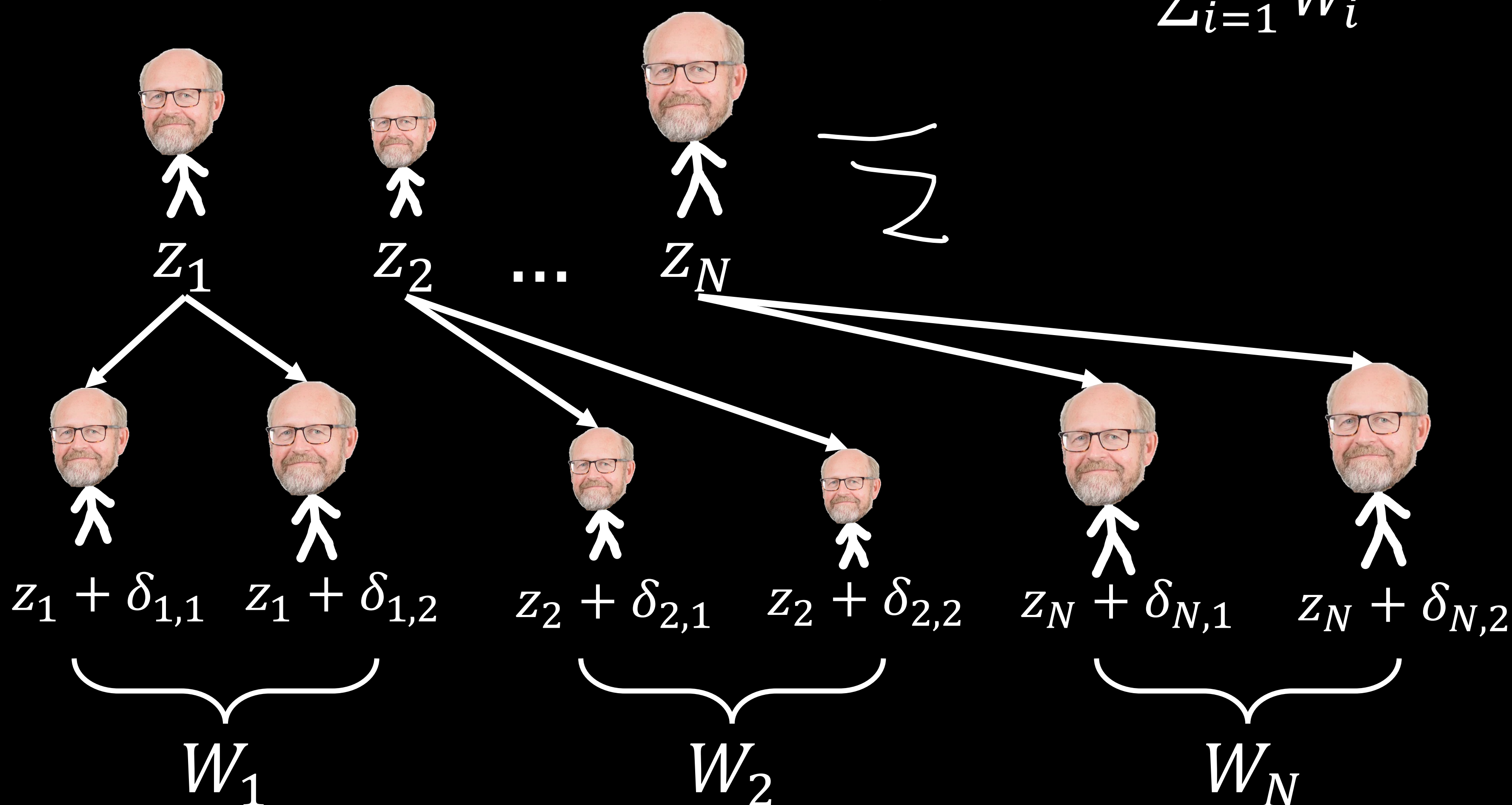
Evolutionary change



$N_t \longrightarrow N_{t+1}$

Trait value of individual i	z_i
Trait deviation from parent *to* offspring	$\delta_{i,j}$
Number of offspring of individual i	W_i
Population size	N

$$\overline{z'} = \frac{\sum_{i=1}^{N} \sum_{j=1}^{W_i} (z_i + \delta_{i,j})}{\sum_{i=1}^{N} W_i}$$



Trait value of individual i	z_i
Trait deviation from parent *to* offspring	$\delta_{i,j}$
Number of offspring of individual i	W_i
Population size	N

$$\overline{z'} = \frac{\sum_{i=1}^{N}\sum_{j=1}^{W_i}(z_i + \delta_{i,j})}{\sum_{i=1}^{N} W_i}$$

$$\sum_{j=1}^{W_i} z_i = W_i z_i$$

$$\sum_{j=1}^{W_i} \delta_{i,j} = W_i \bar{\delta}_i$$

$$\sum_{i=1}^{N} W_i = N\bar{W}$$

$$\overline{z'} = \frac{\sum_{i=1}^{N} W_i z_i + \sum_{i=1}^{N} W_i \bar{\delta}_i}{N\bar{W}}$$

$$\overline{z'} = \frac{1}{N\bar{W}}\left[\sum_{i=1}^{N} W_i z_i + \sum_{i=1}^{N} W_i \bar{\delta}_i\right]$$

$$\overline{z'} = \frac{1}{\bar{W}}\left[E(Wz) + E(W\bar{\delta})\right]$$

$$\overline{z'} = \frac{1}{\bar{W}}\left[cov(W,z) + \bar{W}\bar{z} + E(W\bar{\delta})\right]$$

$$\overline{z'} = \frac{1}{\bar{W}}\left[cov(W,z) + E(W\bar{\delta})\right] + \bar{z}$$

$$\overline{z'} - \bar{z} = \Delta\bar{z} = \frac{1}{\bar{W}}\left[cov(W,z) + E(W\bar{\delta})\right]$$

