An Introduction to the Price Equation with Application to the Evolution of Multicellularity

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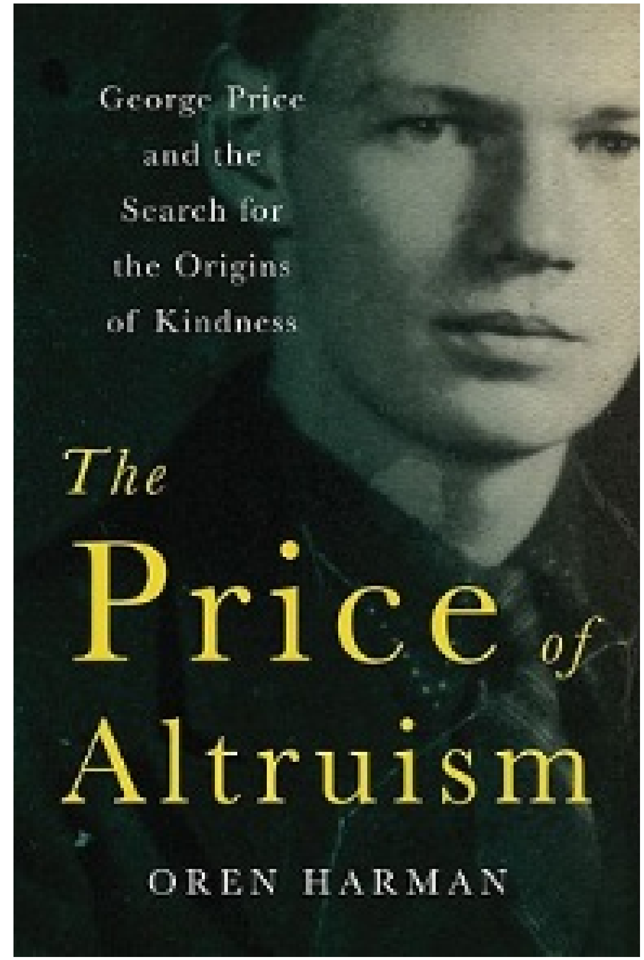
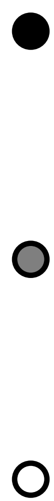
A little background

- George Price (1922-1975)
- American, moved to London in 1967. Galton Laboratory
- Collaborated with W.D. Hamilton and J. Maynard Smith
- 1970. Selection and Covariance. Nature 277: 520-521.
- 1972. Extension of covariance selection mathematics. Ann. Hum. Genet. Lond. 35:485-490.



Time 0



Time 0

i	z_i	q_i
1	1	1/3
2	0.5	1/3
3	0	1/3

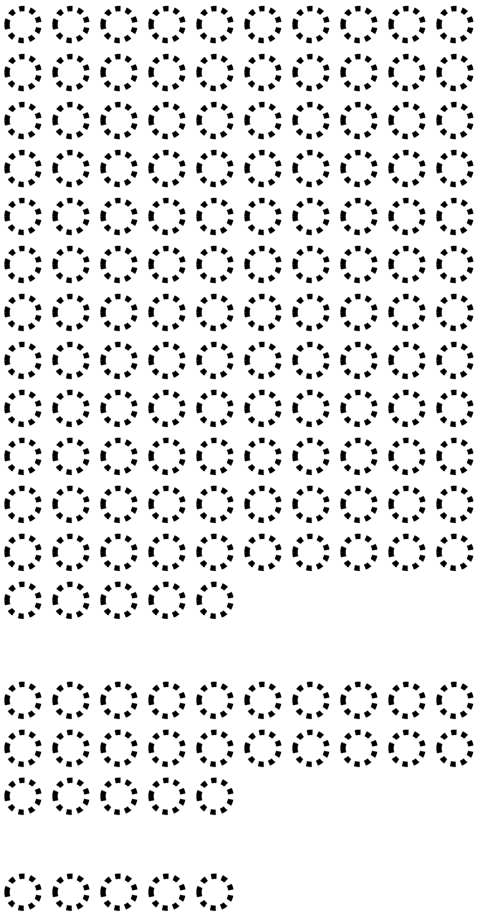
$$\bar{z} = \sum_{i=1}^{N} q_i z_i$$

Time 0

i	z_i	q_i
1	1	1/3
2	0.5	1/3
3	0	1/3

$$\bar{z} = \sum_{i=1}^{N} q_i z_i$$

Time 1



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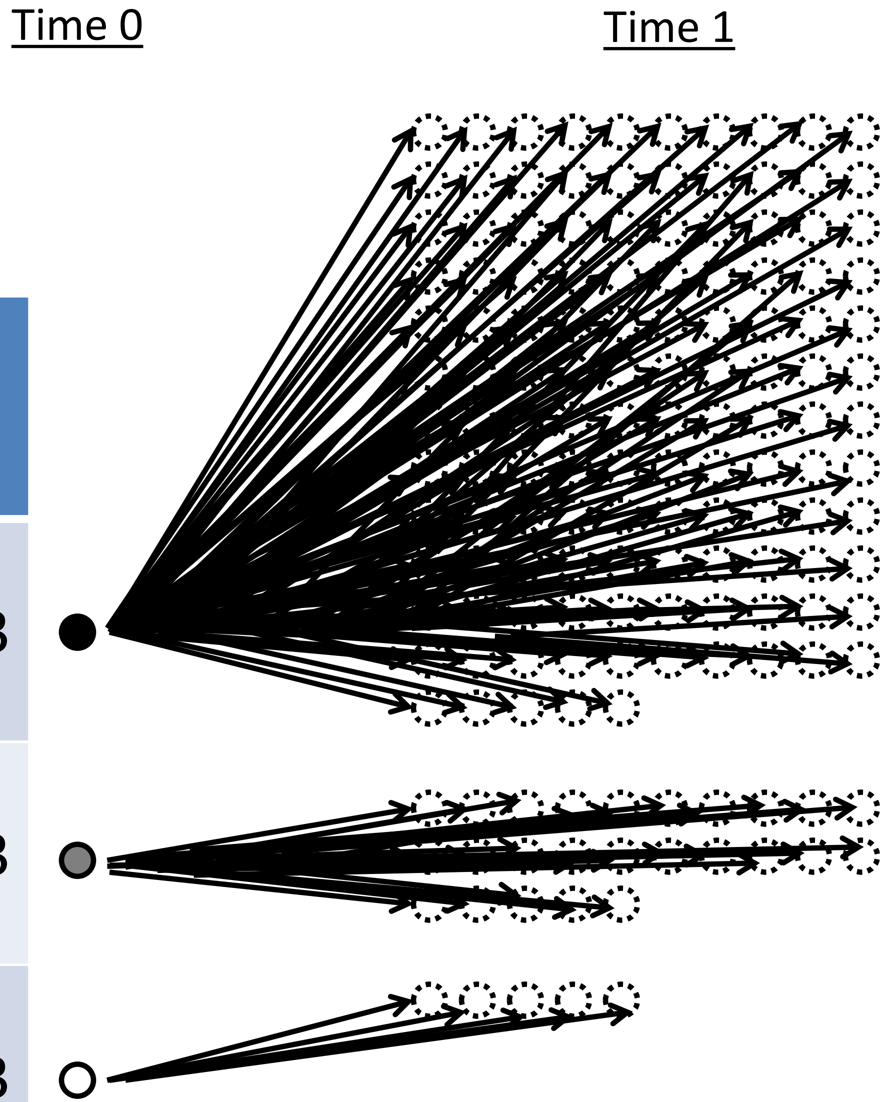
1	1	1/3
2	0.5	1/3
3	0	1/3



$$\bar{z} = \sum_{i=1}^{N} q_i z_i$$

Time 0

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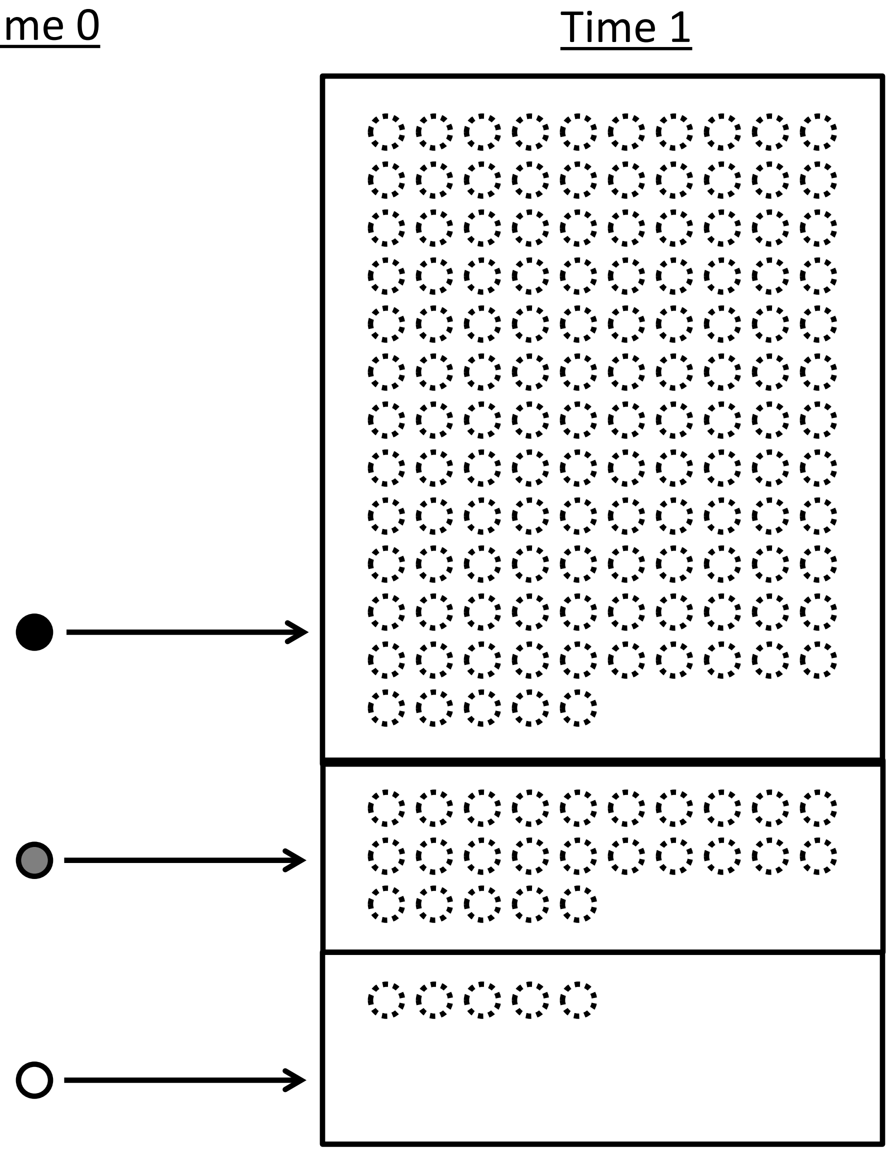


