
THE PHENOTYPIC SIGNATURE OF HOST-PARASITE COEVOLUTION IN CONTINUOUS SPACE

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Abstract

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

Keywords 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 The Model

2.1 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.

2.2 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.

2.3 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:

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

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

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.

2.4 Random Genetic Drift

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

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

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

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 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 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.

3.1 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 inherent 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

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

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

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

A.1 Spatial Autocorrelation and Cross-correlation

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

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

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

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

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

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

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

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

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

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

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

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

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

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

This linear system is uniquely solved by

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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 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?

F Application

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

G Applying (Hu et al. 2013) to Compute Covariance Functions

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, the stationary system (15) becomes

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

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

To consolidate notation, we set

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

$$\bar{\zeta} = \begin{pmatrix} \bar{\zeta}_H \\ \bar{\zeta}_P \end{pmatrix}, \quad \mathbf{V} = \begin{pmatrix} -\sqrt{\frac{G_H}{N_H}} \dot{W}_H \\ -\sqrt{\frac{G_P}{N_P}} \dot{W}_P \end{pmatrix}. \quad (21b)$$

Then, the stationary system can equally be written as

$$\mathcal{L} \bar{\zeta} = \mathbf{V}. \quad (22)$$

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

$$\mathcal{H} \hat{\zeta} = \hat{\mathbf{V}}, \quad (23)$$

where

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

$$\hat{\zeta} = \begin{pmatrix} \hat{\zeta}_H \\ \hat{\zeta}_P \end{pmatrix}, \quad \hat{\mathbf{V}} = \begin{pmatrix} \hat{V}_H \\ \hat{V}_P \end{pmatrix}, \quad (24b)$$

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

$$\mathbf{S}_{\bar{\zeta}} = \begin{pmatrix} S_{\bar{\zeta}_{HH}} & S_{\bar{\zeta}_{HP}} \\ S_{\bar{\zeta}_{PH}} & S_{\bar{\zeta}_{PP}} \end{pmatrix} = \begin{pmatrix} \mathbb{E}[\hat{\zeta}_H \hat{\zeta}_H] & \mathbb{E}[\hat{\zeta}_H \hat{\zeta}_P] \\ \mathbb{E}[\hat{\zeta}_H \hat{\zeta}_P] & \mathbb{E}[\hat{\zeta}_P \hat{\zeta}_P] \end{pmatrix} = \mathcal{H}^{-1} \mathbf{S}_{\mathbf{V}} \mathcal{H}^{-H}, \quad (25)$$

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

$$\hat{\mathbf{V}} = \begin{pmatrix} (2\pi)^{-1} \sqrt{G_H/N_H} \\ (2\pi)^{-1} \sqrt{G_P/N_P} \end{pmatrix}. \quad (26)$$

Since we assume the white noise processes \dot{W}_H and \dot{W}_P are independent we have

$$\mathbf{S}_V = \begin{pmatrix} S_{V_H} & 0 \\ 0 & S_{V_P} \end{pmatrix} = \begin{pmatrix} (2\pi)^{-2} G_H/N_H & 0 \\ 0 & (2\pi)^{-2} G_P/N_P \end{pmatrix}. \quad (27)$$

Putting it all together, we compute $\mathbf{S}_{\bar{\zeta}}$ from

$$S_{\bar{\zeta}_{HH}} = \frac{S_{V_H} |\mathcal{H}_{22}^2| + S_{V_P} |\mathcal{H}_{12}^2|}{|(\mathcal{H}_{11}\mathcal{H}_{22} - \mathcal{H}_{12}\mathcal{H}_{21})^2|}, \quad (28a)$$

$$S_{\bar{\zeta}_{HP}} = -\frac{\mathcal{H}_{22}S_{V_H} |\mathcal{H}_{21}^2| \mathcal{H}_{11} + \mathcal{H}_{12}S_{V_P} |\mathcal{H}_{11}^2| \mathcal{H}_{21}}{|(\mathcal{H}_{11}\mathcal{H}_{22} - \mathcal{H}_{12}\mathcal{H}_{21})^2| \mathcal{H}_{21}\mathcal{H}_{11}}, \quad (28b)$$

$$S_{\bar{\zeta}_{PH}} = -\frac{\mathcal{H}_{21}S_{V_H} |\mathcal{H}_{22}^2| \mathcal{H}_{12} + \mathcal{H}_{11}S_{V_P} |\mathcal{H}_{12}^2| \mathcal{H}_{22}}{|(\mathcal{H}_{11}\mathcal{H}_{22} - \mathcal{H}_{12}\mathcal{H}_{21})^2| \mathcal{H}_{22}\mathcal{H}_{12}}, \quad (28c)$$

$$S_{\bar{\zeta}_{PP}} = \frac{S_{V_H} |\mathcal{H}_{21}^2| + S_{V_P} |\mathcal{H}_{11}^2|}{|(\mathcal{H}_{11}\mathcal{H}_{22} - \mathcal{H}_{12}\mathcal{H}_{21})^2|}. \quad (28d)$$

G.1 Multivariate Matern covariance function

The Matern covariance matrix function

$$C(\mathbf{x}) = \begin{pmatrix} a_H \sigma_H^2 \|\mathbf{x}\| K_1(a_H \|\mathbf{x}\|) & a_{HP} \rho_{HP} \sigma_H \sigma_P \|\mathbf{x}\| K_1(a_{HP} \|\mathbf{x}\|) \\ a_{PH} \rho_{PH} \sigma_H \sigma_P \|\mathbf{x}\| K_1(a_{PH} \|\mathbf{x}\|) & a_P \sigma_P^2 \|\mathbf{x}\| K_1(a_P \|\mathbf{x}\|) \end{pmatrix}$$

has power spectrum matrix

$$\frac{\frac{4BH^2GH^2GP}{\pi^2NP} + \frac{(DPs^2 + 2(AP+BP)GP)^2GH}{\pi^2NH}}{(4BHBPGHGP + (DHS^2 + 2(AH - BH)GH)(DPs^2 + 2(AP + BP)GP))^2}$$

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