(Price 1970)

The Price Equation

$$\bar{W}\Delta\bar{z} = cov(W, z) + E(W\bar{\delta})$$

$$\Delta\bar{z} = \frac{cov(W, z)}{\bar{W}} + \frac{E(W\bar{\delta})}{\bar{W}}$$

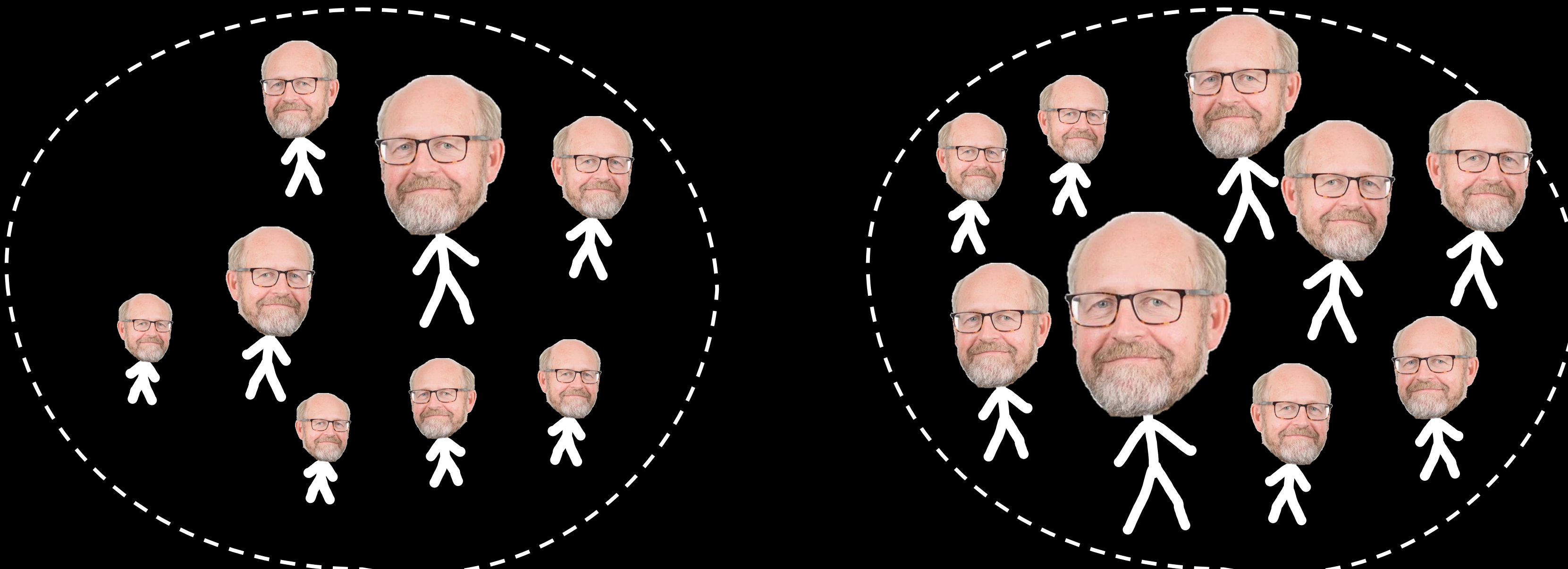
The Price Equation

$$\Delta\bar{z} = \frac{cov(W,z)}{\bar{W}} + \frac{E(W\bar{\delta})}{\bar{W}}$$

- Differential survival and reproduction
- Natural selection
- Genetic drift

The Price Equation

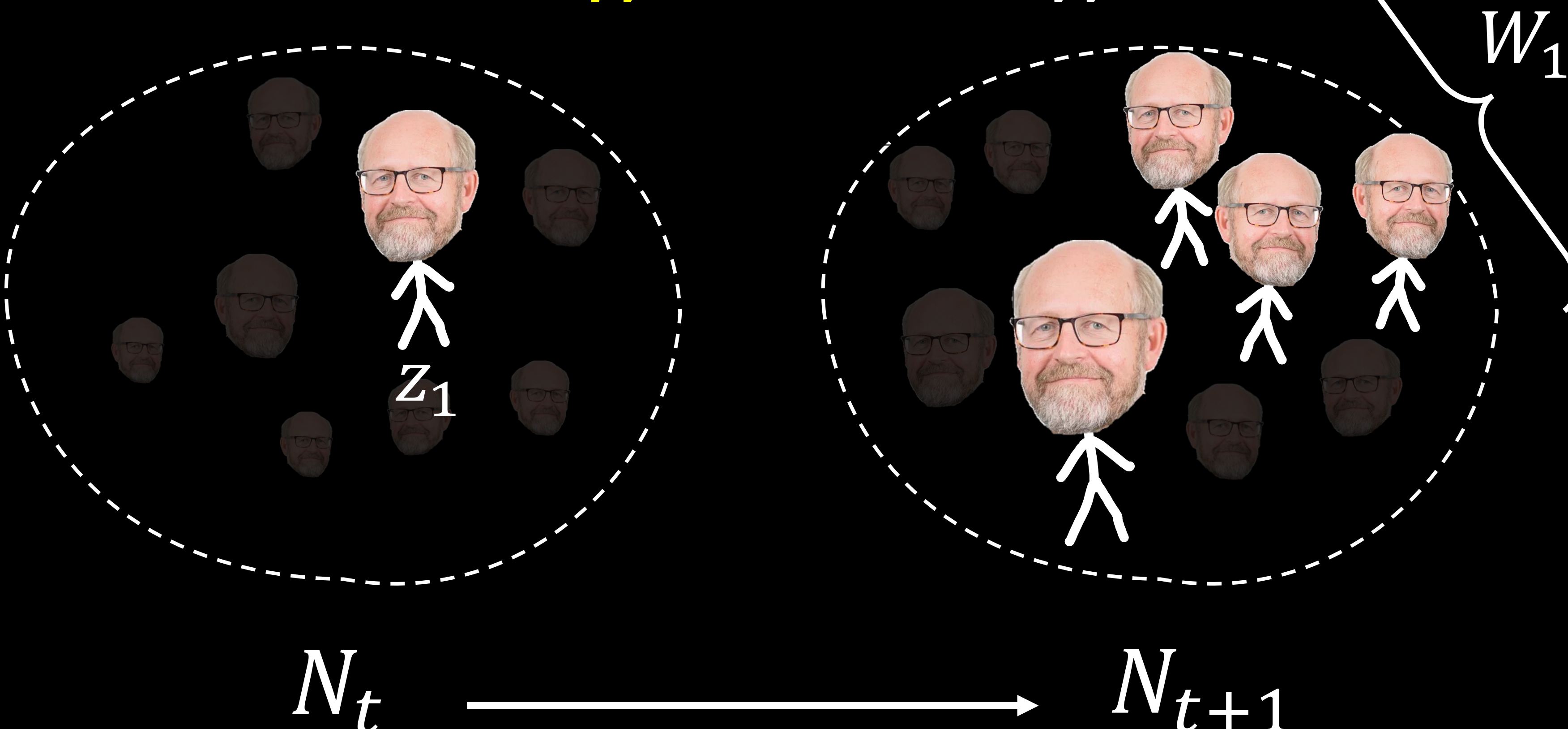
$$\Delta\bar{z} = \frac{cov(W, z)}{\bar{W}} + \frac{E(W\bar{\delta})}{\bar{W}}$$



