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# A CONTINUOUS SPACE MODEL OF PHENOTYPIC COEVOLUTION BETWEEN HOSTS AND PARASITES

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## Abstract

## 1 Introduction

Space is hypothesized to play a fundamental role in the coevolutionary process. In particular, the combined effects of local co-adaptation and spatial movement are thought to produce complex spatial patterns of matched and mismatched traits. However, theoretical studies investigating the spatial signal of coevolution have for the most part restricted themselves to understanding patterns of spatial correlation using spatially implicit models. Hence, the fine-grained details that can be produced in spatially explicit settings have yet to be understood. Here we close this gap in the context of host-parasite coevolution using continuous-space models inspired by classical quantitative genetic theory. In particular, we study the autocorrelations of mean traits within species and the cross-correlation of mean traits between species when trait dynamics are driven by (1) random genetic drift, gene-flow and abiotic stabilizing selection, (2) drift, gene-flow, abiotic stabilizing selection and unilateral adaptation of the host species, (3) drift, gene-flow, stabilizing selection and unilateral adaptation of the parasite species and (4) drift, gene-flow, stabilizing selection and host-parasite coevolution. In each case we assuming abiotic stabilizing selection is spatially homogeneous. By comparing patterns of spatial autocorrelation and cross-correlation in these four scenarios we are able to elucidate the signature of coevolution.

## 2 Questions

- Are we aiming to describe the spatial signature of coevolution? Or are we aiming to explain spatial patterns of traits and local adaptation when species may be coevolving?
  - The first question takes a more reductionist view by focusing on coevolution.
  - The second question takes a more holistic view by embracing the complexity of natural systems.
- What are the characteristic spatial scales of local adaptation in each species?
  - How do these depend on rates/distances of dispersal and strengths of selection?
- What is the characteristic spatial scale at which coevolution becomes visible?
  - How does this depend on dispersal distances, strengths of selection, effective densities and local additive genetic variation?
- What are the characteristic scales of spatial autocorrelation and cross-correlation?
  - Does this answer both questions above?

- How do these answers change when selection, effective densities or local additive genetic variances are spatially heterogeneous (but temporally fixed)?
  - What if these parameters follow deterministic clines? Linear or quadratic?
  - What if they follow stochastic patterns such as Gaussian fields?
    - \* In particular, consider the characteristic scale of environmental heterogeneity.
  - In these scenarios, how does autocorrelation and cross-correlation change across space? What is the characteristic scale at which their characteristic scales change?
- Considering answers to all of the above, what is the best sampling scheme for detecting coevolution?
  - More intensive sampling at a few locations?
  - Less intensive sampling at many locations?
- Future directions:
  - Does the interplay between coevolution and abundance dynamics lead to patchy distributions?
  - When does local adaptation occur in host and/or parasite?
    - \* Are there winners/losers? (ref scott perspective piece)
    - \* When do host or parasite remain generalized?
    - \* Does this agree with past theory?
      - I imagine the stochastic dynamics change the picture

### 3 The Model

#### 3.1 Fitness

The host is denoted  $H$  and the parasite  $P$ . Individual trait values of hosts and parasites are respectively denoted by  $z_H, z_P \in \mathbb{R}$ . Assuming a trait-matching model, where host fitness is minimized and parasite fitness is maximized when  $z_H = z_P$ , we have the following two fitness functions:

$$w_H(z_H, z_P) \propto \exp \left( -\frac{A_H}{2}(\theta_H - z_H)^2 + \frac{B_H}{2}(z_P - z_H)^2 \right), \quad (1a)$$

$$w_P(z_P, z_H) \propto \exp \left( -\frac{A_P}{2}(\theta_P - z_P)^2 - \frac{B_P}{2}(z_H - z_P)^2 \right), \quad (1b)$$

where  $A_H, A_P > 0$  capture the strengths of abiotic stabilizing selection,  $\theta_H, \theta_P \in \mathbb{R}$  are the abiotic optimal phenotypes and  $B_H, B_P > 0$  capture the strengths of biotic selection experienced by each species.

#### 3.2 Non-spatial Dynamics

Using a standard approach, we use the above fitness functions to derive the following non-spatial coevolutionary model:

$$\frac{d\bar{z}_H}{dt} = G_H A_H (\theta_H - \bar{z}_H) - G_H B_H (\bar{z}_P - \bar{z}_H), \quad (2a)$$

$$\frac{d\bar{z}_P}{dt} = G_P A_P (\theta_P - \bar{z}_P) + G_P B_P (\bar{z}_H - \bar{z}_P), \quad (2b)$$

where  $G_H, G_P > 0$  denote the additive genetic variances of each species. In this linear set of equations, when abiotic stabilizing selection is absent ( $A_H = A_P = 0$ ), the parasite mean trait  $\bar{z}_P$  evolves to match the host mean trait  $\bar{z}_H$ . Simultaneously  $\bar{z}_H$  evolves away from  $\bar{z}_P$ . In particular, when  $\bar{z}_H > \bar{z}_P$ , the host mean trait will evolve upwards. Similarly, when  $\bar{z}_H < \bar{z}_P$ , the host mean trait will evolve downwards. This and related models have been thoroughly studied by Sergey Gavrillets and others. For the case when  $A_H = A_P = 0$  two possible outcomes have been demonstrated. First, when  $G_P B_P > G_H B_H$  so that the parasite evolves faster than the host, the system asymptotically evolves to the equilibrium  $\bar{z}_H = \bar{z}_P$ . Second, when  $G_P B_P < G_H B_H$  so that the host evolves faster than the parasite, there is no stable equilibrium. This implies the host evolves to escape the interaction. In the case when  $A_H, A_P \neq 0$  limit cycles can emerge.

