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# SPATIAL SCALES OF LOCAL ADAPTATION AND HOST-PARASITE COEVOLUTION

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A PREPRINT

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## Abstract

Studies of local adaptation between coevolving hosts and parasites have profited from theory that assumes a discrete set of populations. However, when dispersal is limited continuous patterns of phenotypic variation may emerge. Thus, patterns of local adaptation may occur on characteristic spatial scales determined by relative dispersal distances and strengths of selection. Here we study a two-dimensional continuous space model of host-parasite coevolution to elucidate the spatial scales of phenotypic turnover and local adaptation. We find that the species with more limited dispersal tends to be locally adapted, but XYZ about it being ahead in the coevolutionary race. To verify our results when model assumptions are broken, we use individual based simulations. We find XYZ about our results when coevolution is strong and XYZ when population densities significantly vary across space.

**Keywords** coevolution · local adaptation · continuous space · characteristic scales · spde

## 1 Introduction

Local adaptation occurs when individuals reared in the same geographic location as their ancestors exhibit higher fitness than when reared elsewhere. This phenomenon is thought to occur (or has been show to occur) when selection is spatially heterogeneous and strong relative to dispersal (refs).

- It seems an old motivation for studying local adaptation in host-parasite coevolution comes from trying to make sense of the GMTTC. So I think it would be good to include this.
- Need to do lit review of local adaptation in coevolving host-parasite systems.
- We should also tie in previous work on understand spatial scales of phenotypic variation (ie, Slatkin's 1978 ppr). Need to do lit review in this area too.

## 2 Methods

To understand patterns of phenotypic variation and local adaptation in continuous space, we introduce and analyze a pair of stochastic partial partial differential equations (SPDE) that account for coevolution between host and parasite, abiotic stabilizing selection and random genetic drift. In particular, SPDE are stochastic generalizations of deterministic PDE which in turn have been widely employed in theoretical evolutionary ecology to study continuous space population dynamics (refs), the evolution of continuous trait distributions (refs) and feedbacks between the two (refs). Here we employ the SPDE framework to model the evolution of mean traits in coevolving hosts and parasites. By assuming additive genetic variances and population sizes are spatially and temporally homogeneous, we arrive at a pair of linear SPDE driven by space-time

white noise processes. Linearity of the model allows us to employ spectral methods to approximate spatial auto-covariance functions of both mean traits along with a spatial cross-covariance function between the two mean traits. Finally, using the spatial auto-covariance functions, we identify spatial scales of phenotypic turnover.

In section 2.1 we introduce our model and briefly outline our approach using spectral methods. More information on this approach is provided in Appendix A. We then adapt classical measures of local adaptation to the case of limited dispersal. Using these adapted measures, we apply our model results to illustrate the spatial scales of local adaptation and to determine which species has a coevolutionary advantage. These definitions are provided in section 2.2 and further details are located in Appendix B. To test our analytical results, we employ individual-based simulations conducted in the language Julia. In section 2.3, we provide a brief overview of our simulation model. Further details on the individual-based model can be found in Appendix C

## 2.1 SPDE model

We employ a pair of stochastic partial differential equations to track the evolution of mean traits in the host,  $\bar{z}_H(x_1, x_2)$ , and the parasite,  $\bar{z}_P(x_1, x_2)$ , as functions of the two-dimensional spatial coordinates  $(x_1, x_2)$ . We assume geographical space is unbounded so that  $(x_1, x_2)$  span the entire plane. We account for the effects of host parasite coevolution using a trait-matching model (ref other pprs using this model). Under this model, fitness of the host is minimized and fitness of the parasite is maximized when traits are matching. This induces a local coevolutionary chase, where the parasite evolves to match the host, but the host evolves to escape the parasite (this should be stated in the introduction somewhere). The strength of biotic selection (i.e., selection that is induced by the interaction between hosts and parasites) is denoted by  $B_H > 0$  for the host and  $B_P > 0$  for the parasite. We assume these strengths of selection are temporally and spatially homogeneous. To obtain an equilibrium solution to our model, we also account for the effects of abiotic stabilizing selection. Here, we assume abiotic optimal traits and strengths of abiotic selection for both species are temporally and spatially homogeneous. We denote by  $\theta_H, \theta_P$  the abiotic optimal traits and by  $A_H, A_P > 0$  the strengths of abiotic stabilizing selection in the host and parasite respectively. Finally, our model also accounts for the effects of limited dispersal by assuming individuals disperse following a bivariate Gaussian distribution with mean zero and equal standard deviations in both directions. We denote by  $\sigma_H, \sigma_P$  the standard deviations of individual movement in the host and parasite respectively. In our SPDE model, this translates to diffusion with coefficients  $\sigma_H/2$  and  $\sigma_P/2$  (refs). For the sake of mathematical tractability, we also assume the additive genetic variances  $G_H, G_P > 0$  and population densities  $\rho_H, \rho_P > 0$  are temporally and spatially homogeneous for the host and parasite respectively. With this notation, our model can be written as