N_t → N_{t+1}

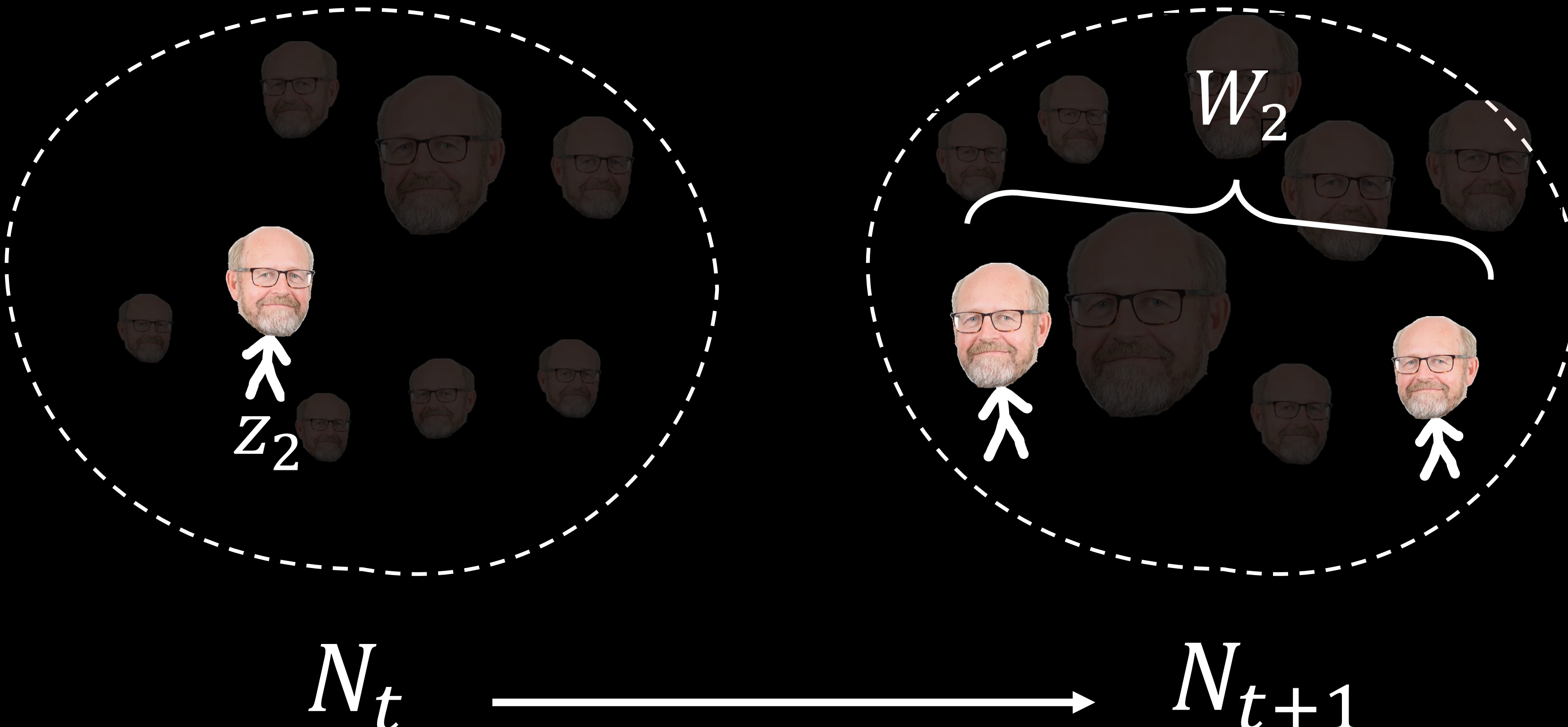
The Price Equation

$$\Delta\bar{z} = \frac{cov(W, z)}{\bar{W}} + \frac{E(W\bar{\delta})}{\bar{W}}$$



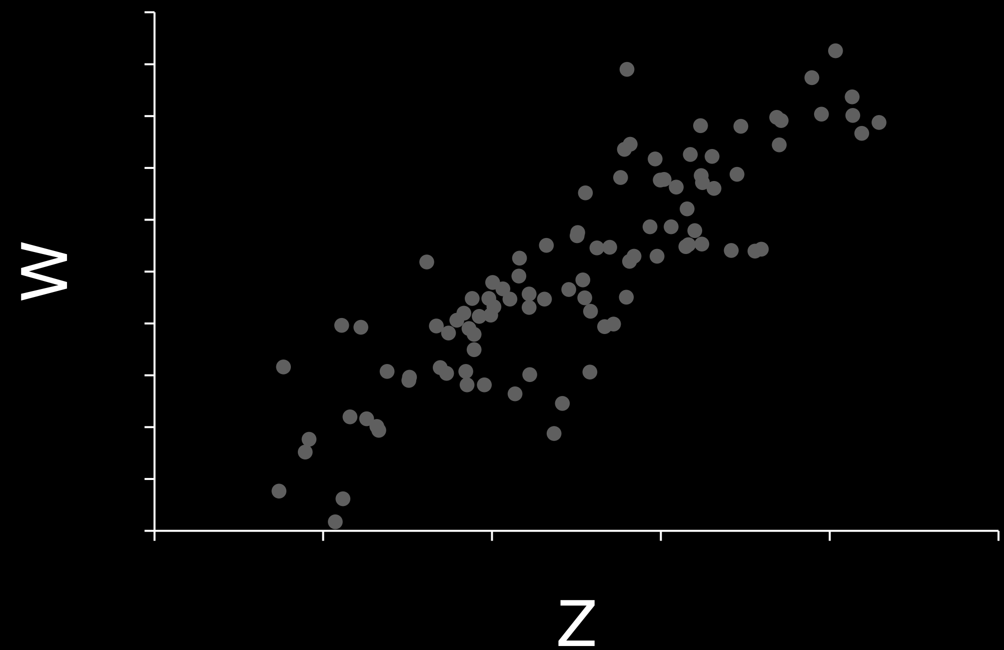
The Price Equation

$$\Delta\bar{z} = \frac{cov(W, z)}{\bar{W}} + \frac{E(W\bar{\delta})}{\bar{W}}$$



The Price Equation

$$\Delta\bar{z} = \frac{cov(W,z)}{\bar{W}} + \frac{E(W\bar{\delta})}{\bar{W}}$$



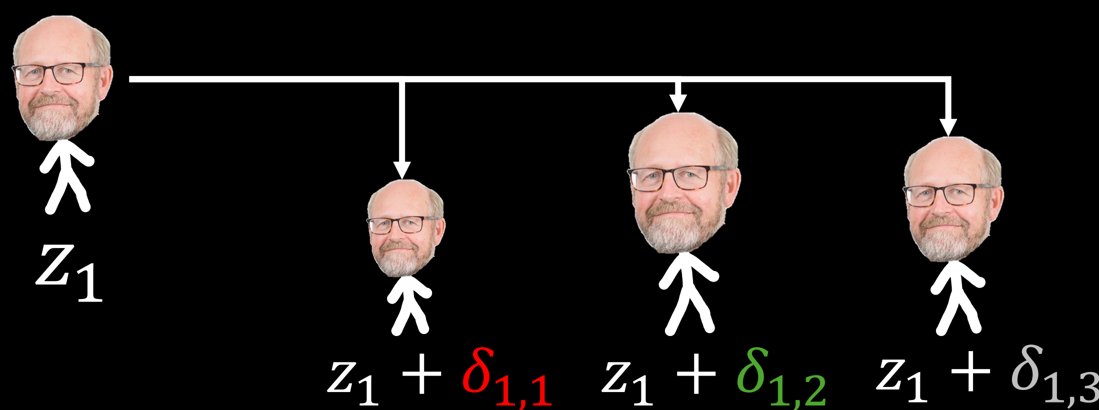
The Price Equation

$$\Delta\bar{z} = \frac{cov(W, z)}{\bar{W}} + \frac{E(W\bar{\delta})}{\bar{W}}$$

- Deviations between parent-offspring (ancestor-descendent) due to transmission
- Mutation, recombination etc
- Other levels of selection (gametic, group)

The Price Equation

$$\Delta\bar{z} = \frac{cov(W, z)}{\bar{W}} + \frac{E(W\bar{\delta})}{\bar{W}}$$



Evolutionary change

$$\bar{W}\Delta\bar{z} = cov(W, z) + E(W\bar{\delta})$$

"In evolutionary biology, the Price equation (Box 1) provides a unifying framework for evolutionary theory by exhaustively and exactly describing evolutionary change for any closed population. The Price equation is therefore fundamental, in the sense that it binds together all of evolutionary theory by formally defining what evolutionary change is and is not."

Duthie & Luque (2025)