### 3.3 Space

In this case mean traits become functions of spatial variables (eg.,  $\bar{z}_H(\mathbf{x})$ ,  $\bar{z}_P(\mathbf{x})$  where  $\mathbf{x} = (x_1, x_2) \in \mathbb{R}^2$ ). As a first step, we assume all model parameters are spatially homogeneous. If we assume interactions occur locally (individuals interact only when they ‘collide’) and abundance densities are spatially homogeneous, then we can obtain the following continuous space model:

$$\frac{\partial \bar{z}_H}{\partial t} = G_H A_H(\theta_H - \bar{z}_H) - G_H B_H(\bar{z}_P - \bar{z}_H) + \frac{\sigma_H^2}{2} \Delta \bar{z}_H, \quad (3a)$$

$$\frac{\partial \bar{z}_P}{\partial t} = G_P A_P(\theta_P - \bar{z}_P) + G_P B_P(\bar{z}_H - \bar{z}_P) + \frac{\sigma_P^2}{2} \Delta \bar{z}_P, \quad (3b)$$

where  $\sigma_H^2, \sigma_P^2 > 0$  are dispersal rates for each species and  $\Delta = \frac{\partial^2}{\partial x_1^2} + \frac{\partial^2}{\partial x_2^2}$  is the Laplacian operator representing spatial movement.

### 3.4 Random Genetic Drift

To incorporate the effects of random genetic drift, we should be able to justify the following SPDE model:

$$\frac{\partial \bar{Z}_H}{\partial t} = G_H A_H(\theta_H - \bar{Z}_H) - G_H B_H(\bar{Z}_P - \bar{Z}_H) + \frac{\sigma_H^2}{2} \Delta \bar{Z}_H + \sqrt{\frac{G_H}{N_H}} \dot{W}_H, \quad (4a)$$

$$\frac{\partial \bar{Z}_P}{\partial t} = G_P A_P(\theta_P - \bar{Z}_P) + G_P B_P(\bar{Z}_H - \bar{Z}_P) + \frac{\sigma_P^2}{2} \Delta \bar{Z}_P + \sqrt{\frac{G_P}{N_P}} \dot{W}_P, \quad (4b)$$

where  $N_P, N_H$  are the effective population densities (here assumed to be constant in space and time),  $\dot{W}_H, \dot{W}_P$  are space-time white noise processes and we use capital  $\bar{Z}_H, \bar{Z}_P$  to emphasize that these are now random quantities. This SPDE model may possess some major benefits over more traditional continuous-space models of population genetics. In particular, it is known to have solutions for all spatial dimensions. The effect of abiotic stabilizing selection may also imply function-valued solutions.

### 3.5 Possible extensions to spatially heterogeneous abiotic optima

- linear clines, eg:  $\theta_H(\mathbf{x}) = \alpha_H + \beta_{H,1}x_1 + \beta_{H,2}x_2$
- quadratic clines, eg:  $\theta_H(\mathbf{x}) = \alpha_H + \beta_{H,1}x_1 + \beta_{H,2}x_2 + \gamma_{H,11}x_1^2 + \gamma_{H,22}x_2^2 + \gamma_{H,12}x_1x_2$
- stochastic fields, eg:  $\theta_H(\mathbf{x})$  follows a fractional Brownian surface, but is fixed in time

## 4 Methods

We use results connecting theory of SPDE, random fields and geostatistics to calculate characteristic spatial scales at which various phenomena become visible. In particular, we take advantage of the approach outlined by (Hu et al. 2013) to obtain spatial (intraspecific) covariance and (interspecific) cross-covariance functions of mean traits separated by a distance  $h$ .

Below, we show under the deterministic model (eqn 3) that when the abiotic optima  $\theta_H, \theta_P$  are spatially homogeneous and when biotic selection on the host is sufficiently weak, mean trait values for both species converge to spatially homogeneous values.

Building off (Hu et al. 2013) and others, we know that the solution to SPDE (4) converges to a stationary isotropic Gaussian random field on  $\mathbb{R}^2$ .

### 4.1 A Stable Equilibrium of PDE (3)

To find an equilibrium of the deterministic PDE (3) we set the time derivatives of  $\bar{z}_H$  and  $\bar{z}_P$  equal to zero. This leads to following systems of ODE's

$$0 = G_H A_H(\theta_H - \bar{z}_H) - G_H B_H(\bar{z}_P - \bar{z}_H) + \frac{\sigma_H^2}{2} \Delta \bar{z}_H, \quad (5a)$$

Table 1: Summary of notation.

Variable/Parameter	Description	Range
$\mathbf{x} = (x_1, x_2)$	Spatial coordinates	$\mathbf{x} \in \mathbb{R}^2$
$z_H, z_P$	Individual trait values	$z_H, z_P \in \mathbb{R}$
$w_H(z_H, z_P), w_P(z_P, z_H)$	Individual fitness	$w_H, w_P > 0$
$A_H, A_P$	Strengths of abiotic stabilizing selection	$A_H, A_P \geq 0$
$\theta_H(\mathbf{x}), \theta_P(\mathbf{x})$	Abiotic trait optima at location $\mathbf{x}$	$\theta_H(\mathbf{x}), \theta_P(\mathbf{x}) \in \mathbb{R}$
$B_H, B_P$	Strengths of biotic selection	$B_H, B_P \geq 0$
$G_H, G_P$	Additive genetic variances	$G_H, G_P \geq 0$
$\sigma_H^2, \sigma_P^2$	Dispersal coefficients	$\sigma_H^2, \sigma_P^2 \geq 0$
$N_H, N_P$	Effective population densities	$N_H, N_P \geq 0$
$\dot{W}_H, \dot{W}_P$	Independent space-time white noise processes	$\dot{W}_H(\mathbf{x}), \dot{W}_P(\mathbf{x})$ random variables in $\mathbb{R}$
$\bar{Z}_H(\mathbf{x}), \bar{Z}_P(\mathbf{x})$	Local mean traits at $\mathbf{x}$	$\bar{Z}_H(\mathbf{x}), \bar{Z}_P(\mathbf{x})$ random variables in $\mathbb{R}$
$\bar{z}_H(\mathbf{x}), \bar{z}_P(\mathbf{x})$	Expected local mean traits at $\mathbf{x}$	$\bar{z}_H(\mathbf{x}), \bar{z}_P(\mathbf{x}) \in \mathbb{R}$

$$0 = G_P A_P (\theta_P - \bar{z}_P) + G_P B_P (\bar{z}_H - \bar{z}_P) + \frac{\sigma_P^2}{2} \Delta \bar{z}_P. \quad (5b)$$