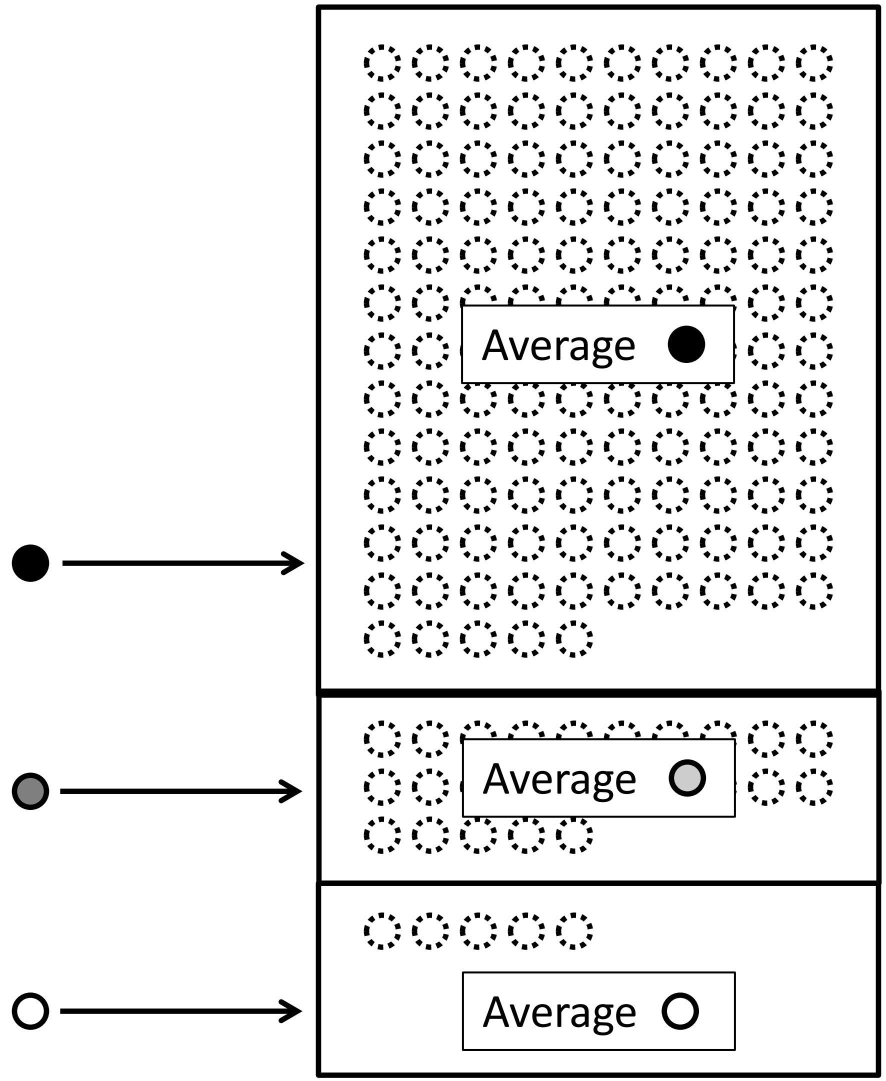
i		q_i'
1		125/155
2		25/155
3		5/155

Time 0

i	z_i	q_i
1	1	1/3
2	0.5	1/3
3	0	1/3

$$\bar{z} = \sum_{i=1}^{N} q_i z_i$$

Time 1



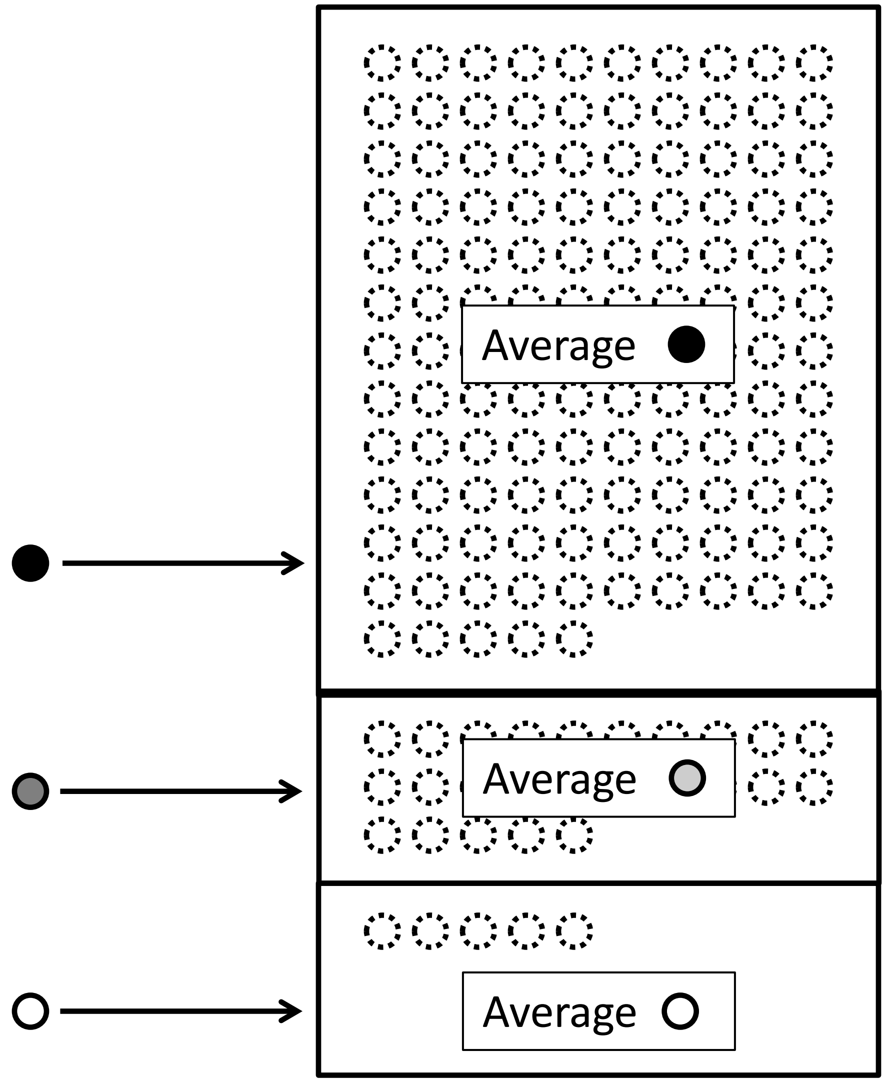
i	z_i'	q_i'
1	1	125/155
2	0.2	25/155
3	0	5/155

