

Seasonally fluctuating selection can maintain polymorphism

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Seasonally fluctuating selection can maintain polymorphism at many loci via segregation lift

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Most natural populations are affected by seasonal changes in temperature, rainfall, or resource availability. Seasonally fluctuating selection could potentially make a large contribution to maintaining genetic polymorphism in populations. However, previous theory suggests that the conditions for multilocus polymorphism are restrictive. Here, we explore a more general class of models with multilocus seasonally fluctuating selection in diploids. In these models, the multilocus genotype is mapped to fitness in

(11) and genotypes (12). In fact, most organisms with multiple generations per year experience a particular type of temporal heterogeneity: seasonality, for example, in temperature, rainfall, resource availability, or in the abundance of predators, competitors, or parasites. Even tropical populations usually experience some seasonality. For example, flowering and fruiting in tropical forests is often synchronized within and between tree species, leading to seasonal changes in food availability for ani-

Claim: Seasonally fluctuating selection can maintain polymorphism simultaneously at many loci in the genome.

Model

- 1 Seasonal score z , "counter of favoured alleles".

$$z_s = n_s + d_s \cdot n_{het}$$

$$z_w = n_w + d_w \cdot n_{het}$$

Model

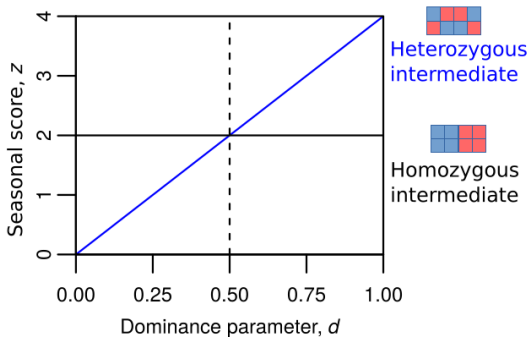
- 1 Seasonal score z , "counter of favoured alleles".

$$z_s = n_s + d_s \cdot n_{het}$$

$$z_w = n_w + d_w \cdot n_{het}$$

Assume *reversal of dominance*.

$$d_w = d_s = d$$



- 2 Map z to fitness $w(z)$ monotonically increasing.

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Case 1: no epistasis

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Achieved with $w(z) = e^z$.

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Case 2: with epistasis

$$v(z) := \ln w(z)$$

For multiplicative model $v'' = 0 \Rightarrow$ use v'' as measure for epistasis.

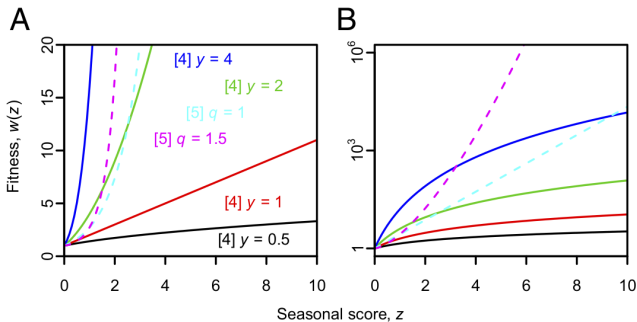
Model

- $v'' > 0$ positive epistasis $\Rightarrow v = \ln w$ increases faster than linearly.
Achieved with

$$w(z) = \exp(z^q), \quad q \geq 1$$

- $v'' < 0$ negative epistasis $\Rightarrow v = \ln w$ decreases faster than linearly.
Achieved with

$$w(z) = (1 + z)^y, \quad y > 0$$



Analysis and simulations

Case 1: $d = 0.5$ (additive contributions to seasonal score z)

$$\Rightarrow z_s + z_w = L, \text{ mean over time is } z^* = \frac{L}{2}.$$

Long-term selection strength depends on geometric mean of $w(z)$ or, equivalently, arithmetic mean of $v(z)$.

