

# Equations of Local Adaptation

Bob Week

6/23/2021

For the sake of brevity, we focus on equations describing parasite local adaptation. Equations for the host are expressed in an analogous manner.

## Classic index of local adaptation in terms of absolute fitness and genotype frequencies

- $K$  = number of populations
- $\overline{W}_P(k, l)$  = expected fitness of a parasite drawn from population  $k$  when confronted with a host drawn from population  $l$
- $\overline{\overline{W}}_P = \frac{1}{K} \sum_{k=1}^K \overline{W}_P(k, k)$  = spatial average of local fitness
- $\mathcal{G}_P = \frac{1}{K^2} \sum_{k=1}^K \sum_{l=1}^K \overline{W}_P(k, l)$  = global adaptation of parasite, assuming an island model of dispersal
- $\mathcal{L}_P = \overline{\overline{W}}_P - \mathcal{G}_P$  = local adaptation of parasite, also assuming an island model of dispersal

$$\mathcal{L} = \overline{\overline{W}} - \mathcal{G}$$

$$\mathcal{L} = \frac{1}{K} \sum_{k=1}^K \overline{W}(k, k) - \frac{1}{K^2} \sum_{k=1}^K \sum_{l=1}^K \overline{W}(k, l)$$

- $n_P, n_H$  = numbers of parasite and host genotype frequencies respectively
- $\varphi_P(k, i), \varphi_H(l, j)$  frequencies of parasite genotype  $i$  in population  $k$  and host genotype  $j$  in population  $l$
- $W_P(i, j)$  = absolute fitness of a parasite with genotype  $i$  when confronted with a host having genotype  $j$ 
  - Then,  $\overline{W}_P(k, l) = \sum_{i=1}^{n_P} \sum_{j=1}^{n_H} W_P(i, j) \varphi_P(k, i) \varphi_H(l, j)$
- $\text{Cov}(\varphi_P(i), \varphi_H(j))$  = spatial covariance between frequency of parasite genotype  $i$  and frequency of host genotype  $j$ 
  - Then,  $\mathcal{L}_P = \sum_{i=1}^{n_P} \sum_{j=1}^{n_H} W_P(i, j) \text{Cov}(\varphi_P(i), \varphi_H(j))$

## Classic index of local adaptation in terms of population growth rate and mean traits under trait matching/mis-matching

- $\bar{m}_P(k, l)$  = expected population growth rate of parasite population  $k$  when confronted with host population  $l$
- $\bar{\bar{m}}_P = \frac{1}{K} \sum_{k=1}^K \bar{m}_P(k, k)$  = spatial average of population growth rates
- $g_P = \frac{1}{K^2} \sum_{k=1}^K \sum_{l=1}^K \bar{m}_P(k, l)$  = global adaptation of parasite, assuming an island model of dispersal
- $\ell_P = \bar{\bar{m}}_P - g_P$  = local adaptation of parasite, also assuming an island model of dispersal

$$\ell = \bar{\bar{m}} - g$$

$$\ell = \frac{1}{K} \sum_{k=1}^K \bar{m}(k, k) - \frac{1}{K^2} \sum_{k=1}^K \sum_{l=1}^K \bar{m}(k, l)$$

- $\varphi_P(k, z_P), \varphi_H(l, z_H)$  frequencies of trait  $z_P$  in parasite population  $k$  and  $z_H$  in host population  $l$
- $m_P(z_P, z_H)$  growth rate of a parasite subpopulation consisting of individuals with trait  $z_P$  when confronting hosts with trait  $z_H$

$$- \text{Then } \bar{m}_P(k, l) = \int \int m_P(z_P, z_H) \varphi_P(k, z_P) \varphi_H(l, z_H) dz_P dz_H$$

Everything above this is general and independent of the trait matching model

- Under trait matching  $m_P(z_P, z_H) = r_P - \frac{B_P}{2}(z_H - z_P)^2$ 
  - $r_P$  = intrinsic growth rate of parasite populations (assumed spatially homogeneous)
  - $B_P$  = strength of biotic selection on parasite (assumed spatially homogeneous)
- $\bar{z}_P(k), \bar{z}_H(l)$  = mean traits of parasite population  $k$  and host population  $l$
- $v_H, v_P$  = local trait variances (assumed spatially homogeneous)
  - Then  $\bar{m}_P = r_P - \frac{B_P}{2} [(\bar{z}_H(l) - \bar{z}_P(k))^2 + v_H + v_P]$
- $\bar{\bar{z}}_P, \bar{\bar{z}}_H$  = spatial averages of local mean traits for parasite and host respectively
- $V_P, V_H$  = spatial variances of local mean traits for parasite and host respectively
- $C_{HP}$  spatial covariance of local mean traits for parasite and host respectively
  - Then  $\bar{\bar{m}}_P = r_P - \frac{B_P}{2} [(\bar{\bar{z}}_H - \bar{\bar{z}}_P)^2 + V_H + V_P - 2C_{HP} + v_H + v_P]$
  - and  $g_P = r_P - \frac{B_P}{2} [(\bar{\bar{z}}_H - \bar{\bar{z}}_P)^2 + V_H + V_P + v_H + v_P]$
  - hence  $\ell_P = B_P C_{HP}$