Time 0

i	z_i	q_i
1	1	1/3
2	0.5	1/3
3	0	1/3

$$\bar{z} = \sum_{i=1}^{N} q_i z_i$$

Time 1



i	z_i'	q_i'
1	1	125/155
2	0.2	25/155
3	0	5/155

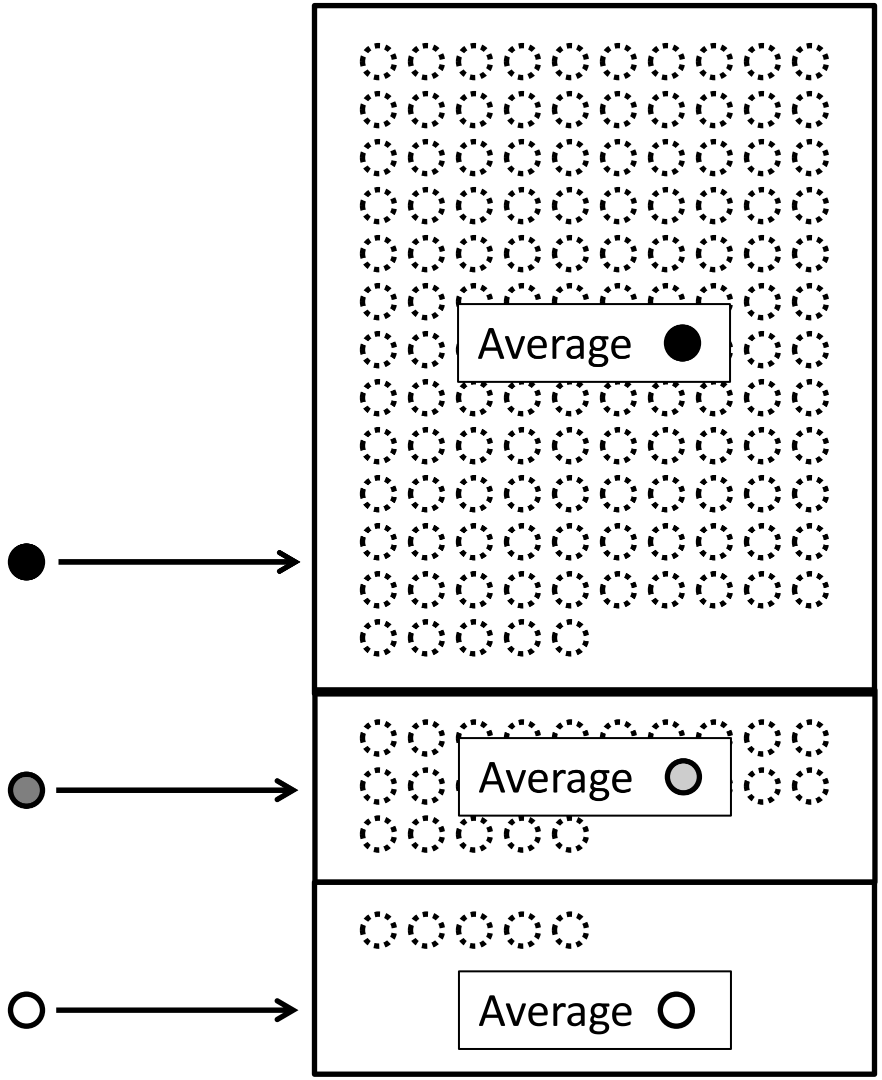
$$\bar{z}' = \sum_{i=1}^{N} q_i' z_i'$$

Time 0

i	z_i	q_i
1	1	1/3
2	0.5	1/3
3	0	1/3

$$\bar{z} = \sum_{i=1}^{N} q_i z_i$$

Time 1



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

$$\Delta\bar{z} \approx 0.839 - 0.5 = 0.339$$

i	z_i'	q_i'
1	1	125/155
2	0.2	25/155
3	0	5/155

$$\bar{z}' = \sum_{i=1}^{N} q_i' z_i'$$

z_i	Trait value for *i*-type individuals in ancestor population
$z_i^{'}$	Average trait value in descendants of *i*-type individuals
q_i	Frequency of *i*-type individuals in ancestor population
$q_i^{'}$	Frequency of descendants of *i*-type individuals in descendant population
Δq_i	$q_i^{'} - q_i$
Δz_i	$z_i^{'} - z_i$

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

$$= \sum_{i=1}^{N} q_i' z_i' - \sum_{i=1}^{N} q_i z_i$$

z_i	Trait value for *i*-type individuals in ancestor population
z_i'	Average trait value in descendants of *i*-type individuals
q_i	Frequency of *i*-type individuals in ancestor population
q_i'	Frequency of descendants of *i*-type individuals in descendant population
Δq_i	$q_i' - q_i$
Δz_i	$z_i' - z_i$

$$\Delta\bar{z} = \bar{z}' - \bar{z}$$
$$= \sum_{i=1}^{N} q_i^{'} z_i^{'} - \sum_{i=1}^{N} q_i z_i$$
$$= \sum_{i=1}^{N} q_i^{'} z_i^{'} - \sum_{i=1}^{N} q_i^{'} z_i + \sum_{i=1}^{N} q_i^{'} z_i - \sum_{i=1}^{N} q_i z_i$$

z_i	Trait value for *i*-type individuals in ancestor population
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Δq_i	$q_i^{'} - q_i$
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$$\Delta\bar{z} = \bar{z}' - \bar{z}$$

$$= \sum_{i=1}^{N} q_i^{'} z_i^{'} - \sum_{i=1}^{N} q_i z_i$$

$$= \sum_{i=1}^{N} q_i^{'} z_i^{'} - \sum_{i=1}^{N} q_i^{'} z_i + \sum_{i=1}^{N} q_i^{'} z_i - \sum_{i=1}^{N} q_i z_i$$

$$= \sum_{i=1}^{N} q_i^{'} (z_i^{'} - z_i) + \sum_{i=1}^{N} z_i (q_i^{'} - q_i)$$

z_i	Trait value for *i*-type individuals in ancestor population
$z_i^{'}$	Average trait value in descendants of *i*-type individuals
q_i	Frequency of *i*-type individuals in ancestor population
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Δq_i	$q_i^{'} - q_i$
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$$\Delta\bar{z} = \bar{z}' - \bar{z}$$

$$= \sum_{i=1}^{N} q_i^{'} z_i^{'} - \sum_{i=1}^{N} q_i z_i$$

$$= \sum_{i=1}^{N} q_i^{'} z_i^{'} - \sum_{i=1}^{N} q_i^{'} z_i + \sum_{i=1}^{N} q_i^{'} z_i - \sum_{i=1}^{N} q_i z_i$$

$$= \sum_{i=1}^{N} q_i^{'} (z_i^{'} - z_i) + \sum_{i=1}^{N} z_i (q_i^{'} - q_i)$$

$$= \sum_{i=1}^{N} q_i^{'} (\Delta z_i) + \sum_{i=1}^{N} (\Delta q_i) z_i$$

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

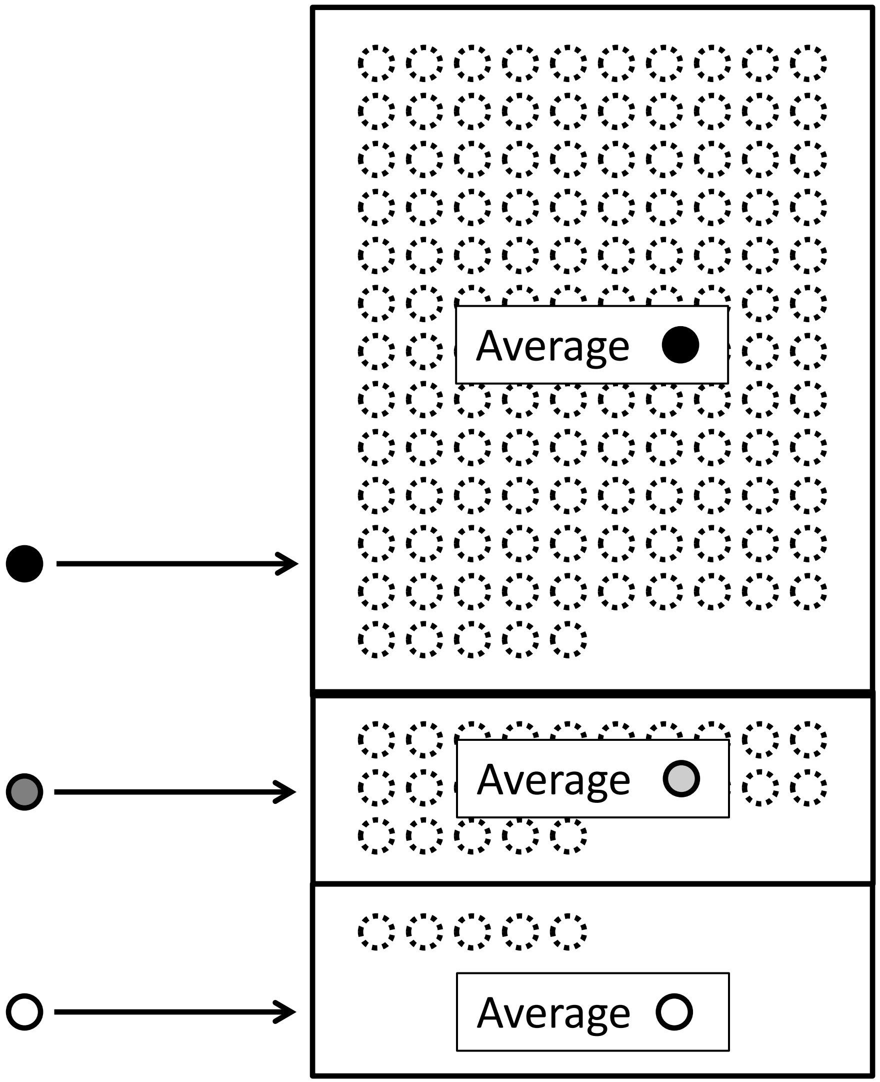
$$= \sum_{i=1}^{N} q_i^{'} z_i^{'} - \sum_{i=1}^{N} q_i z_i$$

$$= \sum_{i=1}^{N} q_i^{'} z_i^{'} - \sum_{i=1}^{N} q_i^{'} z_i + \sum_{i=1}^{N} q_i^{'} z_i - \sum_{i=1}^{N} q_i z_i$$

$$= \sum_{i=1}^{N} q_i^{'} (z_i^{'} - z_i) + \sum_{i=1}^{N} z_i (q_i^{'} - q_i)$$

$$= \sum_{i=1}^{N} q_i^{'} (\Delta z_i) + \sum_{i=1}^{N} (\Delta q_i) z_i$$

$$\boxed{\Delta\bar{z} = \sum_{i=1}^{N} (\Delta q_i) z_i + \sum_{i=1}^{N} q_i^{'} (\Delta z_i)}$$