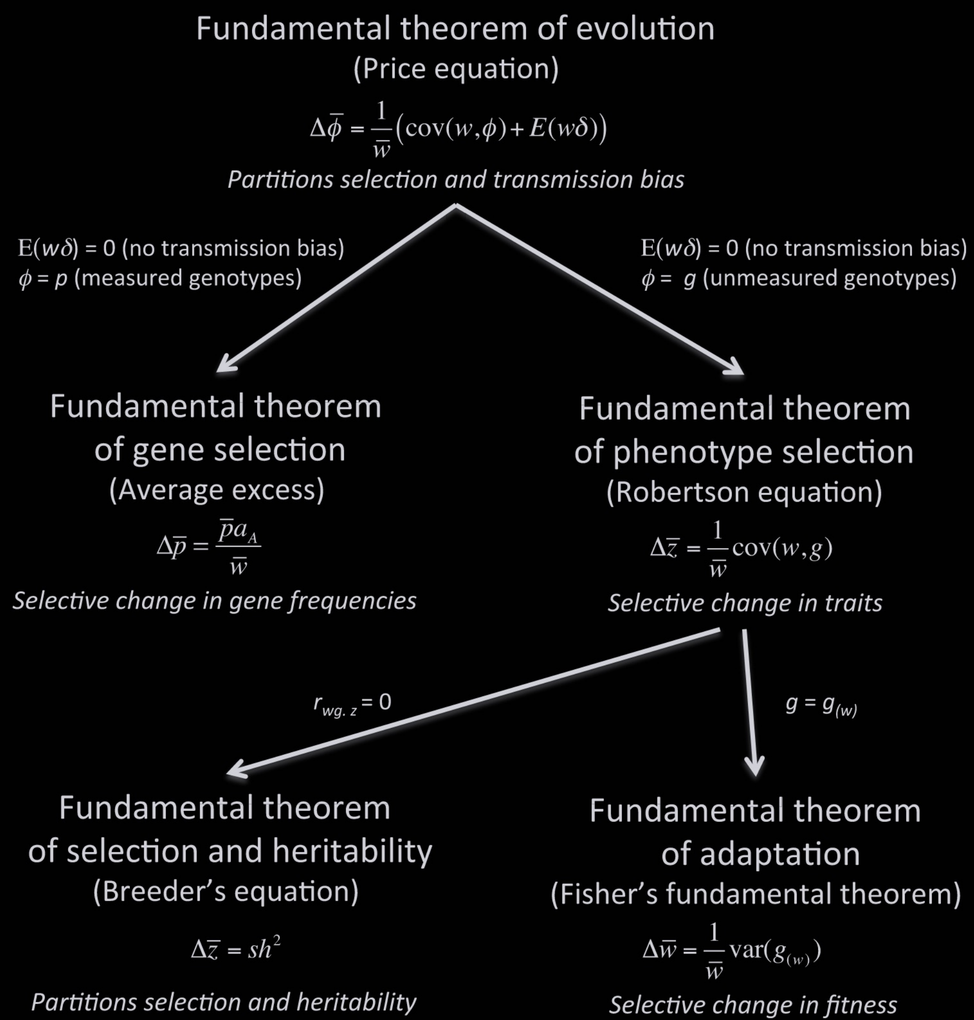


Figure 1: Fundamental theorems and their relationships. Arrows indicate derivation, with required assumptions or domain restrictions written beside them. ϕ = any trait value; δ = the change in ϕ from parent to offspring; w = fitness; p = allele frequency; a_A = average excess; g = breeding value; z = phenotype value; r = partial correlation; s = selection differential, h^2 = heritability. The i subscripts for individuals used in the text are omitted for economy.

Queller (2017)

Evolutionary change

$$\bar{W}\Delta\bar{z} = cov(W, z) + E(W\bar{\delta})$$

Ecological change

$$N_{t+1} = N_t + Births\ - Deaths$$

Eco-evolutionary change

Goal:

- A fundamental model that formally defines eco-evolutionary change
- Must be able to derive both Price Equation and B-D model from it.

Difficulties:

- Price equation deals in relative frequencies, which would prevent recovering exponential growth.

Axioms:

- Diversity is discontinuous.

Duthie & Luque (2025)

Eco-evolutionary change

$$\Omega = \sum_{i=1}^{N} (\beta_i - \delta_i + 1)(z_i + \Delta z_i)$$

Ω	Some summed quantity
N	Population size
i	Individuals in population
β_i	Births attributable to *i*
δ_i	Death indicator variable for *i*
z_i	Character of *i*

Duthie & Luque (2025)

Duthie & Luque (2025)

$z_i = 1$

$\Delta z_i = 0$

Ecological change

$$\Omega = \sum_{i=1}^{N} (\beta_i - \delta_i + 1)(z_i + \Delta z_i)$$

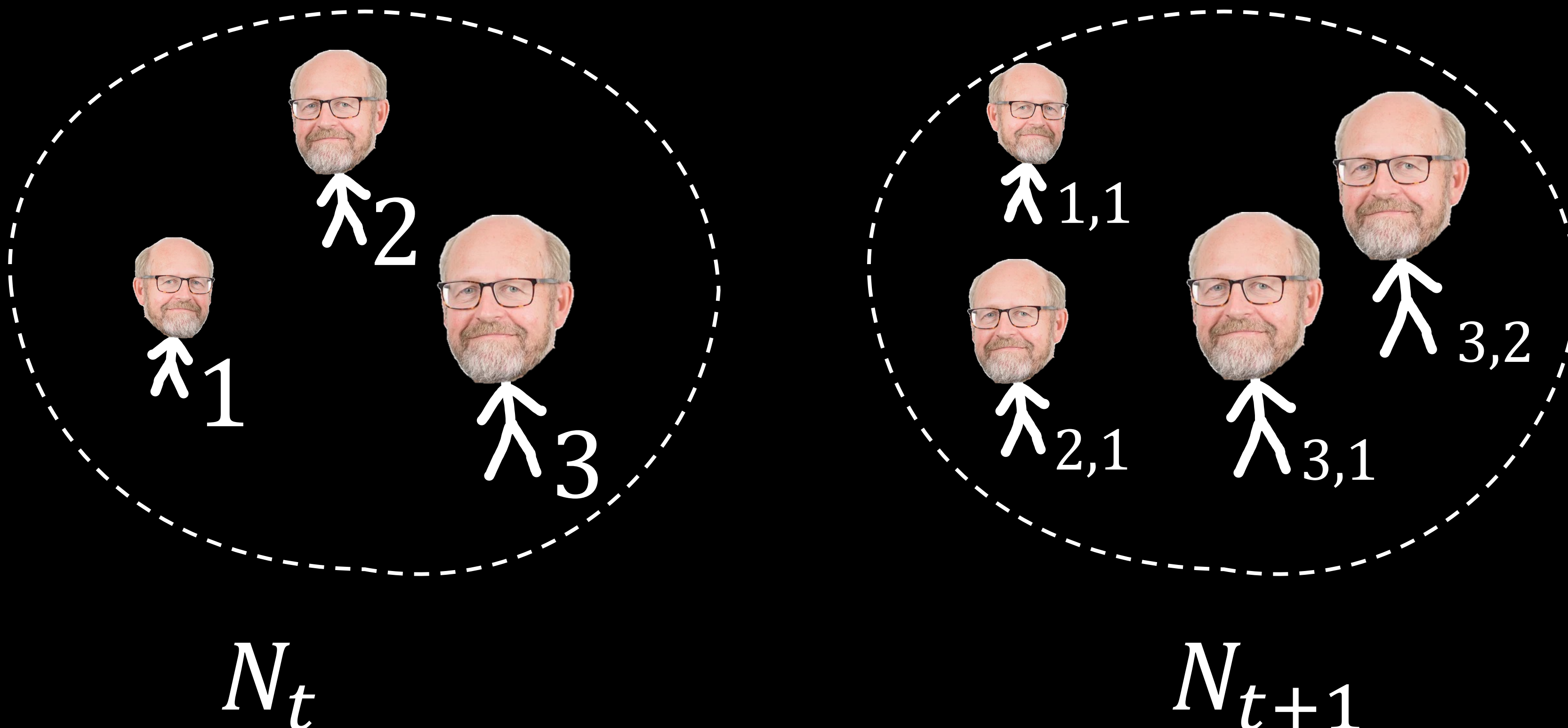
$$\Omega = \sum_{i=1}^{N} (\beta_i - \delta_i + 1)$$