Solving this system for the mean traits  $\bar{z}_H(\mathbf{x})$  and  $\bar{z}_P(\mathbf{x})$  as spatial functions then returns equilibrium solutions to PDE (3). However, we can start simple by considering spatially homogeneous solutions. In these cases the spatial derivatives will return zero (in particular,  $\Delta \bar{z}_H = \Delta \bar{z}_P = 0$ ). Finding these solutions amounts to solve the following system of algebraic equations

$$0 = G_H A_H (\theta_H - \bar{z}_H) - G_H B_H (\bar{z}_P - \bar{z}_H), \quad (6a)$$

$$0 = G_P A_P (\theta_P - \bar{z}_P) + G_P B_P (\bar{z}_H - \bar{z}_P). \quad (6b)$$

This linear system is uniquely solved by

$$\bar{z}_H(\mathbf{x}) \equiv \frac{(A_P + B_P)A_H \theta_H - B_H A_P \theta_P}{(A_P + B_P)A_H - B_H A_P}, \quad (7a)$$

$$\bar{z}_P(\mathbf{x}) \equiv \frac{(A_H - B_H)A_P \theta_P + B_P A_H \theta_H}{(A_H - B_H)A_P + B_P A_H}, \quad (7b)$$

where the symbol  $\equiv$  is used in place of  $=$  to emphasize these functions are constant across space.

To understand whether this equilibrium is stable we perform stability analysis on the non-spatial model. Notice that system (2) can be rewritten in matrix notation as  $\vec{z} = M\vec{z} + \vec{b}$  where

$$\vec{z} = \begin{pmatrix} \bar{z}_H \\ \bar{z}_P \end{pmatrix}, \quad \vec{b} = \begin{pmatrix} G_H A_H \theta_H \\ G_P A_P \theta_P \end{pmatrix}, \quad (8a)$$

$$M = \begin{pmatrix} G_H(B_H - A_H) & -G_H B_H \\ G_P B_P & -G_P(A_P + B_P) \end{pmatrix}. \quad (8b)$$

It turns that if the real parts of the eigenvalues of  $M$  are negative then equilibrium (7) is stable. This condition holds in general when  $B_H < A_H + (A_P + B_P)G_P/G_H$  and  $B_H < A_H(1 + B_P/A_P)$ . A sufficient condition with clear biological intuition is  $B_H < A_H$ , which just means the strength of biotic selection on the host is less than the strength of abiotic stabilizing selection. In this case abiotic stabilizing selection prevents the host from escaping via evolution.

## 5 Stationary Solutions of SPDE (4)

To focus on stationary solutions of the stochastic system (4) we set the time derivatives to zero to obtain the following system

$$G_H A_H(\theta_H - \bar{Z}_H) - G_H B_H(\bar{Z}_P - \bar{Z}_H) + \frac{\sigma_H^2}{2} \Delta \bar{Z}_H = \sqrt{\frac{G_H}{N_H}} \dot{W}_H, \quad (9a)$$

$$G_P A_P(\theta_P - \bar{Z}_P) + G_P B_P(\bar{Z}_H - \bar{Z}_P) + \frac{\sigma_P^2}{2} \Delta \bar{Z}_P = \sqrt{\frac{G_P}{N_P}} \dot{W}_P. \quad (9b)$$

If we further restrict our focus to the single species case we recover a SPDE of the form

$$b^2(a - u) + \Delta u = \sigma \dot{W}. \quad (10)$$

In the case of two spatial dimensions, it is known that equation (10) is satisfied by a Gaussian field with a Whittle covariance function (Whittle 1963; Sigrist, Künsch, and Stahel 2014). Denoting  $K_1$  the modified Bessel function of the second kind, order 1, the Whittle covariance function is given by  $C(r) = \frac{\sigma^2 r}{2b} K_1(br)$ . Hence, we can postulate that solutions of the stationary system (9) will have Whittle cross-covariance matrix-valued functions.

## 6 Computing Covariance Matrix from Spectral Representation

In the technical note of (Hu et al. 2013), a method to compute covariance functions of multivariate Gaussian random fields from systems of SPDE was outlined. The approach begins with a stationary system such as (9) and applies a Fourier transform  $\mathcal{F}$  to convert derivatives into algebraic expressions. The Fourier transform acts to switch perspective from the two-dimensional spatial variable  $\mathbf{x} = (x_1, x_2)$  to a two-dimensional frequency variable (also referred to as wavenumber)  $\mathbf{k} = (k_1, k_2)$ , with  $k_1, k_2$  being complex numbers. We can provide a spectral characterization of the system by considering the behavior of a system across a spectrum of frequencies. Once solving for the quantity of interest in the spectral representation we can use the inverse Fourier transform  $\mathcal{F}^{-1}$  to obtain the associated quantity as a function of space.

To apply this method to our model, we start by using a change of variables to obtain an equivalent system where each spatial variable has zero mean. In particular, we set  $\bar{\zeta}_H = \bar{Z}_H - \bar{z}_H$  and  $\bar{\zeta}_P = \bar{Z}_P - \bar{z}_P$  where  $(\bar{z}_H, \bar{z}_P)$  is the spatially homogeneous equilibrium of the deterministic system reported in equation (7). Under this change of variables, an Itô formula can be applied (need to fact-check) to show the stationary system (9) becomes

$$\left( \frac{\sigma_H^2}{2} \Delta - G_H(A_H - B_H) \right) \bar{\zeta}_H - G_H B_H \bar{\zeta}_P = \sqrt{\frac{G_H}{N_H}} \dot{W}_H, \quad (11a)$$

$$G_P B_P \bar{\zeta}_H + \left( \frac{\sigma_P^2}{2} \Delta - G_P(A_P + B_P) \right) \bar{\zeta}_P = \sqrt{\frac{G_P}{N_P}} \dot{W}_P. \quad (11b)$$

To consolidate notation, we set

$$\mathcal{L} = \begin{pmatrix} G_H(A_H - B_H) - \frac{\sigma_H^2}{2}\Delta & G_H B_H \\ -G_P B_P & G_P(A_P + B_P) - \frac{\sigma_P^2}{2}\Delta \end{pmatrix}, \quad (12a)$$

$$\bar{\zeta} = \begin{pmatrix} \bar{\zeta}_H \\ \bar{\zeta}_P \end{pmatrix}, \quad \mathbf{V} = \begin{pmatrix} -\sqrt{\frac{G_H}{N_H}}\dot{W}_H \\ -\sqrt{\frac{G_P}{N_P}}\dot{W}_P \end{pmatrix}. \quad (12b)$$