Average
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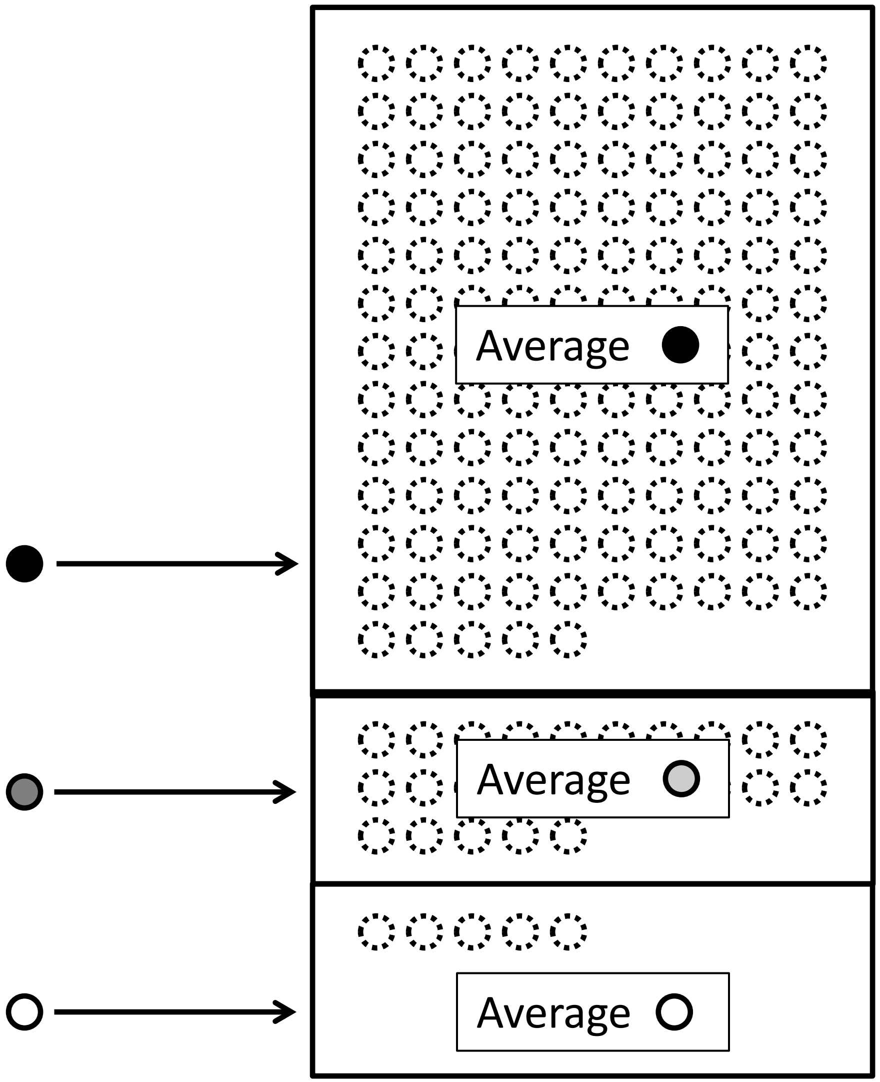


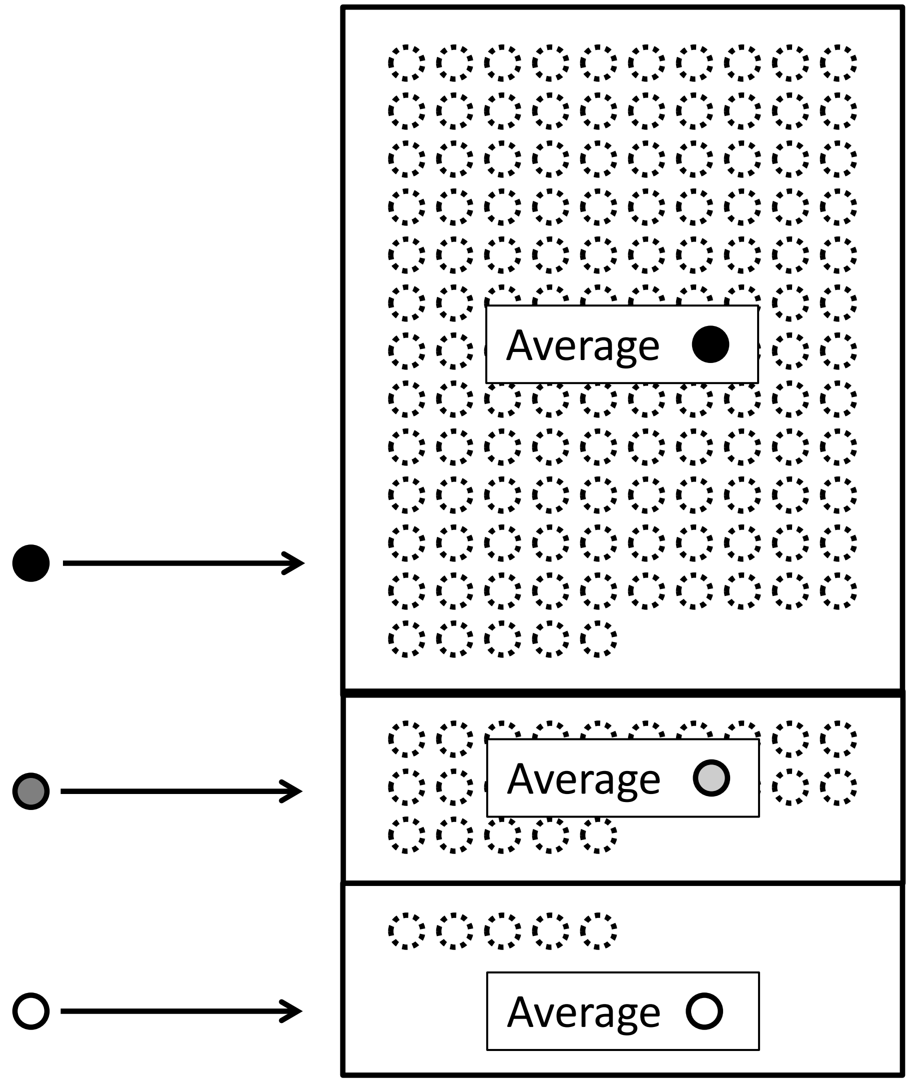
$$\Delta\bar{z} = \sum_{i=1}^{N}(\Delta q_i)z_i + \sum_{i=1}^{N} q_i^{'}(\Delta z_i)$$

$$\Delta\bar{z} = 0.387 - 0.048 = 0.339$$

i	$(\Delta q_i)z_i$	$q_i^{'}(\Delta z_i)$	
1	(0.473)*1 = 0.473	(0.806)*0 = 0	
2	(-0.172)*0.5 = -0.086	(0.161)*-0.3 = -0.048	
3	(-0.301)*0 = 0	(0.032)*0 = 0	
	0.387	-0.048	

Time 0

i	z_i	q_i	w_i
1	1	1/3	125
2	0.5	1/3	25
3	0	1/3	5



Time 1

i	z_i'
1	1
2	0.2
3	0

$$q_i^{'} = \frac{m_i w_i}{\sum_{i=1}^{N} m_i w_i}$$

$$q_i^{'} = \frac{\frac{m_i}{M} w_i}{\sum_{i=1}^{N} \frac{m_i}{M} w_i}$$

$$q_i^{'} = \frac{q_i w_i}{\sum_{i=1}^{N} q_i w_i}$$

$$\boxed{q_i^{'} = q_i \left(\frac{w_i}{\overline{w}}\right)}$$

m_i	Number of *i*-type individuals in ancestor population
M	The total number of individuals in the ancestor population ($\sum_{i=1}^{N} m_i$)
N	Total number of types in ancestor population
w_i	Number of offspring (absolute fitness) of the *i*-type
$\overline{w}$	Average number of offspring produced by ancestral population (average fitness)
q_i	Frequency of *i*-type individuals in ancestor population
$q_i^{'}$	Frequency of descendants of *i*-type individuals in descendant population

$$\Delta\bar{z} = \sum_{i=1}^{N}(\Delta q_i)z_i + \sum_{i=1}^{N} q_i^{'}(\Delta z_i)$$

$$\boxed{q_i^{'} = q_i\left(\frac{w_i}{\bar{w}}\right)}$$

For the first term:

$$\Delta\bar{z} = \sum_{i=1}^{N}(\Delta q_i)z_i + \sum_{i=1}^{N} q_i^{'}(\Delta z_i)$$

$$\sum_{i=1}^{N}(\Delta q_i)z_i = \sum_{i=1}^{N}(q_i^{'} - q_i)z_i$$

$$= \sum_{i=1}^{N}\left(q_i\left(\frac{w_i}{\bar{w}}\right) - q_i\right)z_i$$

$$q_i^{'} = q_i\left(\frac{w_i}{\bar{w}}\right)$$

$$= \sum_{i=1}^{N} q_i z_i\left(\frac{w_i}{\bar{w}}\right) - q_i z_i$$

$$= \frac{1}{\bar{w}}\left(\sum_{i=1}^{N} q_i z_i w_i - \sum_{i=1}^{N} q_i z_i \bar{w}\right)$$

$$= \frac{1}{\bar{w}}(\mathrm{E}(zw) - \mathrm{E}(z)\mathrm{E}(w))$$

$$= \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}}$$

$$\mathrm{Cov}(z_i, w_i) = \mathrm{E}\big[\big(z - \mathrm{E}(z)\big)\big(w - \mathrm{E}(w)\big)\big]$$

