The Phenotypic Signature of Host-Parasite Coevolution in Continuous Space

A Preprint

Bob Week
Integrative Biology
Michigan State University
East Lansing, MI 48824
weekrobe@msu.edu

Gideon Bradburd
Integrative Biology
Michigan State University
East Lansing, MI 48824
bradburd@msu.edu

February 26, 2021

Abstract

Here we identify the phenotypic signature of host-parasite coevolution in continuous space.

***K*eywords** blah · blee · bloo · these are optional and can be removed

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, local effective sizes 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, local effective sizes 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:

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

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

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:

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

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

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 Gavrilets 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., $\bar{z}_H(x), \bar{z}_P(x)$ where $x = (x_1, x_2) \in \mathbb{R}^2$). 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:

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

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

where $D_H, D_P > 0$ are dispersal rates for each species and $\Delta = \frac{\partial^2}{\partial x_1^2} + \frac{\partial^2}{\partial x_2^2}$ is the diffusion 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:

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

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

where N_P, N_H are the local abundance 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 capitol $\bar{Z}_H, \bar{Z}_P$ 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 Extensions

3.5.1 Heterogeneous aboitic optima

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

4 Methods

To study the continuous-space signature of coevolution, we can start with an analytical approach. However, if the corresponding calculations prove to be analytically intractable or time costly, we can employ simulation-based methods to describe the shape of the autocorrelations and cross-correlation in relevant regions of parameters space. The analytical approach would begin by identifying stable attractors of the deterministic system using classical PDE theory. Following this, we may possibly apply theory of SPDE to describe stationary distributions associated with each attractor. This may lend analytical solutions for the expectation and variance of intraspecific autocorrelations and the interspecific cross-correlation, which are defined in Appendix A.1 below.

4.1 Nondimensional Analysis

Nondimensional analysis is an approach to simplify mathematical models by transforming them into equations without units. In particular, traits $\bar{Z}_H, \bar{Z}_P$ are in phenotypic units, additive genetic variances G_H, G_P are in squared phenotypic units, spatial coordinates $x = (x_1, x_2)$ are in units of distance and dispersal coefficients D_H, D_P are in units of distance squared. By removing these units, we can pinpoint characteristic scales emerging from the interactions of different processes. From Murray 2003:

Table 1: Summary of notation.

Variable/Parameter	Description	Range
$x = (x_1, x_2)$	Spatial coordinates	$x \in \mathbb{R}^2$
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	$A_H, A_P \geq 0$
$\theta_H(x), \theta_P(x)$	Abiotic trait optima at location x	$\theta_H(x), \theta_P(x) \in \mathbb{R}$
B_H, B_P	Strengths of biotic selection	$B_H, B_P \geq 0$
G_H, G_P	Additive genetic variances	$G_H, G_P \geq 0$
D_H, D_P	Dispersal coefficients	$D_H, D_P \geq 0$
N_H, N_P	Local effective population sizes	$N_H, N_P \geq 0$
$\dot{W}_H, \dot{W}_P$	Independent space-time white noise processes	$\dot{W}_H(x), \dot{W}_P(x)$ random variables in $\mathbb{R}$
$\bar{Z}_H(x), \bar{Z}_P(x)$	Local mean traits at x	$\bar{Z}_H(x), \bar{Z}_P(x)$ random variables in $\mathbb{R}$
$\bar{z}_H(x), \bar{z}_P(x)$	Expected local mean traits at x	$\bar{z}_H(x), \bar{z}_P(x) \in \mathbb{R}$

> One of the most useful aspects of a nondimensional analysis, with resulting nondimensional groupings of the parameters, is that it is possible to assess how different physical effects, quantified by the parameters in the nondimensionalisation, trade off against one another.

Hence, we can use nondimensional analysis to assess how selection, dispersal and drift interact to determine characteristic spatial scales. The difficulty here is that there's two species with different dispersal coefficients. This leads to two distinct characteristic spatial scales at which patterns emerge. Perhaps we can focus on patterns of matching/mis-matching by tracking $Y(x) := \bar{Z}_H(x) - \bar{Z}_P(x)$? The trouble with this is that the species are evolving to different strengths of abiotic selection. Hence, it's not clear what rescaling would nondimensionalize Y.

5 Discussion

5.1 A Note on Biological Diversity vs Statistical Uncertainty

An important distinction to make when analyzing spatial patterns of coevolving species is the difference between statistical uncertainty and biological variation across space. In particular, we can ignore the stochastic effects of random genetic drift and focus on patterns produced by deterministic processes through studying the PDE (3). In this case, we might study quantities such as the global mean trait values (ie., mean trait values averaged across space) and the spatial variance of mean trait values. These quantities are purely functions of existing biological diversity and do not take into account uncertainties inherit in the process of evolution (eg., random genetic drift). Once drift is accounted for, the global mean and spatial variance of local mean trait values themselves become random variables.