$$N_{t+1} = N_t + Births\ - Deaths$$

Ω	Some summed quantity (in this case, population size at t+1)
N	Population size
i	Individuals in population
β_i	Births attributable to *i*
δ_i	Death indicator variable for *i*
z_i	Character of *i* (in this case, as the identity of i belonging to the population, a count)

Ω Some summed quantity
N Population size
i Individuals in population
β_i Births attributable to Erik *i*
δ_i Death indicator variable for *Erik i (Eriks are annual so = 1)*
z_i Character of Erik *i*

$$\beta_1 = 1$$
$$\beta_2 = 1$$
$$\beta_3 = 2$$



$z_i = 1$

$\Delta z_i = 0$

$N = 3$

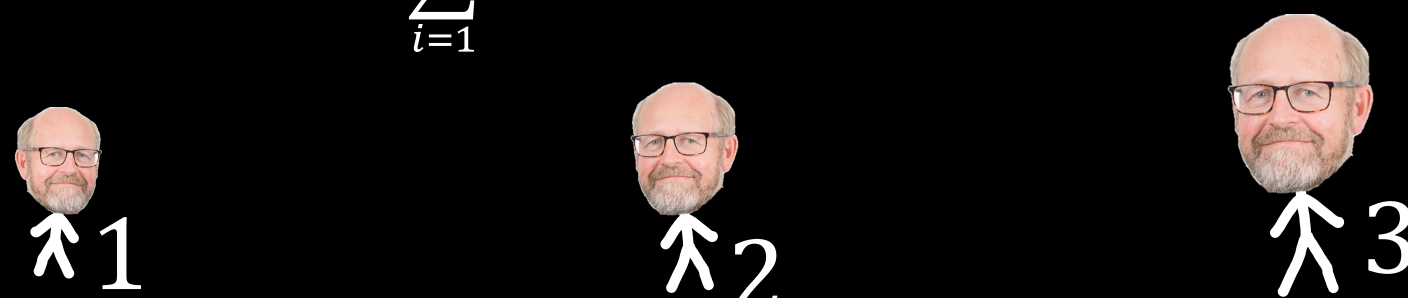
Ecological change

$\beta_1 = 1$

$\beta_2 = 1$

$\beta_3 = 2$

$$\Omega = \sum_{i=1}^{N} (\beta_i - \delta_i + 1)(z_i + \Delta z_i)$$



$$(\beta_1 - \delta_1 + 1)(z_1 + \Delta z_1) + (\beta_2 - \delta_2 + 1)(z_2 + \Delta z_2) + (\beta_3 - \delta_3 + 1)(z_3 + \Delta z_3)$$

$$(1 - 1 + 1)(1 + 0) \quad (1 - 1 + 1)(1 + 0) \quad (2 - 1 + 1)(1 + 0)$$

$$1 \quad 1 \quad 2$$

$$= 4$$

Ω N at t+1

N Population size (at t+1)