For the second term:

$$\Delta \bar{z} = \sum_{i=1}^{N} (\Delta q_i) z_i + \sum_{i=1}^{N} q_i^{'} (\Delta z_i)$$

$$\sum_{i=1}^{N} q_i^{'} (\Delta z_i) = \sum_{i=1}^{N} q_i \left(\frac{w_i}{\bar{w}}\right) \Delta z_i$$

$$= \frac{\sum_{i=1}^{N} q_i w_i \Delta z_i}{\bar{w}}$$

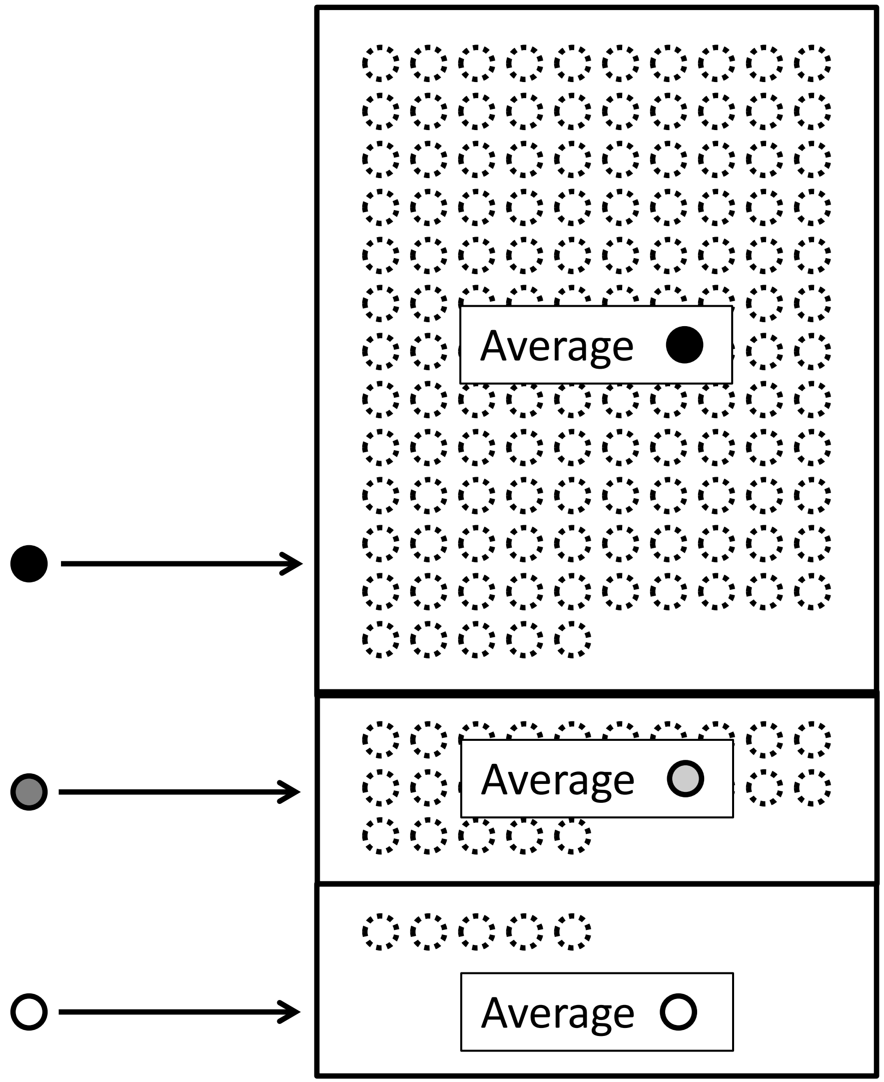
$$= \frac{\mathrm{E}(w \Delta z)}{\bar{w}}$$

$$\boxed{q_i^{'} = q_i \left(\frac{w_i}{\bar{w}}\right)}$$

$$\Delta\bar{z} = \sum_{i=1}^{N} (\Delta q_i) z_i + \sum_{i=1}^{N} q_i^{'} (\Delta z_i)$$

$$q_i^{'} = q_i \left(\frac{w_i}{\bar{w}}\right)$$

$$\boxed{\Delta\bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \frac{\mathrm{E}(w\Delta z)}{\bar{w}}}$$

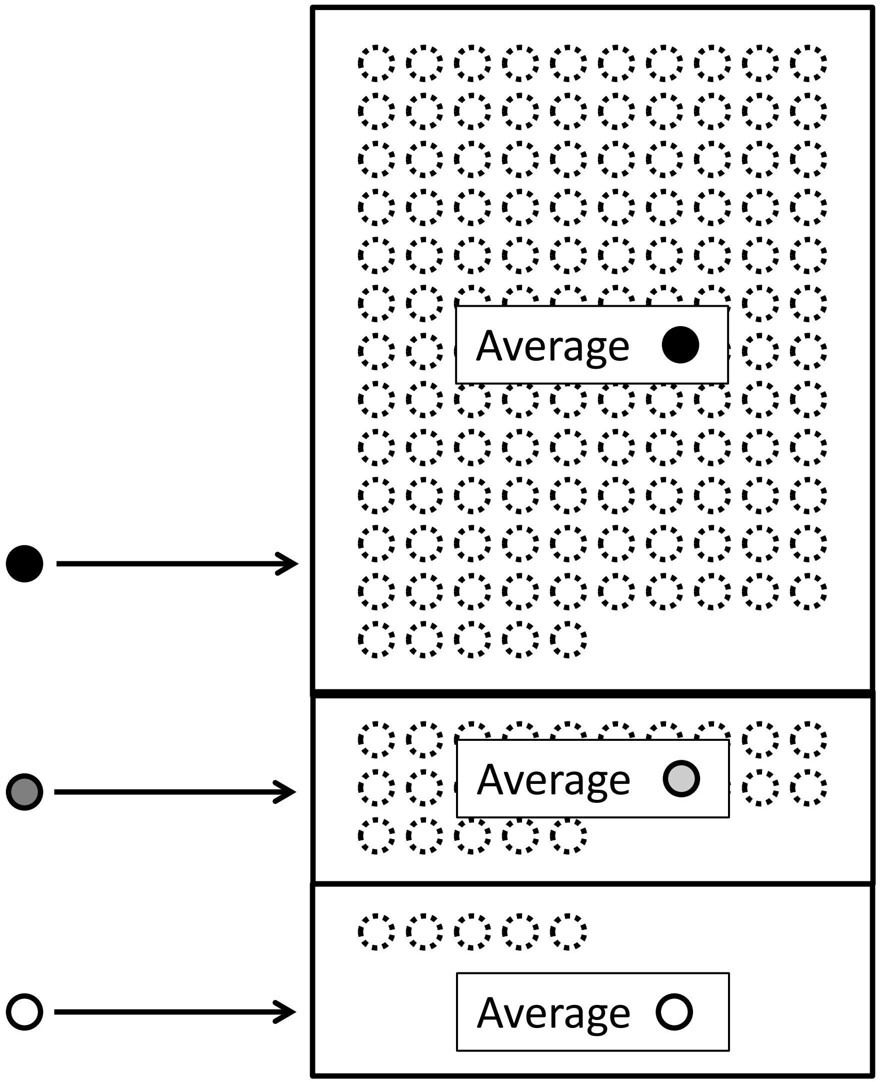


Change due to natural selection

Change due to transmission bias

$$\Delta\bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \frac{\mathrm{E}(w\Delta z)}{\bar{w}}$$

$$\Delta\bar{z} = 0.387 - 0.048 = 0.339$$



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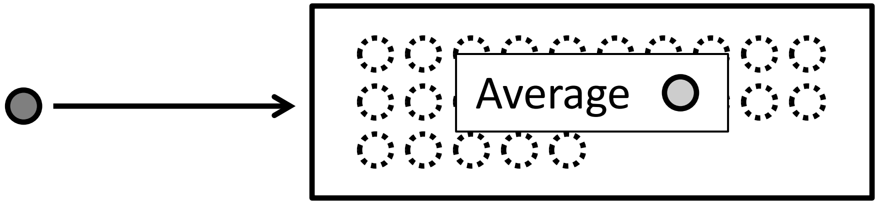
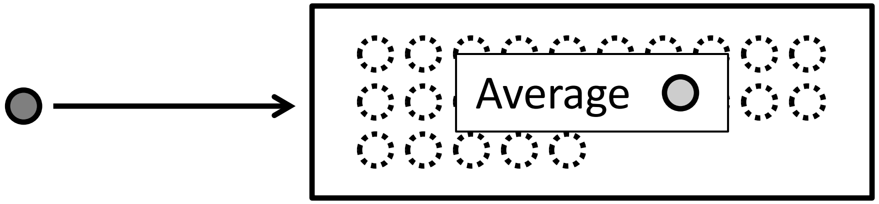
Can zoom in here and apply the Price equation again



$$\Delta z_2 = 0.2 - 0.5 = -0.3$$



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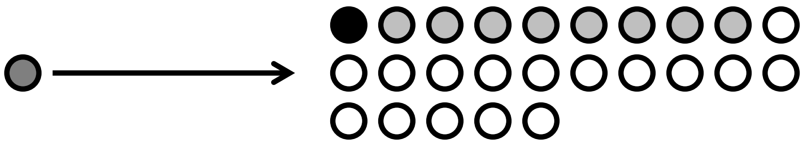