$$\ell_P = B_P C_{HP}$$

$$\ell_H = -B_H C_{HP}$$

## Modified index of local adaptation accounting for limited dispersal under trait matching/mis-matching

- $\bar{m}_P(x, y)$  = expected population growth rate of parasite population at location  $x = (x_1, x_2)$  when confronted with host population at location  $y = (y_1, y_2)$ .
  - **From here on we write  $\bar{m}_P(\mathcal{d})$**  as the expected population growth rate of a parasite population when confronted with host population located a distance  $\mathcal{d}$  away. That is, for  $\|x - y\| = \mathcal{d}$ ,  $\bar{m}_P(\mathcal{d}) = \bar{m}_P(x, y)$ .
- $\bar{\bar{m}}_P = \mathbb{E}(\bar{m}_P(0))$  = spatial average of population growth rates
- $\tilde{g}_P(\mathcal{d}) = \mathbb{E}(\bar{m}_P(\mathcal{d}))$  = a pseudo measure of parasite global adaptation for all distances  $\mathcal{d} \geq 0$
- $D(\mathcal{d})$  = the probability density function for the distance  $\mathcal{d}$  between two interacting individuals before dispersal
- $g_P = \int_0^\infty \tilde{g}_P(\mathcal{d}) D(\mathcal{d}) d\mathcal{d}$  = a measure of parasite global adaptation accounting for limited dispersal within each species
- $\tilde{\ell}_P(\mathcal{d}) = \bar{\bar{m}}_P - \tilde{g}_P(\mathcal{d})$  = a psuedo measure of parasite local adaptation for all distances  $\mathcal{d} \geq 0$
- $\ell_P = \int_0^\infty \tilde{\ell}_P(\mathcal{d}) D(\mathcal{d}) d\mathcal{d} = \bar{\bar{m}}_P - g_P$  = a measure of parasite local adaptation accounting for limited dispersal in each species

### Everything above this is independent of the trait matching model

- Assuming Gaussian dispersal in each species and the trait matching model we find

$$\bar{\bar{m}}_P = r_P - \frac{B_P}{2} ((\bar{\bar{z}}_H - \bar{\bar{z}}_P)^2 + V_H + V_P - 2C_{HP} + v_H + v_P)$$

$$\tilde{g}_P(\mathcal{d}) = r_P - \frac{B_P}{2} ((\bar{\bar{z}}_H - \bar{\bar{z}}_P)^2 + V_H + V_P - 2C_{HP}(\mathcal{d}) + v_H + v_P)$$

- $C_{HP} = C_{HP}(0)$  = the marginal covariance of mean traits (same thing as  $C_{HP}$  above)
- $C_{HP}(\mathcal{d})$  = the spatial cross-covariance of host-parasite mean traits at the distance  $\mathcal{d}$
- $\bar{C}_{HP} = \int_0^\infty C_{HP}(\mathcal{d}) D(\mathcal{d}) d\mathcal{d}$  = expected covariance of mean traits of interacting individuals
- Then, the psuedo measures of local adaptation work out to be

$$\begin{aligned}\tilde{\ell}_P(\mathcal{d}) &= B_P(C_{HP} - C_{HP}(\mathcal{d})) \\ \tilde{\ell}_H(\mathcal{d}) &= B_H(C_{HP}(\mathcal{d}) - C_{HP})\end{aligned}$$

- Since  $\lim_{\mathcal{d} \rightarrow \infty} C_{HP}(\mathcal{d}) = 0$ , we see  $\lim_{\mathcal{d} \rightarrow \infty} \tilde{\ell}_P(\mathcal{d})$  = the classical measure of parasite local adaptation above
- The measure of local adaptation accounting for limited dispersal the works out to be

$$\ell_P = B_P(C_{HP} - \bar{C}_{HP})$$

$$\ell_H = B_H(\bar{C}_{HP} - C_{HP})$$