To understand why spatial expectations and variances become random variables in the presence of drift, we can think of each possible instance of the white-noise processes $\dot{W}_H, \dot{W}_P$. In probability theory these instances are called sample paths and are typically denoted by the variable ω. The set of all ω is denoted Ω and is referred to as the probability space. Hence, we would refer to $\dot{W}_H(\omega), \dot{W}_P(\omega)$ as particular sample

paths of the processes $\dot{W}_H, \dot{W}_P$. This implies that a solution to the stochastic system (4) is really a set of solutions indexed by $\omega \in \Omega$. For each ω we can compute spatial averages, variances and covariance of mean traits. Hence, the probabilistic expectation and variance of these spatial statistics are found by integrating across Ω.

This heavily theoretical discussion is important for understanding the difference between spatial autocorrelation and the covariance function of a spatial stochastic process. In particular, the spatial autocorrelation we are interested in (denoted $\rho_{ff}(r)$ for a spatial function f) corresponds to deterministic patterns. Hence, when accounting for random genetic drift, ρ_{ff} will be a random function. To compute the expectation, variance and covariance of this function, we can use properties of the associated spatial stochastic process (the expectation and covariance function, in particular).

Finally, for the sake of completion it is worthwhile to note that sampling error adds a second layer of stochasticity.

Appendices

A Spatial Moments

Suppose $f(x)$ is a function of a two-dimensional spatial parameter $x = (x_1, x_2)$. For simplicity, let's consider a rectangular subset Γ of $\mathbb{R}^2$ with periodic boundaries (ie., the surface of a torus). Then we can compute the spatial average of $f(x)$ via

$$\bar{f} = \frac{1}{|\Gamma|} \int_\Gamma f(x) dx, \tag{5}$$

where $|\Gamma|$ is the size of the subset Γ. The spatial variance of f is then

$$\mathrm{Var}(f) = \frac{1}{|\Gamma|} \int_\Gamma (f(x) - \bar{f})^2 dx, \tag{6}$$

A.1 Spatial Autocorrelation and Cross-correlation

The cross-correlation of two functions f, g is defined by

$$\rho_{fg}(x) = \int_\Gamma f(y) g(y - x) dy. \tag{7}$$

We can reduce this quantity to a function of distance $r = \sqrt{x_1^2 + x_2^2}$ using the average

$$\bar{\rho}_{fg}(r) = \frac{1}{2\pi r} \int_0^{2\pi} \rho_{fg}((r\cos\theta, r\sin\theta)) d\theta. \tag{8}$$

The autocorrelation of f is then ρ_{ff}.

A.2 Cross-covariance

Following the above definitions of spatial moments and cross-correlation, we compute the cross-covariance of two spatial functions f and g (in 2D space) via

$$K_{fg}(x) = \sqrt{\mathrm{Var}(f)\mathrm{Var}(g)} \rho_{f,g}(x). \tag{9}$$

Hence, inspired by the definition of $\bar{\rho}_{fg}$, we can define the cross covariance between spatial functions f and g at two locations separated by distance r via

$$\bar{K}_{fg}(r) = \frac{1}{2\pi r} \sqrt{\mathrm{Var}(f)\mathrm{Var}(g)} \int_0^{2\pi} K_{fg}((r\cos\theta, r\sin\theta)) d\theta. \tag{10}$$

B 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

$$0 = G_H A_H (\theta_H - \bar{z}_H) - G_H B_H (\bar{z}_P - \bar{z}_H) + \frac{D_H}{2} \Delta \bar{z}_H, \tag{11a}$$

$$0 = G_P A_P (\theta_P - \bar{z}_P) + G_P B_P (\bar{z}_H - \bar{z}_P) + \frac{D_P}{2} \Delta \bar{z}_P. \tag{11b}$$

Solving this system for the mean traits $\bar{z}_H(x_1, x_2)$ and $\bar{z}_P(x_1, x_2)$ 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

$$0 = G_H A_H (\theta_H - \bar{z}_H) - G_H B_H (\bar{z}_P - \bar{z}_H), \tag{12a}$$

$$0 = G_P A_P (\theta_P - \bar{z}_P) + G_P B_P (\bar{z}_H - \bar{z}_P). \tag{12b}$$