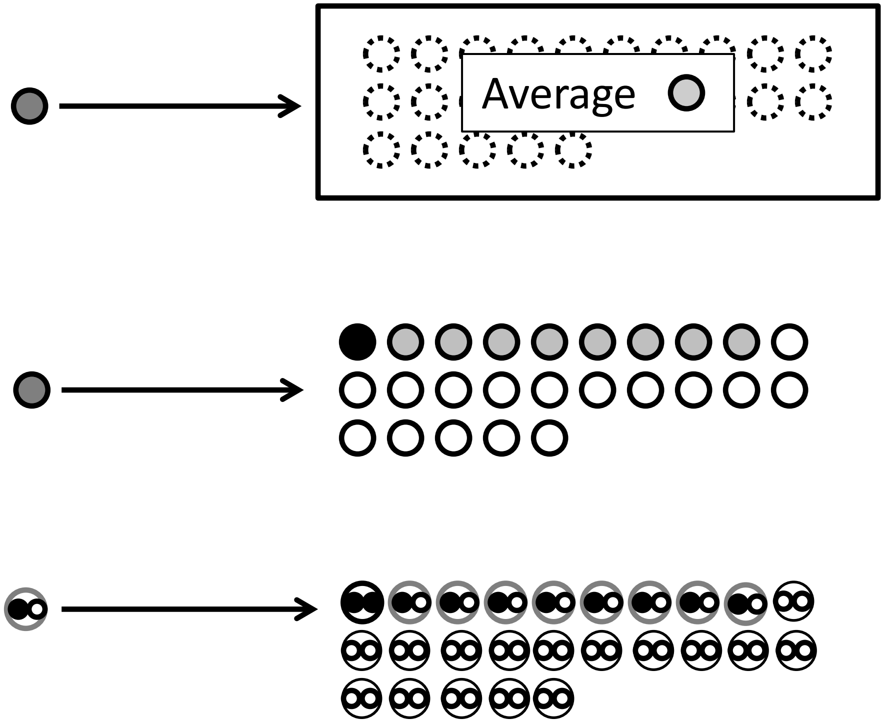

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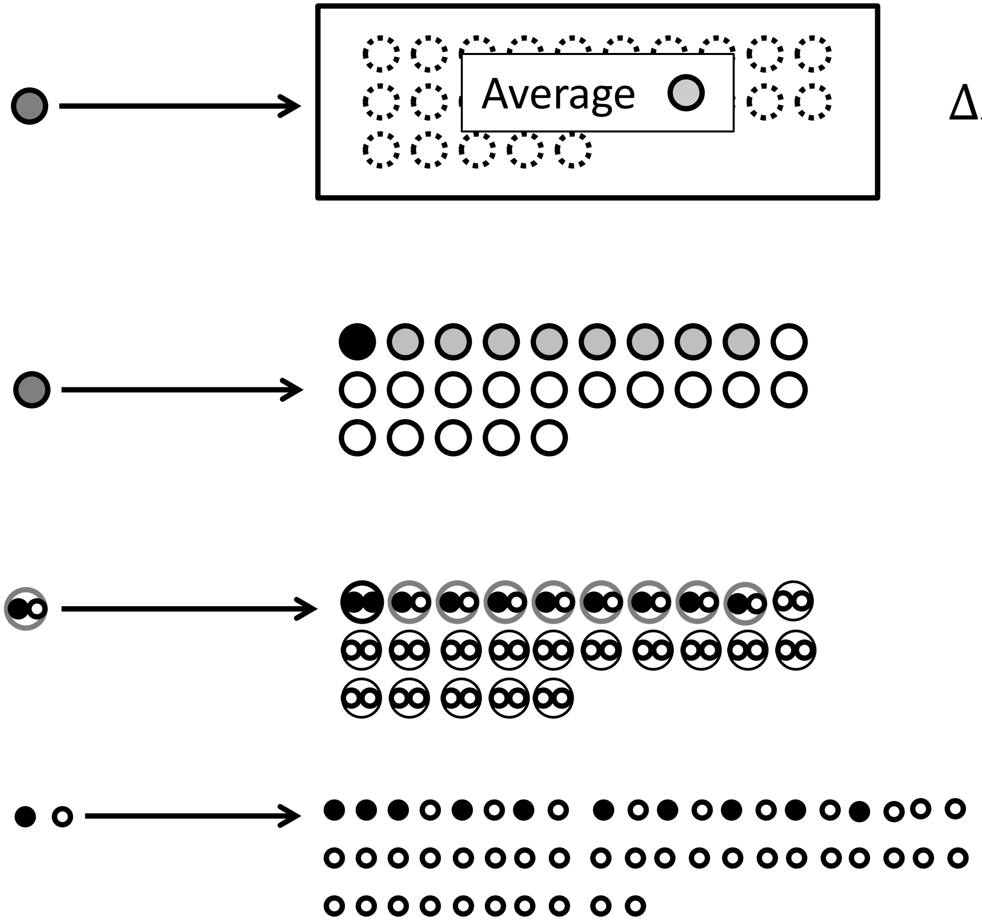

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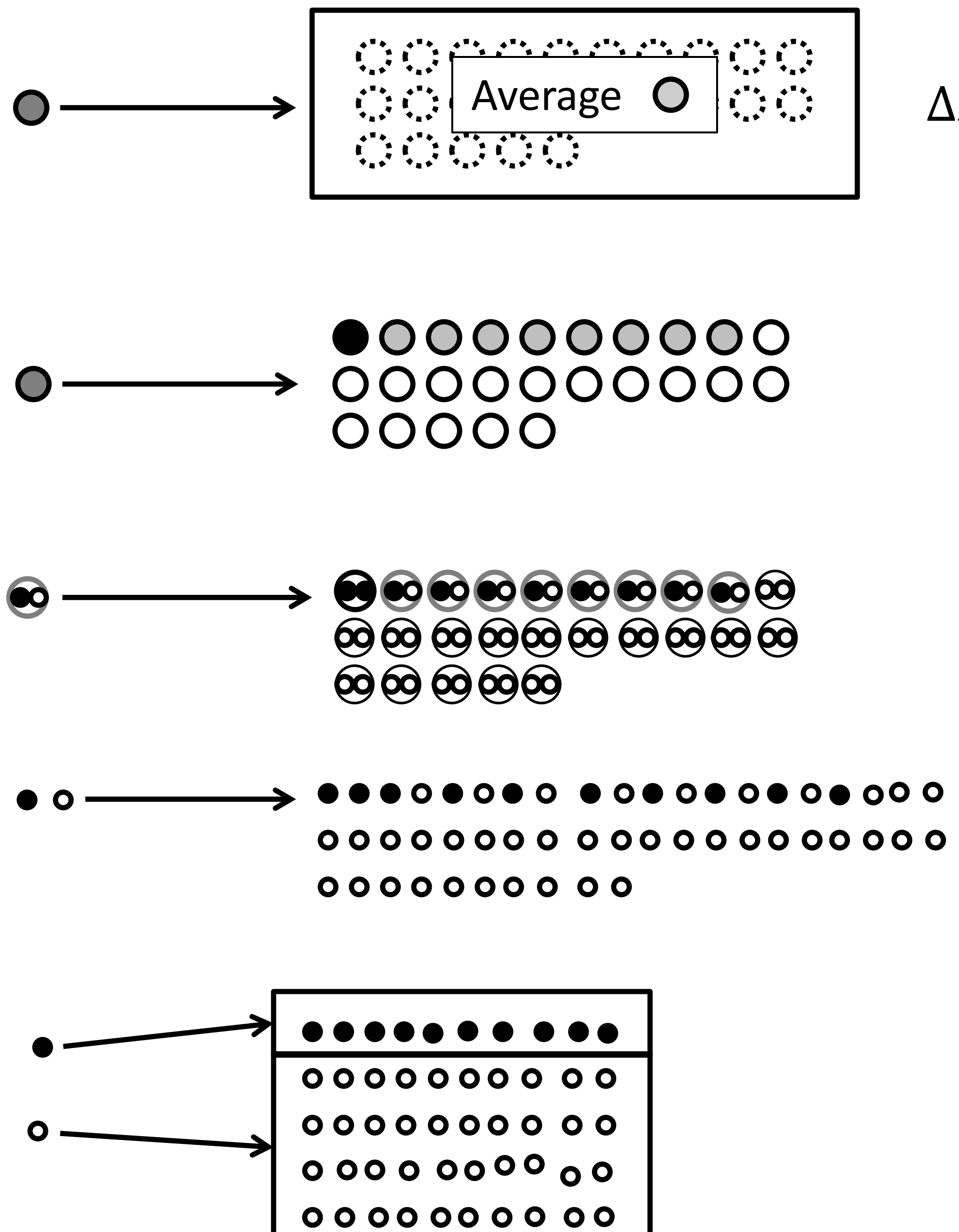
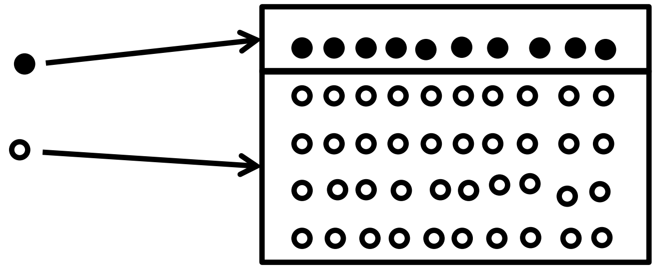


