

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

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

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