This linear system is uniquely solved by

$$\bar{z}_H(x_1, x_2) \equiv \frac{(A_P + B_P) A_H \theta_H - B_H A_P \theta_P}{(A_P + B_P) A_H - B_H A_P}, \tag{13a}$$

$$\bar{z}_P(x_1, x_2) \equiv \frac{(A_H - B_H) A_P \theta_P + B_P A_H \theta_H}{(A_H - B_H) A_P + B_P A_H}, \tag{13b}$$

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

$$\vec{z} = \begin{pmatrix} \bar{z}_H \\ \bar{z}_P \end{pmatrix}, \ \vec{b} = \begin{pmatrix} G_H A_H \theta_H \\ G_P A_P \theta_P \end{pmatrix}, \tag{14a}$$

$$M = \begin{pmatrix} G_H(B_H - A_H) & -G_H B_H \\ G_P B_P & -G_P(A_P + B_P) \end{pmatrix}. \tag{14b}$$

It turns that if the real parts of the eigenvalues of M are negative then equilibrium (13) 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.

C   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

$$G_H A_H (\theta_H - \bar{Z}_H) - G_H B_H (\bar{Z}_P - \bar{Z}_H) + \frac{D_H}{2} \Delta \bar{Z}_H = \sqrt{\frac{G_H}{N_H}} \dot{W}_H, \tag{15a}$$

$$G_P A_P (\theta_P - \bar{Z}_P) + G_P B_P (\bar{Z}_H - \bar{Z}_P) + \frac{D_P}{2} \Delta \bar{Z}_P = \sqrt{\frac{G_P}{N_P}} \dot{W}_P. \tag{15b}$$

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

$$b^2(a - u) + \Delta u = \sigma \dot{W}. \tag{16}$$

In the case of two spatial dimensions, it is known that equation (16) 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 (15) will have Whittle cross-covariance matrix-valued functions.

D   The autocovariances and cross-covariance of $\bar{Z}_H$ and $\bar{Z}_P$

Set $\bar{z}_H(x) = \mathbb{E}[\bar{Z}_H(x)]$ and $\bar{z}_P(x) = \mathbb{E}[\bar{Z}_P(x)]$. Since the system (15) is linear, we can expect $(\bar{z}_H, \bar{z}_P)$ to solve the associated deterministic system. Then, it seems reasonable to expect the cross-covariance of $\bar{Z}_H$ and $\bar{Z}_P$ across space to satisfy

$$K_{\bar{Z}_H \bar{Z}_P}(x) = K_{\bar{z}_H \bar{z}_P}(x) + \mathcal{A}_{HP}(x) + \mathcal{B}_{HP}(x), \tag{17}$$

where $\mathcal{A}_{HP}(x)$ is the cross-covariance of $\bar{Z}_H$ and $\bar{Z}_P$ generated by abiotic stabilizing selection and $\mathcal{B}_{HP}(x)$ is the cross-covariance generated by coevolutionary selection.

- **Note:** In the case of the stable equilibrium considered above, $\bar{z}_H$ and $\bar{z}_P$ are spatially homogeneous which implies $K_{\bar{z}_H \bar{z}_P}(x) \equiv \sqrt{\text{Var}(\bar{z}_H)\text{Var}(\bar{z}_P)} = 0$ since $\text{Var}(\bar{z}_H) = \text{Var}(\bar{z}_P) = 0$.

Similarly, we might expect the autocovariances of $\bar{Z}_H$ and $\bar{Z}_P$ to satisfy

$$K_{\bar{Z}_H \bar{Z}_H}(x) = K_{\bar{z}_H \bar{z}_H}(x) + \mathcal{A}_H(x) + \mathcal{B}_H(x), \tag{18}$$

$$K_{\bar{Z}_P \bar{Z}_P}(x) = K_{\bar{z}_P \bar{z}_P}(x) + \mathcal{A}_P(x) + \mathcal{B}_P(x), \tag{19}$$

where $\mathcal{A}_X(x)$ is the autocovariance of species X generated by abiotic stabilizing selection and $\mathcal{B}_X(x)$ is the autocovariance generated by unilateral biotic selection on species X. In general, the signature of coevolution is likely to be found in the six covariance functions: $K_{\bar{z}_H \bar{z}_P}(x), K_{\bar{z}_H \bar{z}_H}(x), K_{\bar{z}_P \bar{z}_P}(x), \mathcal{B}_{HP}(x), \mathcal{B}_H(x)$ and $\mathcal{B}_P(x)$.

E   Nondimensionalization

Our approach to nondimensionalize system (4) is borrowed from Polechova & Barton (2015). In particular, these authors nondimensionalize the SPDE

$$\frac{\partial \bar{Z}}{\partial t} = G \frac{\partial \bar{r}}{\partial \bar{Z}} + \frac{D}{2} \Delta \bar{z} + \sqrt{\frac{G}{N}} \dot{W},$$

where $\bar{r}$ is the population growth rate and its derivative with respect to $\bar{Z}$ represents selection.