Then, the stationary system can equally be written as

$$\mathcal{L}\bar{\zeta} = \mathbf{V}. \quad (13)$$

Setting  $\hat{\zeta}_H = \mathcal{F}[\bar{\zeta}_H]$ ,  $\hat{\zeta}_P = \mathcal{F}[\bar{\zeta}_P]$ ,  $\hat{V}_H = \mathcal{F}[-\sqrt{\frac{G_H}{N_H}}\dot{W}_H]$ ,  $\hat{V}_P = \mathcal{F}[-\sqrt{\frac{G_P}{N_P}}\dot{W}_P]$ , we can Fourier transform the whole dang thing to get

$$\mathcal{H}\hat{\zeta} = \hat{\mathbf{V}}, \quad (14)$$

where

$$\mathcal{H} = \begin{pmatrix} G_H(A_H - B_H) + \frac{\sigma_H^2}{2}\|\mathbf{k}\|^2 & G_H B_H \\ -G_P B_P & G_P(A_P + B_P) + \frac{\sigma_P^2}{2}\|\mathbf{k}\|^2 \end{pmatrix}, \quad (15a)$$

$$\hat{\zeta} = \begin{pmatrix} \hat{\zeta}_H \\ \hat{\zeta}_P \end{pmatrix}, \quad \hat{\mathbf{V}} = \begin{pmatrix} \hat{V}_H \\ \hat{V}_P \end{pmatrix}, \quad (15b)$$

The power spectrum corresponding to  $\bar{\zeta}$  is defined as  $\mathbf{S}_{\bar{\zeta}} = \mathbb{E}[\hat{\zeta}\hat{\zeta}^\top]$ , where  $\top$  denotes matrix transposition. In particular, this provides

$$\mathbf{S}_{\bar{\zeta}} = \begin{pmatrix} S_{\bar{\zeta}_{HH}} & S_{\bar{\zeta}_{HP}} \\ S_{\bar{\zeta}_{PH}} & S_{\bar{\zeta}_{PP}} \end{pmatrix} = \begin{pmatrix} \mathbb{E}[\hat{\zeta}_H \hat{\zeta}_H] & \mathbb{E}[\hat{\zeta}_H \hat{\zeta}_P] \\ \mathbb{E}[\hat{\zeta}_H \hat{\zeta}_P] & \mathbb{E}[\hat{\zeta}_P \hat{\zeta}_P] \end{pmatrix} = \mathcal{H}^{-1} \mathbf{S}_{\mathbf{V}} \mathcal{H}^{-H}, \quad (16)$$

with  $-H$  denoting the inverse of the Hermitian of a matrix and  $\mathbf{S}_{\mathbf{V}} = \mathbb{E}[\hat{\mathbf{V}}\hat{\mathbf{V}}^H]$  denoting the power spectrum of the noise process  $\mathbf{V}$ . Using properties of Fourier transforms, we compute

$$\hat{\mathbf{V}} = \begin{pmatrix} \sqrt{G_H/N_H} \\ \sqrt{G_P/N_P} \end{pmatrix}. \quad (17)$$

Formally, I'm missing some  $2\pi$ 's. However, since our goal is to transform back into geographic space (all this Fourier stuff puts us in frequency space) the missing  $2\pi$ 's should be accounted for. Since we assume the white noise processes  $\dot{W}_H$  and  $\dot{W}_P$  are independent we have

$$\mathbf{S}_{\mathbf{V}} = \begin{pmatrix} S_{V_H} & 0 \\ 0 & S_{V_P} \end{pmatrix} = \begin{pmatrix} G_H/N_H & 0 \\ 0 & G_P/N_P \end{pmatrix}. \quad (18)$$

Plugging into *Mathematica* yields

$$S_{\zeta_{HH}} = \frac{\frac{G_H}{4N_H} (2G_P(A_P + B_P) + \sigma_P^2 \|\mathbf{k}\|^2)^2 + \frac{G_P}{N_P} B_H^2 G_H^2}{\left\{ -B_H B_P G_H G_P - \frac{1}{4} [2G_H(A_H - B_H) + \sigma_H^2 \|\mathbf{k}\|^2] [2G_P(A_P + B_P) + \sigma_P^2 \|\mathbf{k}\|^2] \right\}^2} \quad (19a)$$

$$S_{\zeta_{PP}} = \frac{\frac{G_P}{4N_P} (2G_H(A_H - B_H) + \sigma_H^2 \|\mathbf{k}\|^2)^2 + \frac{G_H}{N_H} B_P^2 G_P^2}{\left\{ -B_H B_P G_H G_P - \frac{1}{4} [2G_H(A_H - B_H) + \sigma_H^2 \|\mathbf{k}\|^2] [2G_P(A_P + B_P) + \sigma_P^2 \|\mathbf{k}\|^2] \right\}^2} \quad (19b)$$

$$S_{\zeta_{HP}} = \frac{\frac{G_H G_P}{2} \left[ \frac{B_P}{N_H} (2G_P(A_P + B_P) + \sigma_P^2 \|\mathbf{k}\|^2) + \frac{B_H}{N_P} (2G_H(A_H - B_H) + \sigma_H^2 \|\mathbf{k}\|^2) \right]}{\left\{ -B_H B_P G_H G_P - \frac{1}{4} [2G_H(A_H - B_H) + \sigma_H^2 \|\mathbf{k}\|^2] [2G_P(A_P + B_P) + \sigma_P^2 \|\mathbf{k}\|^2] \right\}^2}. \quad (19c)$$

Then, by assuming weak biotic selection so that  $B_H^2, B_P^2, B_H B_P \approx 0$ , we get

$$S_{\zeta_{HH}}(\mathbf{k}) \approx \frac{4G_H/N_H}{[2G_H(A_H - B_H) + \sigma_H^2 \|\mathbf{k}\|^2]^2}, \quad (20a)$$

$$S_{\zeta_{PP}}(\mathbf{k}) \approx \frac{4G_P/N_P}{[2G_P(A_P + B_P) + \sigma_P^2 \|\mathbf{k}\|^2]^2}, \quad (20b)$$

$$S_{\zeta_{HP}}(\mathbf{k}) \approx 8G_H G_P \left( \frac{B_H/N_P}{[2G_H(A_H - B_H) + \sigma_H^2 \|\mathbf{k}\|^2] [2G_P(A_P + B_P) + \sigma_P^2 \|\mathbf{k}\|^2]^2} + \frac{B_P/N_H}{[2G_H(A_H - B_H) + \sigma_H^2 \|\mathbf{k}\|^2]^2 [2G_P(A_P + B_P) + \sigma_P^2 \|\mathbf{k}\|^2]} \right). \quad (20c)$$

It may be better to assume weak coupling in the general SPDE model ( $b_{12}, b_{21} \ll 1$ ) to get this result since there is an impulse to distribute the  $B$ 's are continue canceling terms, which makes life harder since the marginal cov's are no longer Whittle.