i Individuals in population

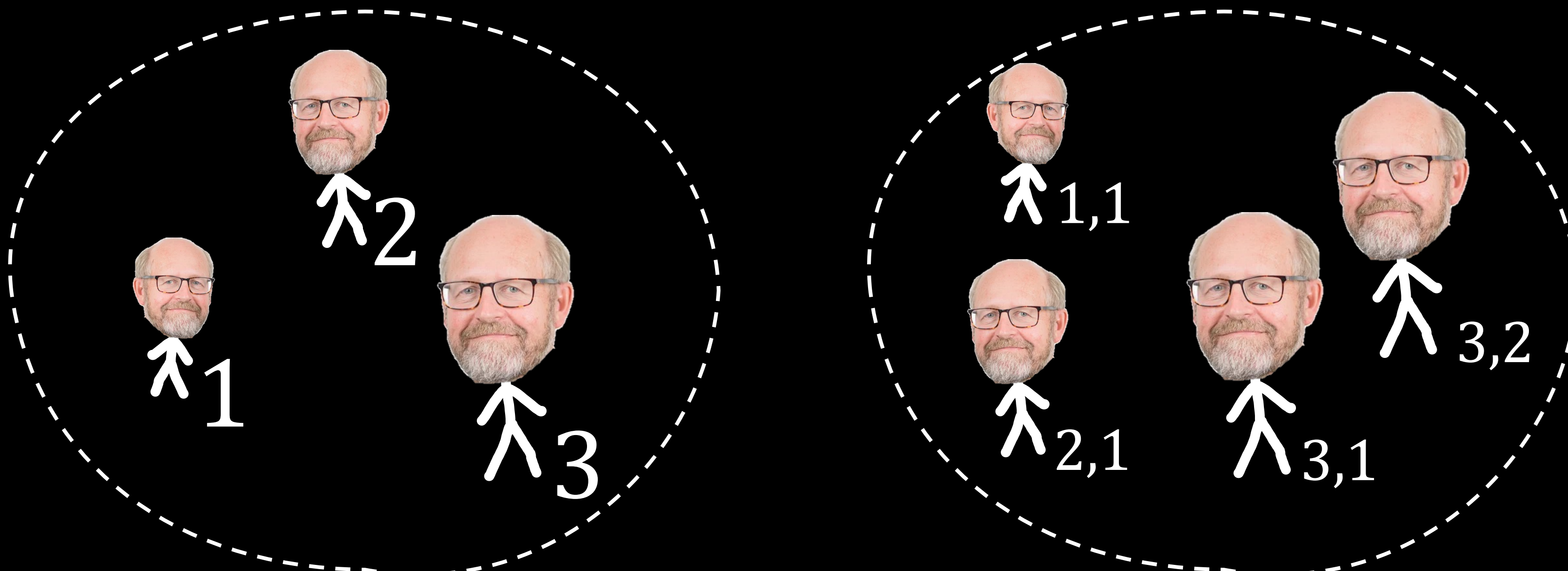
β_i Births attributable to Erik *i*

δ_i Death indicator variable for *Erik i (Eriks are annual so = 1)*

z_i Character identity of Erik (contribution of an Erik to N)

Ω	Some summed quantity
N	Population size
i	Individuals in population
β_i	Births attributable to Erik *i*
δ_i	Death indicator variable for *Erik i (Eriks are annual so = 1)*
z_i	Character of Erik *i*

$$\beta_1 = 1$$
$$\beta_2 = 1$$
$$\beta_3 = 2$$



N_t N_{t+1}

Duthie & Luque (2025)

Evolutionary change

$$W_i = \beta_i - \delta_i + 1$$

$$\Omega = \sum_{i=1}^{N}(\beta_i - \delta_i + 1)(z_i + \Delta z_i)$$

$$\Omega = \sum_{i=1}^{N}(W_i z_i + W_i \Delta z_i)$$

$$\frac{1}{N}\Omega = \frac{1}{N}\sum_{i=1}^{N}(W_i z_i) + \frac{1}{N}\sum_{i=1}^{N}(W_i \Delta z_i)$$

$$\frac{1}{N}\Omega = E(Wz) + E(W\Delta z)$$

Ω	Some summed quantity (trait values)
N	Population size
i	Individuals in population
β_i	Births attributable to *i*
δ_i	Death indicator variable for *i*
z_i	Character of *I (trait)*
W_i	Fitness of *i*

Duthie & Luque (2025)

Evolutionary change

(read paper)

$$\Omega = N\bar{W}\overline{z'}$$

$$\frac{1}{N}\Omega = E(Wz) + E(W\Delta z)$$

$$\bar{W}\overline{z'} = E(Wz) + E(W\Delta z)$$

$$\bar{W}\overline{z'} = Cov(W,z) + \bar{W}\bar{z} + E(W\Delta z)$$

$$\bar{W}(\overline{z'} - \bar{z}) = Cov(W,z) + E(W\Delta z)$$

Ω Some summed quantity (the total sum trait values (zi) across the entire population at t + 1)

N Population size (at time t)

i Individuals in population

β_i Births attributable to *i*

δ_i Death indicator variable for *i*

z_i Character of *I (trait)*

W_i Fitness of *i*

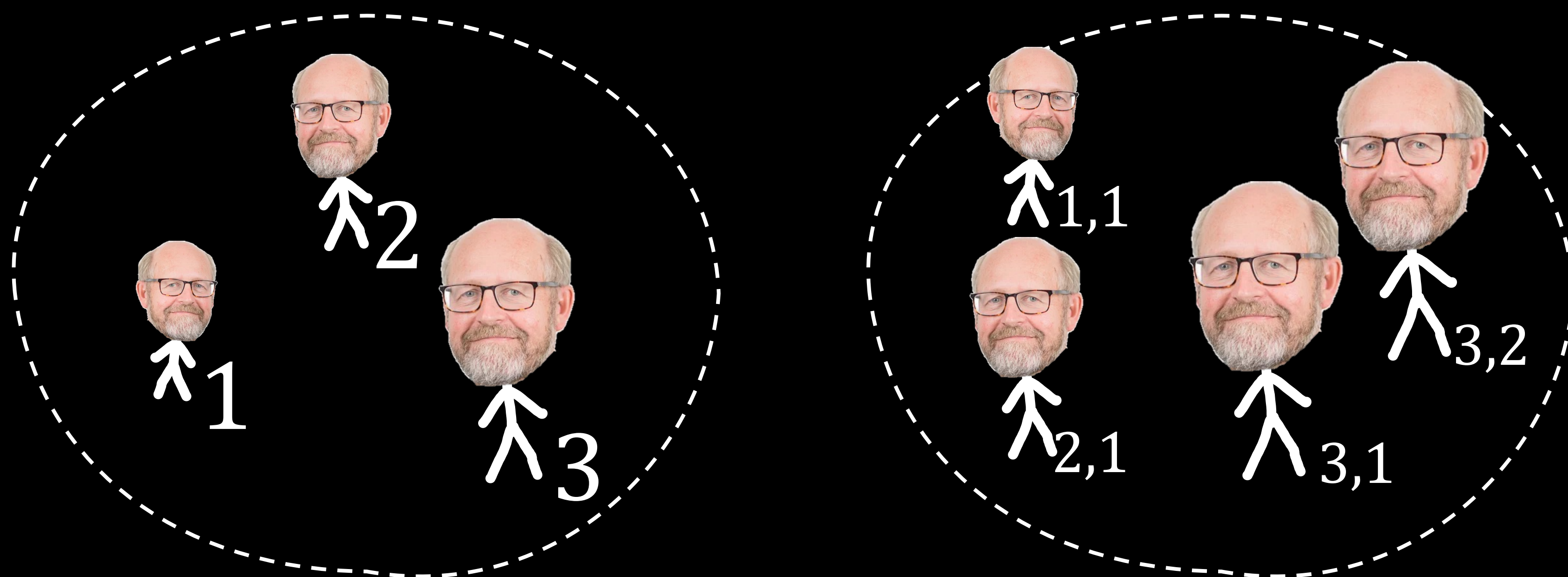
Ω	Some summed quantity
N	Population size
i	Individuals in population
β_i	Births attributable to Erik *i*
δ_i	Death indicator variable for *Erik i (Eriks are annual so = 1)*
z_i	Height of Erik *i*