F   More?

- Explore other patterns of spatial covariance using different models of spatial movement.
  - This leads to other random surfaces such as fractional Brownian surfaces which are characterized by different families of covariance functions.
  - Hence, it may be possible to learn models of spatial movement based on patterns of spatial covariance.
- What happens when interacting species have different movement models?

G   Application

- How tough would it be to revisit toju and pauw data-sets to infer coevolution again?

H   Applying (Hu et al. 2013) to Compute 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 (15) 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 $x = (x_1, x_2)$ to a two-dimensional frequency variable $s = (s_1, s_2)$, where s_1, s_2 are 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 (13). Under this change of variables, an Itô formula can be applied (need to fact-check) to show the stationary system (15) becomes

$$\left(\frac{D_H}{2}\Delta - G_H(A_H - B_H)\right)\bar{\zeta}_H - G_H B_H \bar{\zeta}_P = \sqrt{\frac{G_H}{N_H}}\dot{W}_H, \tag{20a}$$

$$G_P B_P \bar{\zeta}_H + \left(\frac{D_P}{2}\Delta - G_P(A_P + B_P)\right)\bar{\zeta}_P = \sqrt{\frac{G_P}{N_P}}\dot{W}_P. \tag{20b}$$

To consolidate notation, we set

$$\mathscr{L} = \begin{pmatrix} G_H(A_H - B_H) - \frac{D_H}{2}\Delta & G_H B_H \\ -G_P B_P & G_P(A_P + B_P) - \frac{D_P}{2}\Delta \end{pmatrix}, \tag{21a}$$

$$\bar{\boldsymbol{\zeta}} = \begin{pmatrix} \bar{\zeta}_H \\ \bar{\zeta}_P \end{pmatrix}, \; \boldsymbol{V} = \begin{pmatrix} -\sqrt{\frac{G_H}{N_H}}\dot{W}_H \\ -\sqrt{\frac{G_P}{N_P}}\dot{W}_P \end{pmatrix}. \tag{21b}$$

Then, the stationary system can equally be written as

$$\mathscr{L}\bar{\boldsymbol{\zeta}} = \boldsymbol{V}. \tag{22}$$

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

$$\boldsymbol{\mathcal{H}}\hat{\boldsymbol{\zeta}} = \hat{\boldsymbol{V}}, \tag{23}$$

where

$$\mathscr{H} = \begin{pmatrix} G_H(A_H - B_H) + \frac{D_H}{2}\|\boldsymbol{k}\|^2 & G_H B_H \\ -G_P B_P & G_P(A_P + B_P) + \frac{D_P}{2}\|\boldsymbol{k}\|^2 \end{pmatrix}, \tag{24a}$$

$$\hat{\boldsymbol{\zeta}} = \begin{pmatrix} \hat{\zeta}_H \\ \hat{\zeta}_P \end{pmatrix}, \hat{\boldsymbol{V}} = \begin{pmatrix} \hat{V}_H \\ \hat{V}_P \end{pmatrix}, \tag{24b}$$

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

$$\boldsymbol{S}_{\bar{\boldsymbol{\zeta}}} = \begin{pmatrix} S_{\bar{\zeta}_{HH}} & S_{\bar{\zeta}_{HP}} \\ S_{\bar{\zeta}_{PH}} & S_{\bar{\zeta}_{PP}} \end{pmatrix} = \begin{pmatrix} \mathbb{E}[\hat{\zeta}_H \hat{\zeta}_H] & \mathbb{E}[\hat{\zeta}_H \hat{\zeta}_P] \\ \mathbb{E}[\hat{\zeta}_H \hat{\zeta}_P] & \mathbb{E}[\hat{\zeta}_P \hat{\zeta}_P] \end{pmatrix} = \mathscr{H}^{-1} \boldsymbol{S_V} \mathscr{H}^{-H}, \tag{25}$$

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

$$\hat{\boldsymbol{V}} = \begin{pmatrix} \sqrt{G_H/N_H} \\ \sqrt{G_P/N_P} \end{pmatrix}. \tag{26}$$

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

$$\boldsymbol{S_V} = \begin{pmatrix} S_{V_H} & 0 \\ 0 & S_{V_P} \end{pmatrix} = \begin{pmatrix} G_H/N_H & 0 \\ 0 & G_P/N_P \end{pmatrix}. \tag{27}$$