Taking the inverse Fourier transform of the power spectra  $S_{\zeta_{HH}}(\mathbf{k})$  and  $S_{\zeta_{PP}}(\mathbf{k})$  yields the (intraspecific) spatial covariance functions  $C_{HH}(\mathbf{x})$ ,  $C_{PP}(\mathbf{x})$  and the inverse Fourier transform of  $S_{\zeta_{HP}}$  provides the (interspecific) spatial cross-covariance function  $C_{HP}(\mathbf{x})$ . The intraspecific covariance functions are straightforward to calculate, leading to the Whittle covariance functions:

$$C_{HH}(\mathbf{x}) \approx \frac{M(\mathbf{x}|1, \sqrt{2G_H(A_H - B_H)/\sigma_H^2})}{N_H \sigma_H^2 (A_H - B_H)}, \quad (21a)$$

$$C_{PP}(\mathbf{x}) \approx \frac{M(\mathbf{x}|1, \sqrt{2G_P(A_P + B_P)/\sigma_P^2})}{N_P \sigma_P^2 (A_P + B_P)}, \quad (21b)$$

where  $M(\mathbf{x}|\nu, \kappa) = \frac{2^{1-\nu}}{\Gamma(\nu)} (\kappa \|\mathbf{x}\|)^\nu K_\nu(\kappa \|\mathbf{x}\|)$  is the Matern spatial correlation function.

The interspecific cross covariance function does not lend to a simple closed form expression. Instead, we can see the corresponding component of the power spectrum matrix is the sum of convolutions of Matern correlation functions with Bessel functions. In particular, denoting  $f * g$  the convolution of two functions  $f(\mathbf{x}), g(\mathbf{x})$ , we have

$$C_{HP}(\mathbf{x}) \approx \frac{2G_P B_P}{N_H \sigma_H^2 \sigma_P^2 (A_H - B_H)} \left[ K_0 \left( \sqrt{\frac{2G_P}{\sigma_P^2} (A_P + B_P)} \|\mathbf{x}\| \right) * M \left( \mathbf{x} | 1, \sqrt{\frac{2G_H}{\sigma_H^2} (A_H - B_H)} \right) \right] - \frac{2G_H B_H}{N_P \sigma_H^2 \sigma_P^2 (A_P + B_P)} \left[ K_0 \left( \sqrt{\frac{2G_H}{\sigma_H^2} (A_H - B_H)} \|\mathbf{x}\| \right) * M \left( \mathbf{x} | 1, \sqrt{\frac{2G_P}{\sigma_P^2} (A_P + B_P)} \right) \right]. \quad (22)$$

Although characteristic length scales are obvious for  $C_{HH}$  and  $C_{PP}$  (by normalizing distance, they are  $\xi_H = \sqrt{\sigma_H^2/[2G_H(A_H - B_H)]}$  and  $\xi_P = \sqrt{\sigma_P^2/[2G_P(A_P + B_P)]}$  respectively), finding a corresponding characteristic length for  $C_{HP}$  is not so obvious. Fortunately there exist alternative measures of spatial scale that we can employ. In particular, we can use a measure called *integral range* to study spatial patterns at a more global scale and a measure called *smoothness microscale* to study the more fine-grained details of spatial patterns.

The *integral range* a stationary isotropic process on  $\mathbb{R}^2$  characterized by a correlation function  $N(\mathbf{x})$  is given by

$$l = \sqrt{\int_{\mathbb{R}^2} N(\mathbf{x}) d\mathbf{x}}.$$

However, since the correlation function we are interested may become negative, we use the modified integral range  $l' = \sqrt{|\int_{\mathbb{R}^2} N(\mathbf{x}) d\mathbf{x}|}$ .

The *smoothness microscale* has a more complex definition, involving the Laplacian of the covariance function evaluated at zero lag in the denominator. This is a potential issue since the Laplacian of  $K_0(\mathbf{x})$  and  $M(\mathbf{x}|\kappa, 1)$  evaluated at zero lag both take infinite values.

The *correlation length* may be a feasible alternative, but what does it tell us that integral range doesn't already cover?

## 6.1 Computing Integral Lengths for General Dispersal Kernels

For more general dispersal kernels, including heavy-tailed kernels, we focus on the more general form of the SPDE:

$$b_H(\kappa_H^2 - \Delta)^{\alpha_H/2} \bar{Z}_H + b_{HP} \bar{Z}_P = \sqrt{V_H} \dot{W}_H \quad (23a)$$

$$b_{PH} \bar{Z}_H + b_P(\kappa_P^2 - \Delta)^{\alpha_P/2} \bar{Z}_P = \sqrt{V_P} \dot{W}_P \quad (23b)$$

The parameters  $\alpha_H$  and  $\alpha_P$  are determined by the dispersal kernel. In particular, under diffusive dispersal (ie., Gaussian kernels) we have  $\alpha_H = \alpha_P = 2$ . In general we can have  $1 < \alpha_H, \alpha_P \leq 2$  where  $\alpha_H, \alpha_P < 2$  implies heavy-tailed dispersal kernels (stable distributions in particular).