$\beta_1 = 1 \qquad z_1 = 0.8\, m$

$\beta_2 = 1 \qquad z_2 = 1.0\, m$

$\beta_3 = 2 \qquad z_3 = 1.5\, m$

$\Delta z = 0.1\, m$



$N_t \qquad N_{t+1}$

$z_1 = 0.8\ m$
$z_2 = 1.0\ m$
$z_3 = 1.5\ m$

Evolutionary change

$\beta_1 = 1$
$\beta_2 = 1$
$\beta_3 = 2$

$\Delta z = 0.1\ m$

$$\Omega = \sum_{i=1}^{N} (\beta_i - \delta_i + 1)(z_i + \Delta z_i)$$


1


2


3

$$(\beta_1 - \delta_1 + 1)(z_1 + \Delta z_1) + (\beta_2 - \delta_2 + 1)(z_2 + \Delta z_2) + (\beta_3 - \delta_3 + 1)(z_3 + \Delta z_3)$$

$(1 - 1 + 1)(0.8 + 0.1)$ $(1 - 1 + 1)(1 + 0.1)$ $(2 - 1 + 1)(1.5 + 0.1)$

$0.9\ m$ $1.1\ m$ $3.2\ m$

$= 5.2\ m$

$\bar{z'} = 5.2/4\ \ m$

$\bar{z} = 3.3/3\ \ m$

Ω Population total height (summed heights at t+1)
N Population size (at t+1)
i Individuals in population
β_i Births attributable to Erik *i*
δ_i Death indicator variable for *Erik i (Eriks are annual so = 1)*
z_i Height of Erik i

$$\overline{z'} = 5.2/4 \ \ m$$

$$\bar{z} = \frac{3.3}{3} = 1.1 \ \ m$$

$$cov(z,W) = \frac{1}{N}\sum_{i=1}^{N}(z_i - \bar{z})(W_i - \bar{W})$$

$$z_1 = 0.8\ m$$
$$z_2 = 1.0\ m$$
$$z_3 = 1.5\ m$$

$$cov(z,W) = \frac{1}{3}\left[(0.8 - 1.1)\left(1 - \frac{4}{3}\right) + \cdots\right]$$

$$cov(z,W) = 2/15$$

$$\Delta \bar{z} =$$

$$E(W\Delta z) = \frac{4}{3}\times 0.1 = 2/15$$

Duthie & Luque (2025)

Some other points

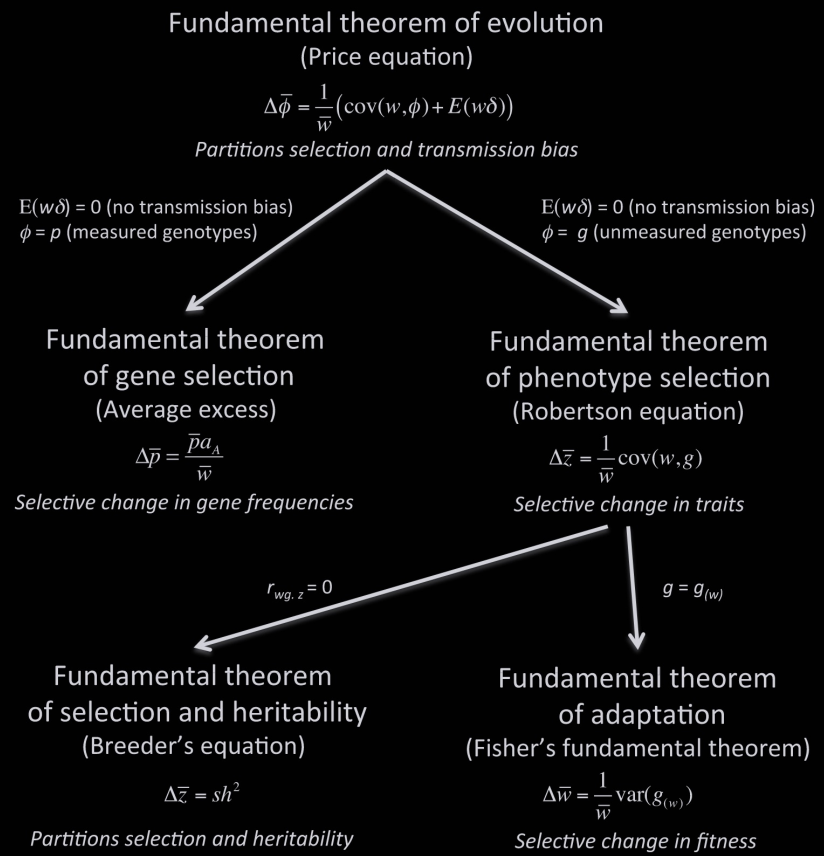


Figure 1: Fundamental theorems and their relationships. Arrows indicate derivation, with required assumptions or domain restrictions written beside them. ϕ = any trait value; δ = the change in ϕ from parent to offspring; w = fitness; p = allele frequency; a_A = average excess; g = breeding value; z = phenotype value; r = partial correlation; s = selection differential, h^2 = heritability. The i subscripts for individuals used in the text are omitted for economy.

The covariance thing

$$cov(x,y) = \frac{1}{N}\sum_{i=1}^{N}(x_i - \bar{x})(y_i - \bar{y})$$

$$cov(x,y) = \frac{1}{N}\sum_{i=1}^{N} x_i y_i - \bar{x}\bar{y}$$

$$cov(x,y) = E(xy) - \bar{x}\bar{y}$$

$$cov(x,y) + \bar{x}\bar{y} = E(xy)$$

*Go look on wikipedia