$$\frac{\partial \bar{z}_H}{\partial t} = G_H B_H (\bar{z}_H - \bar{z}_P) + G_H A_H (\theta_H - \bar{z}_H) + \frac{\sigma_H}{2} \left( \frac{\partial^2 \bar{z}_H}{\partial x_1^2} + \frac{\partial^2 \bar{z}_H}{\partial x_2^2} \right) + \sqrt{\frac{G_H}{\rho_H}} \dot{W}_H, \quad (1a)$$

$$\frac{\partial \bar{z}_P}{\partial t} = G_P B_P (\bar{z}_H - \bar{z}_P) + G_P A_P (\theta_P - \bar{z}_P) + \frac{\sigma_P}{2} \left( \frac{\partial^2 \bar{z}_P}{\partial x_1^2} + \frac{\partial^2 \bar{z}_P}{\partial x_2^2} \right) + \sqrt{\frac{G_P}{\rho_P}} \dot{W}_P. \quad (1b)$$

Here  $\dot{W}_H, \dot{W}_P$  denote independent space-time white noise processes, which are Gaussian processes independent in both space and time. In particular, integrating  $\dot{W}_S$ , for either  $S = H, P$ , over an interval of time  $[t_1, t_2]$  and a geographic region  $U$  returns a normally distributed random variable with mean zero and variance equal to  $(t_2 - t_1)|U|$ , where  $|U|$  denotes the area of  $U$  (refs). Hence, when for an interval of unit length and region of unit area, the integral of  $\sqrt{G_S/\rho_S} \dot{W}_S$  is normal with mean zero and variance  $G_S/\rho_S$  in analogy with classical models of random genetic drift in quantitative genetics (refs).

The assumption of constant effective population size across time and space can be thought of as an extreme form of population regulation. However, the model is agnostic to whether population regulation is caused by top-down forces such as predation, bottom-up forces such as resource competition or some combination of these forces. Similarly, the assumption of constant additive genetic variances can be justified theoretically via mutation-selection balance (refs).

We analyze model (1) at its statistical equilibrium, which exists and is unique when  $A_H > B_H$  (see Appendix A). Following well established results of spatial statistics (refs), we know the stationary solution of model (1) is a bivariate Gaussian random field (refs). An example of a stationary solution to model (1) in an instant of time is illustrated in Figure X. A multivariate Gaussian random field of  $d$  variables has the convenient property

of being characterized by its  $d$ -dimensional mean vector  $\boldsymbol{\mu}(x_1, x_2)$  and  $d \times d$  spatial auto/cross-covariance matrix  $\Sigma(x_1, x_2)$ . Under our model,  $\boldsymbol{\mu}(x_1, x_2) = (\tilde{z}_H, \tilde{z}_P)^\top$  is the expected equilibrium trait values, which are spatially homogeneous and are determined by a balance between biotic and abiotic selection.

## **2.2 Local adaptation in continuous space**

## **2.3 Individual-based simulations**

# **3 Results**

# **4 Discussion**

# **5 Conclusion**

## Appendix

### A Calculating the covariance and cross-covariance functions

Assuming the system has reached a statistical equilibrium, we make use of a Fourier transform convert the model from geographic coordinates to frequency coordinates, where the Fourier transformed solution represents the spatial harmonic content of the solution to the SPDE model. We then use the Fourier transformed model to construct so-called power spectra of the solution, which are exactly the Fourier transformed spatial auto-covariance functions. We then use a weak coevolution approximation to simplify the power spectra so they can be inverted, arriving at analytical expressions for the spatial auto-covariance functions. In turn, the functional form of the spatial auto-covariance functions allows the identification of spatial scales of phenotypic turnover.

To compute formula for the spatial (intraspecific) covariance and (interspecific) cross-covariance functions, we make use of the relation between the covariance functions and power spectra of random fields. In particular, the power spectrum of a multivariate stationary random field  $\mathbf{F}(\mathbf{x})$ ,  $\mathbf{x} = (x_1, x_2)$  being spatial location, is defined by  $S_{\mathbf{F}}(\mathbf{k}) = \mathbb{E} \left( \hat{\mathbf{F}}(\mathbf{k}) \hat{\mathbf{F}}(\mathbf{k})^H \right)$  where  $\hat{\mathbf{F}}(\mathbf{k})$  is the Fourier transform of  $\mathbf{F}$ , the symbol  $^H$  denotes Hessian transpose and  $\mathbf{k} = (k_1, k_2)$  are the Fourier transformed coordinates which represent the frequencies of fluctuations across the two spatial dimensions. Hence,  $\hat{\mathbf{F}}$  represents the harmonic content of the process  $\mathbf{F}$ . The spatial covariance function  $C_{\mathbf{F}}(\mathbf{x})$  is just the inverse Fourier transform of the power spectrum  $S_{\mathbf{F}}(\mathbf{k})$ .