Under our model of coevolution with diffusive dispersal we have the parameterization

- $b_H = (\sigma_H^2/2)^{\alpha_H/2}$ ,
- $b_P = (\sigma_P^2/2)^{\alpha_P/2}$ ,
- $b_{HP} = G_H B_H$ ,
- $b_{PH} = -G_P B_P$ ,
- $\kappa_H^2 = 2G_H(A_H - B_H)/\sigma_H^2$ ,
- $\kappa_P^2 = 2G_P(A_P + B_P)/\sigma_P^2$ ,
- $V_H = G_H/N_H$
- $V_P = G_P/N_P$

with  $\alpha_H = \alpha_P = 2$ . An important question is to understand whether the parameterization of  $\kappa_H$  and  $\kappa_P$  will change when dispersal follows heavy-tailed distributions so that  $\alpha_H, \alpha_P < 2$ . For now we side-step this question by proceeding with the parameterization using  $b$ 's,  $\kappa$ 's,  $\alpha$ 's and  $V$ 's.

Keeping our assumption of weakly coupled stochastic fields so that  $b_{HP}^2, b_{PH}^2, b_{HP}b_{PH} \approx 0$ , we obtain

$$S_{\zeta_{HH}}(\mathbf{k}) \approx \frac{V_H/b_H^2}{(\kappa_H^2 + \|\mathbf{k}\|)^{\alpha_H}}, \quad (24a)$$



$$S_{\bar{\zeta}_{PP}}(\mathbf{k}) \approx \frac{V_P/b_P^2}{(\kappa_P^2 + \|\mathbf{k}\|)^{\alpha_P}}, \quad (24b)$$

$$S_{\bar{\zeta}_{HP}}(\mathbf{k}) \approx -\frac{b_{PH}V_H}{b_P b_H^2}(\kappa_P^2 + \|\mathbf{k}\|)^{-\alpha_P/2}(\kappa_H^2 + \|\mathbf{k}\|)^{-\alpha_H} - \frac{b_{HP}V_P}{b_H b_P^2}(\kappa_H^2 + \|\mathbf{k}\|)^{-\alpha_H/2}(\kappa_P^2 + \|\mathbf{k}\|)^{-\alpha_P}. \quad (24c)$$

Using properties of Fourier transforms, we know the local variance of trait values for each species is given by

$$C_{HH}(\mathbf{0}) = \int_{\mathbb{R}^2} S_{\bar{\zeta}_{HH}}(\mathbf{k}) d\mathbf{k} \approx \frac{V_H/b_H^2}{(\alpha_H - 1)\kappa_H^{2(\alpha_H-1)}}, \quad (25a)$$

$$C_{PP}(\mathbf{0}) = \int_{\mathbb{R}^2} S_{\bar{\zeta}_{PP}}(\mathbf{k}) d\mathbf{k} \approx \frac{V_P/b_P^2}{(\alpha_P - 1)\kappa_P^{2(\alpha_P-1)}}. \quad (25b)$$

Then, the integral ranges for spatial patterns of intraspecific traits are

$$l_H = \sqrt{\frac{S_{\bar{\zeta}_{HH}}(\mathbf{0})}{C_{HH}(\mathbf{0})}} \approx \frac{\alpha_H - 1}{\kappa_H} = (\alpha_H - 1) \sqrt{\frac{\sigma_H^2}{2G_H(A_H - B_H)}}, \quad (26a)$$

$$l_P = \sqrt{\frac{S_{\bar{\zeta}_{PP}}(\mathbf{0})}{C_{PP}(\mathbf{0})}} \approx \frac{\alpha_P - 1}{\kappa_P} = (\alpha_P - 1) \sqrt{\frac{\sigma_P^2}{2G_P(A_P + B_P)}}. \quad (26b)$$

Unfortunately, although the integral  $\int_{\mathbb{R}^2} S_{\bar{\zeta}_{HP}}(\mathbf{k}) d\mathbf{k}$  does have a closed-form expression, it is quite long and filled with many bizarre transcendental functions. Hence, the expression for integral range of interspecific trait patterns may not provide much intuition for the general case. However, in the case of Gaussian dispersal, we have

$$\begin{aligned} C_{HP}(\mathbf{0}) &= \int_{\mathbb{R}^2} S_{\bar{\zeta}_{HP}}(\mathbf{k}) d\mathbf{k} \\ &= \frac{b_{PH}V_H}{b_P b_H^2} \frac{\kappa_H^2(1 - \ln \kappa_H^2) - \kappa_P^2(1 - \ln \kappa_P^2)}{\kappa_H^2(\kappa_H - \kappa_P)^2(\kappa_H + \kappa_P)^2} + \frac{b_{HP}V_P}{b_H b_P^2} \frac{\kappa_P^2(1 - \ln \kappa_P^2) - \kappa_H^2(1 - \ln \kappa_H^2)}{\kappa_H^2(\kappa_H - \kappa_P)^2(\kappa_H + \kappa_P)^2} \end{aligned} \quad (27)$$

Hence, the integral range is slightly easier to read in this case:

$$\begin{aligned} l_{HP} &= \sqrt{\frac{S_{\bar{\zeta}_{HP}}(\mathbf{0})}{C_{HP}(\mathbf{0})}} \\ &= \frac{(\kappa_H^2 - \kappa_P^2)^2(b_P b_{PH} \kappa_P^2 V_H + b_H b_{HP} \kappa_H^2 V_P)}{b_P b_{PH} V_H \kappa_H^2 \kappa_P^4 (\kappa_P^2 - \kappa_H^2 (1 + \ln(\kappa_P^2/\kappa_H^2))) + b_H b_{HP} V_P \kappa_P^2 \kappa_H^4 (\kappa_H^2 - \kappa_P^2 (1 + \ln(\kappa_H^2/\kappa_P^2)))}. \end{aligned} \quad (28)$$

Although it is possible this expression will greatly simplify when model parameters are substituted in, it is also possible it will get even worse. Hence, we might want to search for other ways to quantify characteristic lengths.