$$\Delta z_2 = 0.2 - 0.5 = -0.3$$

Time 0

Time 1

i	z_i	q_i	w_i
1	1	1/2	10
2	0	1/2	40

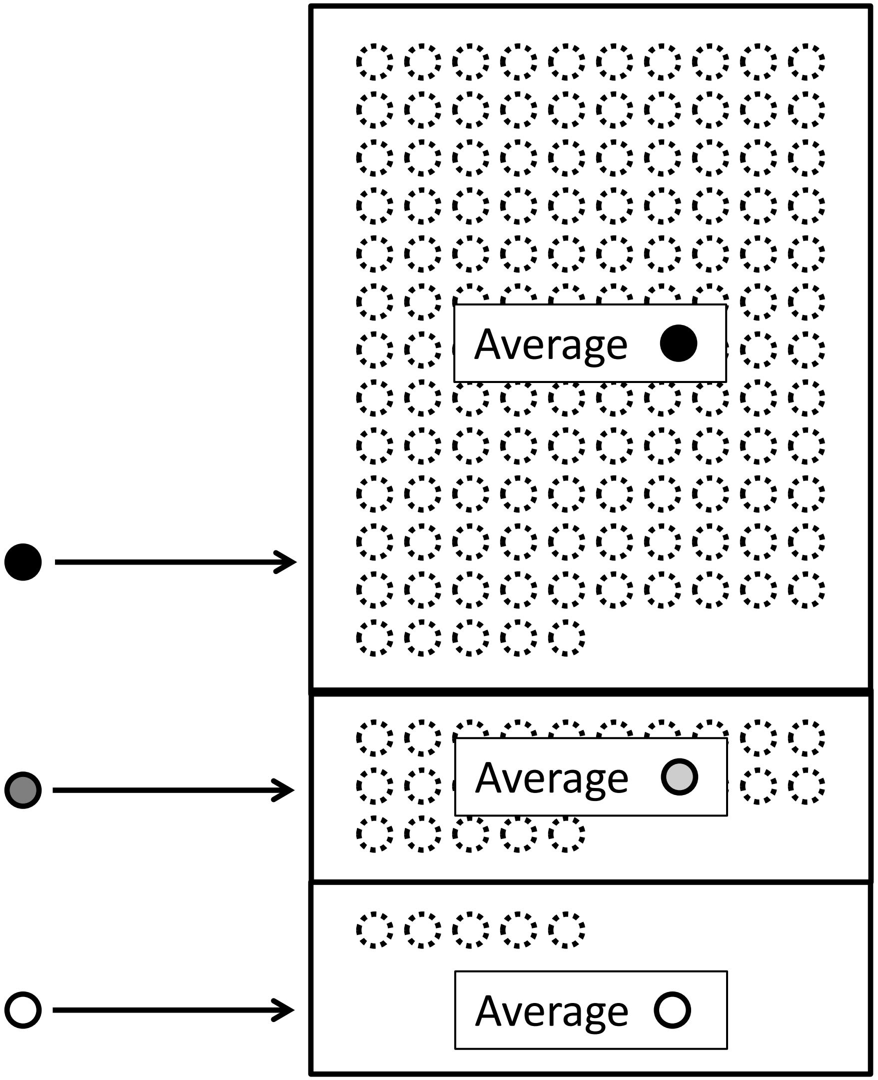


i	z_i'
1	1
2	0

$$\Delta\bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \frac{\mathrm{E}(w\Delta z)}{\bar{w}}$$

$$\Delta\bar{z} = \frac{-7.5}{25} + 0$$

$$\Delta\bar{z} = -0.3$$



$$\Delta\bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \frac{\mathrm{E}(w\Delta z)}{\bar{w}}$$

- Price equation is general and exactly true
- Can aid in specifying what is meant by “change due to natural selection”
- Shows how natural selection at a lower level can look like “transmission bias” at a higher level

Levels of selection during a transition from unicellularity to multicellularity

Levels of selection and multicellularity

- Before multicellularity, all (or most) of natural selection occurs at the cell level.
- After multicellularity, all (or most) of natural selection occurs at the cell-group level.
- The issue of quantifying a transition to multicellularity corresponds to the issue of separating and quantifying the effect of lower- and higher-level selection.

Mathematical vs. causal decomposition

- All of the decompositions shown at right are mathematically true
- However, there is a lack of consensus on the correct decomposition of trait change due to separate causes (e.g. individual and group selection)

$$\Delta\bar{z} = \begin{cases} \dfrac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \dfrac{\mathrm{E}(w\Delta z)}{\bar{w}} \\ \dfrac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \dfrac{\mathrm{Cov}(\Delta z_i, w_i)}{\bar{w}} + \mathrm{E}(\Delta z) \\ \dfrac{\mathrm{Cov}(z_i', w_i)}{\bar{w}} + \mathrm{E}(\Delta z) \end{cases}$$

Problem with the traditional causal interpretation of the Price Equation

Change due to natural selection

Change due to transmission bias

$$\Delta\bar{z} = \frac{\text{Cov}(z_i, w_i)}{\bar{w}} + \frac{\text{E}(w\Delta z)}{\bar{w}}$$

Problem with the traditional causal interpretation of the Price Equation

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$$\Delta\bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \frac{\mathrm{E}(w\Delta z)}{\bar{w}}$$

- Assume z is not correlated with a different fitness-affecting trait

Problem with the traditional causal interpretation of the Price Equation

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$$\Delta\bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \frac{\mathrm{E}(w\Delta z)}{\bar{w}}$$

- Assume z is not correlated with a different fitness-affecting trait
- Further, assume the second term is zero

Problem with the traditional causal interpretation of the Price Equation

Change due to natural selection

Change due to transmission bias

$$\Delta\bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \frac{\mathrm{E}(w\Delta z)}{\bar{w}}$$

- Assume z is not correlated with a different fitness-affecting trait
- Further, assume the second term is zero
- In that case, can we safely say that the change in z is due to natural selection for z?

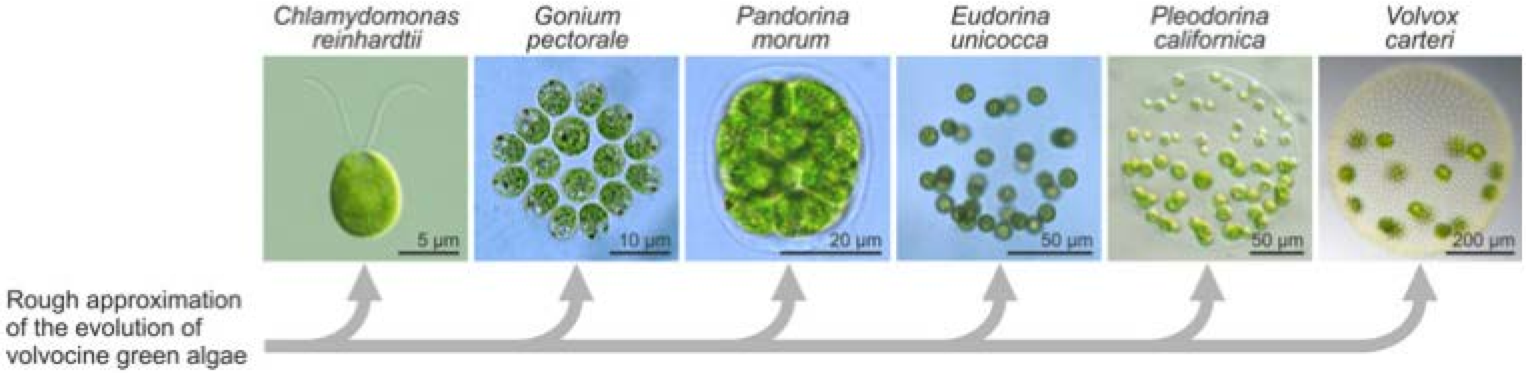
"Fleet deer" problem

- G. C. Williams (1966) *Adaptation and Natural Selection A Critique of Some Current Evolutionary Thought.* Princeton University Press, Princeton.