Plugging into *Mathematica* yields

$$S_{\bar{\zeta}_{HH}} = \frac{\frac{G_H}{4N_H}\left(2G_P(A_P+B_P)+D_P\|\boldsymbol{k}\|^2\right)^2 + \frac{G_P}{N_P}B_H^2 G_H^2}{\left\{-B_H B_P G_H G_P - \frac{1}{4}\left[2G_H(A_H-B_H)+D_H\|\boldsymbol{k}\|^2\right]\left[2G_P(A_P+B_P)+D_P\|\boldsymbol{k}\|^2\right]\right\}^2} \tag{28a}$$

$$S_{\bar{\zeta}_{PP}} = \frac{\frac{G_P}{4N_P}\left(2G_H(A_H-B_H)+D_H\|\boldsymbol{k}\|^2\right)^2 + \frac{G_H}{N_H}B_P^2 G_P^2}{\left\{-B_H B_P G_H G_P - \frac{1}{4}\left[2G_H(A_H-B_H)+D_H\|\boldsymbol{k}\|^2\right]\left[2G_P(A_P+B_P)+D_P\|\boldsymbol{k}\|^2\right]\right\}^2} \tag{28b}$$

$$S_{\bar{\zeta}_{HP}} = \frac{\frac{G_H G_P}{2}\left[\frac{B_P}{N_H}\left(2G_P(A_P+B_P)+D_P\|\boldsymbol{k}\|^2\right)+\frac{B_H}{N_P}\left(2G_H(A_H-B_H)+D_H\|\boldsymbol{k}\|^2\right)\right]}{\left\{-B_H B_P G_H G_P - \frac{1}{4}\left[2G_H(A_H-B_H)+D_H\|\boldsymbol{k}\|^2\right]\left[2G_P(A_P+B_P)+D_P\|\boldsymbol{k}\|^2\right]\right\}^2}. \tag{28c}$$

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

$$S_{\bar{\zeta}_{HH}}(\boldsymbol{k}) \approx \frac{4G_H/N_H}{\left[2G_H(A_H-B_H)+D_H\|\boldsymbol{k}\|^2\right]^2}, \tag{29a}$$

$$S_{\bar{\zeta}_{PP}}(\boldsymbol{k}) \approx \frac{4G_P/N_P}{\left[2G_P(A_P+B_P)+D_P\|\boldsymbol{k}\|^2\right]^2}, \tag{29b}$$

$$S_{\bar{\zeta}_{HP}}(\boldsymbol{k}) \approx 8G_H G_P \left(\frac{B_H/N_P}{\left[2G_H(A_H-B_H)+D_H\|\boldsymbol{k}\|^2\right]\left[2G_P(A_P+B_P)+D_P\|\boldsymbol{k}\|^2\right]^2}\right.$$
$$\left. + \frac{B_P/N_H}{\left[2G_H(A_H-B_H)+D_H\|\boldsymbol{k}\|^2\right]^2\left[2G_P(A_P+B_P)+D_P\|\boldsymbol{k}\|^2\right]}\right). \tag{29c}$$

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

$$C_{HH}(\boldsymbol{x}) \approx \frac{M(\boldsymbol{x}|1, \sqrt{2G_H(A_H - B_H)/D_H})}{N_H D_H (A_H - B_H)}, \tag{30a}$$

$$C_{PP}(\boldsymbol{x}) \approx \frac{M(\boldsymbol{x}|1, \sqrt{2G_P(A_P + B_P)/D_P})}{N_P D_P (A_P + B_P)}, \tag{30b}$$

where $M(\boldsymbol{x}|\nu, \kappa) = \frac{2^{1-\nu}}{\Gamma(\nu)} (\kappa \|\boldsymbol{x}\|)^\nu K_\nu(\kappa \|\boldsymbol{x}\|)$ 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 $f(\boldsymbol{x}), g(\boldsymbol{x})$, we have

$$C_{HP}(\boldsymbol{x}) \approx \frac{2G_H B_H}{N_P D_H D_P (A_P + B_P)} K_0 \left(\sqrt{\frac{2G_H}{D_H}(A_H - B_H)} \|\boldsymbol{x}\| \right) * M \left(\boldsymbol{x} \Big| 1, \sqrt{\frac{2G_P}{D_P}(A_P + B_P)} \right)$$

$$+ \frac{2G_P B_P}{N_H D_H D_P (A_H - B_H)} K_0 \left(\sqrt{\frac{2G_P}{D_P}(A_P + B_P)} \|\boldsymbol{x}\| \right) * M \left(\boldsymbol{x} \Big| 1, \sqrt{\frac{2G_H}{D_H}(A_H - B_H)} \right). \tag{31}$$

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.