**Regardless of the metric chosen, we can at least visualize how the characteristic lengths change as functions of biological parameters, even for heavy-tailed dispersal kernels.**

## 7 Measures of Local Adaptation

To measure local adaptation as a function of spatial lag  $\mathbf{x}$ , we consider the fitness difference for individuals interacting with local partners versus partners located at the spatial lag  $\mathbf{x}$ . In particular, denoting  $\bar{m}_H(\mathbf{x}, \mathbf{y})$

the growth rate of the host from location  $\mathbf{x}$  when confronted with a parasite from location  $\mathbf{y}$  and  $\bar{m}_P(\mathbf{y}, \mathbf{x})$  the growth rate of the parasite from location  $\mathbf{y}$  when confronted with a host from location  $\mathbf{x}$ , we have

$$\bar{m}_H(\mathbf{x}, \mathbf{y}) = r_H - \frac{A_H}{2}(\theta_H - \bar{Z}_H(\mathbf{x}))^2 + \frac{B_H}{2}(\bar{Z}_P(\mathbf{y}) - \bar{Z}_H(\mathbf{x}))^2 - \frac{A_H - B_H}{2}\sigma_H^2 + \frac{B_H}{2}\sigma_P^2, \quad (29a)$$

$$\bar{m}_P(\mathbf{y}, \mathbf{x}) = r_P - \frac{A_P}{2}(\theta_P - \bar{Z}_P(\mathbf{y}))^2 - \frac{B_P}{2}(\bar{Z}_H(\mathbf{x}) - \bar{Z}_P(\mathbf{y}))^2 - \frac{A_P + B_P}{2}\sigma_P^2 - \frac{B_P}{2}\sigma_H^2, \quad (29b)$$

Then, since we consider stationary processes, the fitness difference for confronting individuals at the lag  $\mathbf{x}$  is given by

$$\Delta_H(\mathbf{x}) = \bar{m}_H(\mathbf{0}, \mathbf{0}) - \bar{m}_H(\mathbf{0}, \mathbf{x}) = \frac{B_H}{2} [(\bar{Z}_P(\mathbf{0}) - \bar{Z}_H(\mathbf{0}))^2 - (\bar{Z}_P(\mathbf{x}) - \bar{Z}_H(\mathbf{0}))^2], \quad (30a)$$

$$\Delta_P(\mathbf{x}) = \bar{m}_P(\mathbf{0}, \mathbf{0}) - \bar{m}_P(\mathbf{0}, \mathbf{x}) = \frac{B_P}{2} [(\bar{Z}_H(\mathbf{x}) - \bar{Z}_P(\mathbf{0}))^2 - (\bar{Z}_H(\mathbf{0}) - \bar{Z}_P(\mathbf{0}))^2]. \quad (30b)$$

Taking expectations provides

$$\mathbb{E}[\Delta_H(\mathbf{x})] = \frac{B_H}{2} [(\bar{z}_P - \bar{z}_H)^2 + C_{PP}(\mathbf{0}) + C_{HH}(\mathbf{0}) - 2C_{HP}(\mathbf{0}) - (\bar{z}_P - \bar{z}_H)^2 - C_{PP}(\mathbf{0}) - C_{HH}(\mathbf{0}) + 2C_{HP}(\mathbf{x})], \quad (31a)$$

$$\mathbb{E}[\Delta_P(\mathbf{x})] = \frac{B_P}{2} [(\bar{z}_H - \bar{z}_P)^2 + C_{PP}(\mathbf{0}) + C_{HH}(\mathbf{0}) - 2C_{HP}(\mathbf{x}) - (\bar{z}_H - \bar{z}_P)^2 - C_{PP}(\mathbf{0}) - C_{HH}(\mathbf{0}) + 2C_{HP}(\mathbf{0})]. \quad (31b)$$

Since  $\bar{z}_P, \bar{z}_H$  are spatially homogeneous, this simplifies to

$$\mathbb{E}[\Delta_H(\mathbf{x})] = B_H [C_{HP}(\mathbf{x}) - C_{HP}(\mathbf{0})], \quad (32a)$$

$$\mathbb{E}[\Delta_P(\mathbf{x})] = B_P [C_{HP}(\mathbf{0}) - C_{HP}(\mathbf{x})]. \quad (32b)$$

The classical definition of local adaptation is obtained by sending  $\|\mathbf{x}\| \rightarrow \infty$ . In particular,  $\lim_{\|\mathbf{x}\| \rightarrow \infty} C_{HP}(\mathbf{x}) = 0$ . This can be compared to the case of limited dispersal by evaluating at  $\|\mathbf{x}\| = \sqrt{\pi(\sigma_H^2 + \sigma_P^2)}/2$ , which is the expected distance between interacting individuals before dispersal.

## 7.1 Comparing Interspecific Fitnesses

$$\begin{aligned} \Delta(\mathbf{x}) &= \bar{m}_H(\mathbf{0}, \mathbf{x}) - \bar{m}_P(\mathbf{x}, \mathbf{0}) \\ &= (r_H - r_P) - \frac{1}{2} [A_H(\theta_H - \bar{Z}_H(\mathbf{0}))^2 - A_P(\theta_P - \bar{Z}_P(\mathbf{x}))^2 + (B_H + B_P)(\bar{Z}_H(\mathbf{0}) - \bar{Z}_P(\mathbf{x}))^2 \\ &\quad - (A_H - B_H + B_P)\sigma_H^2 + (A_P + B_P + B_H)\sigma_P^2] \end{aligned} \quad (33)$$

$$\begin{aligned} \mathbb{E}[\Delta(\mathbf{x})] &= (r_H - r_P) - \frac{1}{2} [A_H(\theta_H - \bar{z}_H)^2 + A_H C_{HH}(\mathbf{0}) - A_P(\theta_P - \bar{z}_P(\mathbf{x}))^2 - A_P C_{PP}(\mathbf{0}) \\ &\quad + (B_H + B_P)(\bar{z}_H - \bar{z}_P)^2 + (B_H + B_P)[C_{PP}(\mathbf{0}) + C_{HH}(\mathbf{0}) - 2C_{HP}(\mathbf{x})] \\ &\quad - (A_H - B_H + B_P)\sigma_H^2 + (A_P + B_P + B_H)\sigma_P^2]. \end{aligned} \quad (34)$$

Using equilibrium expressions for  $\bar{z}_H, \bar{z}_P$  and assuming  $\theta_H = \theta_P$ , *Mathematica* yields

$$\begin{aligned} \mathbb{E}[\Delta(\mathbf{x})] &= (r_H - r_P) + \frac{1}{2} [(B_H - A_H - B_P)\sigma_H^2 + (A_P + B_P + B_H)\sigma_P^2 \\ &\quad + (B_P - A_H - B_H)C_{HH}(\mathbf{0}) + (A_P + B_P - B_H)C_{PP}(\mathbf{0})] + (B_P - B_H)C_{HP}(\mathbf{x}) \end{aligned} \quad (35)$$