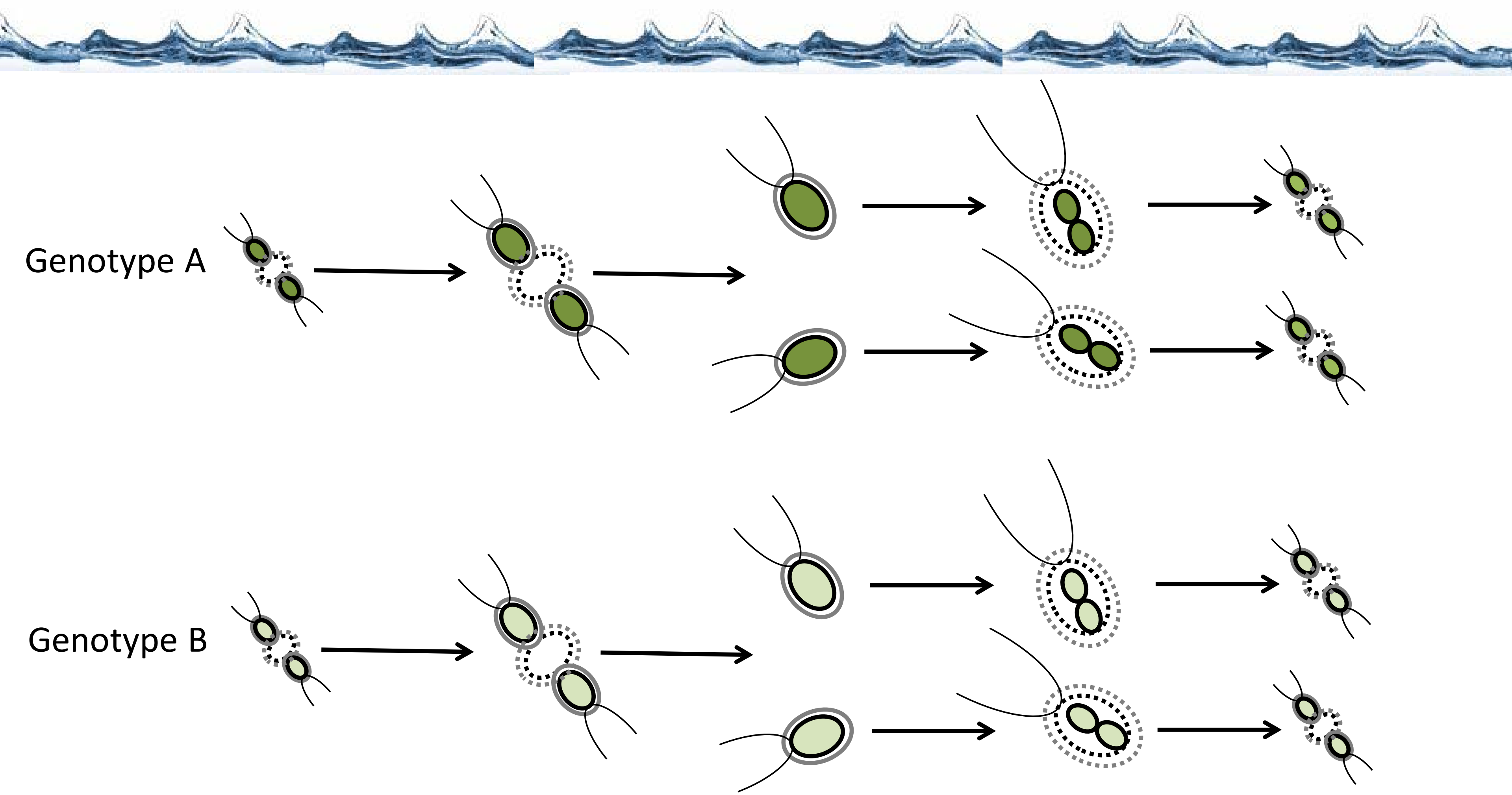
- z is average speed of a herd
- w is fitness of a herd
- Average herd speed would appear to change due to herd-level natural selection

$$\Delta \bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}}$$

- Volvocine species are living, real-world examples that span the unicellular-to-multicellular divide.



Hallmann (2011) *Sex Plant Reprod,* 24: 97-112.


Genotype A
Genotype B

- Did group selection or individual selection cause one strain to out-compete the other?
  - Groups are all homogenous so there definitely was no within-group individual selection

- Did group selection or individual selection cause one strain to out-compete the other?
  - Groups are all homogenous so there definitely was no within-group individual selection
  - But the “fleet deer” idea indicates that there can be individual selection even when all the trait-fitness covariance is between groups

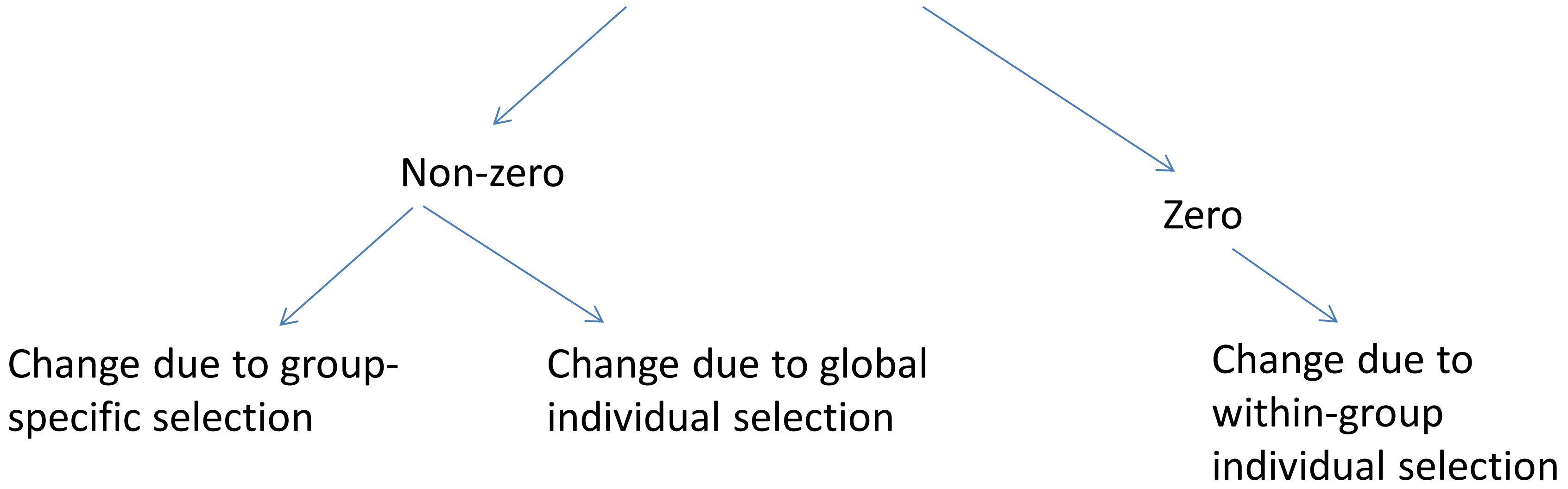
$$\Delta\bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \frac{\mathrm{E}(w_i \Delta z_i)}{\bar{w}}$$

Non-zero

Zero

Change due to
within-group
individual selection

$$\Delta\bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \frac{\mathrm{E}(w_i \Delta z_i)}{\bar{w}}$$



$$w_i = \beta_{wz} z_i + \beta_{w\omega} \omega_i + \varepsilon$$

$$\Delta\bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \frac{\mathrm{E}(w_i \Delta z_i)}{\bar{w}}$$

Non-zero

Zero

Change due to group-specific selection

$$\frac{\beta_{wz}\,\mathrm{Var}(z)}{\bar{w}}$$

Change due to global individual selection

$$\frac{\beta_{w\omega}\,\mathrm{Cov}(\omega, z)}{\bar{w}}$$

Change due to within-group individual selection

$$w_i = \beta_{wz} z_i + \beta_{w\omega} \omega_i + \varepsilon$$

$$\Delta\bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \frac{\mathrm{E}(w_i \Delta z_i)}{\bar{w}}$$

Non-zero

Zero

Change due to group-specific selection

$$\frac{\beta_{wz}\,\mathrm{Var}(z)}{\bar{w}}$$

Change due to global individual selection

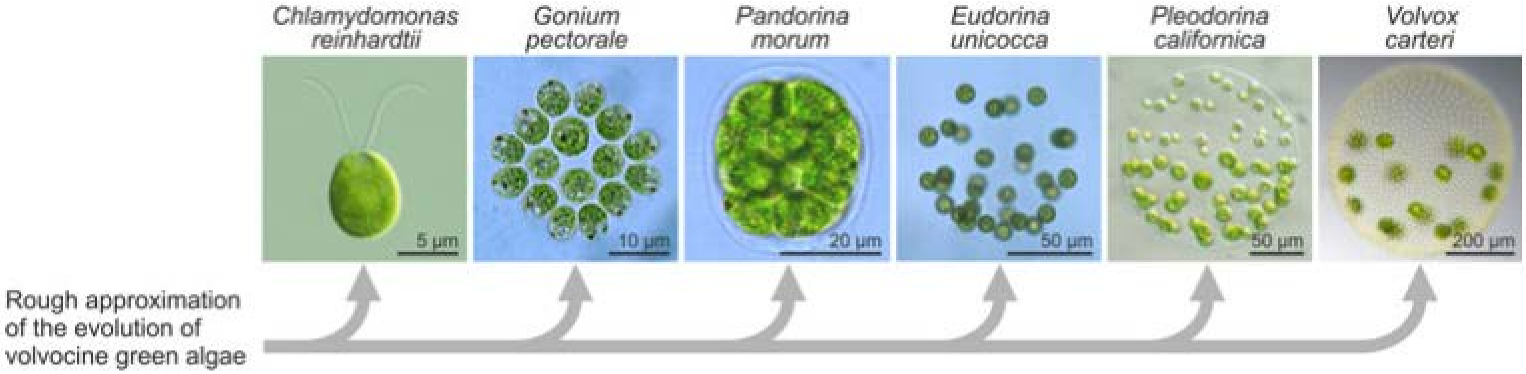
$$\frac{\beta_{w\omega}\,\mathrm{Cov}(\omega, z)}{\bar{w}}$$

Change due to within-group individual selection

- Two hierarchical levels → three categories of natural selection

Summary

$$\Delta\bar{z} = \frac{\mathrm{Cov}(z_i, w_i)}{\bar{w}} + \frac{\mathrm{E}(w_i \Delta z_i)}{\bar{w}}$$



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