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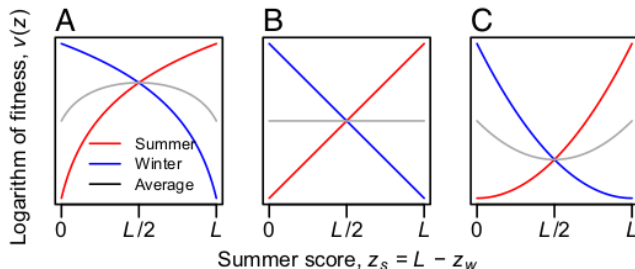
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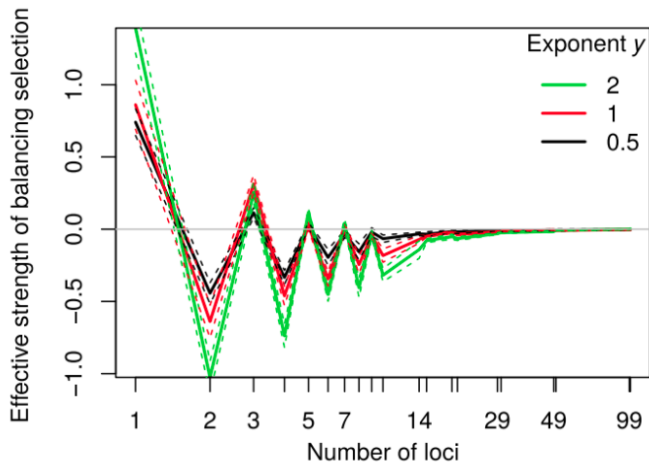
(A) $v'' < 0 \Rightarrow \text{average}(v(z)) \leq v(z^*) \Rightarrow \text{most fitness at } z_s = z_w$

(B) $v'' = 0 \Rightarrow \text{average}(v(z)) = v(z^*)$ neutral \Rightarrow no balancing selection

(C) $v'' > 0 \Rightarrow \text{average}(v(z)) \geq v(z^*) \Rightarrow \text{most fitness at } z_s = L \text{ or } z_w = L$



Case 1: $d = 0.5$



Case 2: $d \neq 0.5$

(i) $v'' = 0$, $w(z) = e^z \Rightarrow$ polymorphism is possible if

$$(e^d)^2 > e^1 \cdot e^0 \Leftrightarrow 2d > 1 \Leftrightarrow d > 0.5$$

Case 2: $d \neq 0.5$

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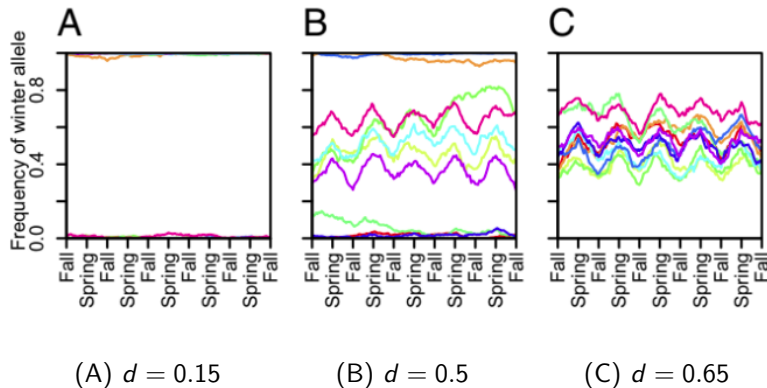
$$(e^d)^2 > e^1 \cdot e^0 \Leftrightarrow 2d > 1 \Leftrightarrow d > 0.5$$

(ii) $v'' > 0$, $w(z) = \exp(z^q) \Rightarrow$ polymorphism can be maintained with $d \rightarrow 1$. Requires large change in dominance.

(iii) $v'' < 0$, $w(z) = (1+z)^y \Rightarrow$ polymorphism can be maintained with $d \rightarrow 0.5$. Smaller change in dominance is sufficient.

Analysis and simulations

Case 2: $d \neq 0.5$



Conclusion

Polymorphism can be maintained with reversal of dominance for $d > 0.5$.