## 7.2 Using Expected Lifetime Reproductive Output

Individual fitness determined by interactions between individuals drawn from different locations and averaged across the diversity found in those locations are given by

$$\bar{w}_H(\mathbf{x}, \mathbf{y}) = \exp \left( r_H - \frac{1}{2} \frac{(\theta_H - \bar{Z}_H(\mathbf{x}))^2}{\sigma_H^2 + 1/A_H} + \frac{1}{2} \frac{(\bar{Z}_P(\mathbf{y}) - \bar{Z}_H(\mathbf{x}))^2}{\sigma_H^2 + \sigma_P^2 + 1/B_H} \right), \quad (36a)$$

$$\bar{w}_P(\mathbf{y}, \mathbf{x}) = \exp \left( r_P - \frac{1}{2} \frac{(\theta_P - \bar{Z}_P(\mathbf{y}))^2}{\sigma_P^2 + 1/A_P} - \frac{1}{2} \frac{(\bar{Z}_H(\mathbf{x}) - \bar{Z}_P(\mathbf{y}))^2}{\sigma_H^2 + \sigma_P^2 + 1/B_P} \right). \quad (36b)$$

Then, an analogous metric for adaptation at spatial lag  $\mathbf{x}$  is given by

$$N_H(\mathbf{x}) = \bar{w}_H(\mathbf{0}, \mathbf{0}) / \bar{w}_H(\mathbf{0}, \mathbf{x}) = \sqrt{\exp \left( \frac{(\bar{Z}_P(\mathbf{0}) - \bar{Z}_H(\mathbf{0}))^2}{\sigma_H^2 + \sigma_P^2 + 1/B_H} - \frac{(\bar{Z}_P(\mathbf{x}) - \bar{Z}_H(\mathbf{0}))^2}{\sigma_H^2 + \sigma_P^2 + 1/B_H} \right)}, \quad (37a)$$

$$N_P(\mathbf{x}) = \bar{w}_P(\mathbf{0}, \mathbf{0}) / \bar{w}_P(\mathbf{0}, \mathbf{x}) = \sqrt{\exp \left( \frac{(\bar{Z}_H(\mathbf{x}) - \bar{Z}_P(\mathbf{0}))^2}{\sigma_H^2 + \sigma_P^2 + 1/B_P} - \frac{(\bar{Z}_H(\mathbf{0}) - \bar{Z}_P(\mathbf{0}))^2}{\sigma_H^2 + \sigma_P^2 + 1/B_P} \right)}. \quad (37b)$$

Not sure this is helping...

## 8 Environmental Heterogeneity

We can extend our model to allow the abiotic optimum, representing environmental condition, to vary across space. We now denote  $\Theta_H(\mathbf{x}), \Theta_P(\mathbf{x})$  the random fields corresponding to the abiotic optimum at location  $\mathbf{x}$  for the host and parasite respectively. Then, assuming the abiotic optima follow Whittle covariance functions, we have

$$G_H A_H (\Theta_H - \bar{Z}_H) - G_H B_H (\bar{Z}_P - \bar{Z}_H) + \frac{\sigma_H^2}{2} \Delta \bar{Z}_H = \sqrt{\frac{G_H}{N_H}} \dot{W}_H, \quad (38a)$$

$$G_P A_P (\Theta_P - \bar{Z}_P) + G_P B_P (\bar{Z}_H - \bar{Z}_P) + \frac{\sigma_P^2}{2} \Delta \bar{Z}_P = \sqrt{\frac{G_P}{N_P}} \dot{W}_P, \quad (38b)$$

$$\gamma_H (\theta_H - \Theta_H) + \frac{R_H}{2} \Delta \Theta_H = \dot{Q}_H, \quad (38c)$$

$$\gamma_P (\theta_P - \Theta_P) + \frac{R_P}{2} \Delta \Theta_P = \dot{Q}_P, \quad (38d)$$

where  $\dot{Q}_H, \dot{Q}_P$  are spatial white-noise processes driving the abiotic optima,  $\gamma_H, \gamma_P$  determine the variance around the deterministic and spatially homogeneous  $\theta_H, \theta_P$  and  $R_H, R_P$  determine the spatial covariance (but not cross-covariance) of the abiotic optima. This model can be further generalized so that  $\Theta_H(\mathbf{x}), \Theta_P(\mathbf{x})$  follow general Matern covariance functions to get

$$G_H A_H (\Theta_H - \bar{Z}_H) - G_H B_H (\bar{Z}_P - \bar{Z}_H) + \frac{\sigma_H^2}{2} \Delta \bar{Z}_H = \sqrt{\frac{G_H}{N_H}} \dot{W}_H, \quad (39a)$$

$$G_P A_P (\Theta_P - \bar{Z}_P) + G_P B_P (\bar{Z}_H - \bar{Z}_P) + \frac{\sigma_P^2}{2} \Delta \bar{Z}_P = \sqrt{\frac{G_P}{N_P}} \dot{W}_P, \quad (39b)$$

$$\gamma_H \theta_H + \left( -\gamma_H + \frac{R_H}{2} \Delta \right)^{\beta_H/2} \Theta_H = \dot{Q}_H, \quad (39c)$$

$$\gamma_P \theta_P + \left( -\gamma_P + \frac{R_P}{2} \Delta \right)^{\beta_P/2} \Theta_P = \dot{Q}_P. \quad (39d)$$

Now  $\beta_H, \beta_P$  determine long-range spatial correlations of the abiotic optima (with themselves, not each other) along with the roughness of the fields  $\Theta_H, \Theta_P$ .

## References

- Hu, Xiangping, Daniel Simpson, Finn Lindgren, and Håvard Rue. 2013. “Multivariate Gaussian Random Fields Using Systems of Stochastic Partial Differential Equations.” *arXiv Preprint arXiv:1307.1379*.
- Sigrist, Fabio, Hans R. Künsch, and Werner A. Stahel. 2014. “Stochastic Partial Differential Equation Based Modelling of Large Space-Time Data Sets.” *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 77 (1): 3–33. <https://doi.org/10.1111/rssb.12061>.
- Whittle, Peter. 1963. “Stochastic-Processes in Several Dimensions.” *Bulletin of the International Statistical Institute* 40 (2): 974–94.