Working with the power spectrum has the advantage of converting differential equations into algebraic equations, making for a more analytically tractable approach. Furthermore, due to the Fourier relationship between  $C_{\mathbf{F}}(\mathbf{x})$  and  $S_{\mathbf{F}}(\mathbf{k})$ , we have the convenient properties  $\int_{\mathbb{R}^2} C_{\mathbf{F}}(\mathbf{x}) d\mathbf{x} = S_{\mathbf{F}}(\mathbf{0})$  and  $\int_{\mathbb{R}^2} S_{\mathbf{F}}(\mathbf{x}) d\mathbf{x} = C_{\mathbf{F}}(\mathbf{0})$ . Both of these properties will aid in calculating results on host-parasite local adaptation.

Using  $\mathbf{k} = (k_1, k_2)$  to denote spatial frequency (the Fourier equivalent to spatial location  $\mathbf{x} = (x_1, x_2)$ ) and  $\hat{\mathbf{z}}(\mathbf{k}) = (\hat{z}_H(\mathbf{k}), \hat{z}_P(\mathbf{k}))^\top$  to denote the Fourier transforms of the equilibrium solution  $\bar{\mathbf{z}}(\mathbf{x}) = (\bar{z}_H(\mathbf{x}), \bar{z}_P(\mathbf{x}))^\top$ , the Fourier transform of our model at equilibrium is

$$\begin{aligned} 0 &= G_H A_H (\theta_H - \hat{z}_H) - G_H B_H (\hat{z}_P - \hat{z}_H) - \frac{\sigma_H^2}{2} \|\mathbf{k}\|^2 \hat{z}_H + \sqrt{\frac{G_H}{N_H}} \widehat{W}_H, \\ 0 &= G_P A_P (\theta_P - \hat{z}_P) + G_P B_P (\hat{z}_H - \hat{z}_P) - \frac{\sigma_P^2}{2} \|\mathbf{k}\|^2 \hat{z}_P + \sqrt{\frac{G_P}{N_P}} \widehat{W}_P, \end{aligned}$$

where  $\|\mathbf{k}\|^2 = k_1^2 + k_2^2$  and  $\widehat{W}_S$  is a heuristic representation for the Fourier transform of the spatial white noise  $\dot{W}_S$  for species  $S = H, P$ . Since the mean vector for equilibrium solution of the SPDE model is spatially homogeneous, we set  $\theta_H = \theta_P = 0$  without loss of generality. This is equivalent to centering the solution by working with  $\bar{z}_H = \bar{z}_H - \mu_H$  and  $\bar{z}_P = \bar{z}_P - \mu_P$  instead of  $\bar{z}_H$  and  $\bar{z}_P$ . The Fourier transformed SPDE model can be rewritten in matrix form as

$$\mathcal{H} \hat{\mathbf{z}} = \widehat{\mathbf{W}}$$

where  $\widehat{\mathbf{W}} = \frac{1}{2\pi} \left( -\sqrt{\frac{G_H}{N_H}} \widehat{W}_H, -\sqrt{\frac{G_P}{N_P}} \widehat{W}_P \right)^\top$  and

$$\mathcal{H} = \frac{1}{2\pi} \begin{pmatrix} -G_H A_H + G_H B_H + \frac{\sigma_H^2}{2} \|\mathbf{k}\|^2 & -G_H B_H \\ G_P B_P & -G_P A_P - G_P B_P + \frac{\sigma_P^2}{2} \|\mathbf{k}\|^2 \end{pmatrix}.$$

Since no complex numbers appear in the above expressions, the power spectrum of the random field  $\bar{\mathbf{z}}$  simplifies to  $S_{\bar{\mathbf{z}}} = \mathbb{E} \left( \hat{\mathbf{z}} \hat{\mathbf{z}}^\top \right)$ . Rearranging the above matrix equation, we find

$$\hat{\mathbf{z}} = \mathcal{H}^{-1} \widehat{\mathbf{W}},$$

$$\hat{\mathbf{z}}^\top = \widehat{\mathbf{W}}^\top (\mathcal{H}^\top)^{-1}.$$

Hence, the power spectrum of  $\bar{\mathbf{z}}$  is

$$S_{\bar{\mathbf{z}}} = \mathcal{H}^{-1} S_{\mathbf{W}} (\mathcal{H}^\top)^{-1}$$

where

$$S_{\mathbf{W}} = \mathbb{E} \left( \widehat{\mathbf{W}} \widehat{\mathbf{W}}^\top \right) = \frac{1}{(2\pi)^2} \begin{pmatrix} G_H/N_H & 0 \\ 0 & G_P/N_P \end{pmatrix}$$

is the power spectrum of the spatial white noise  $\dot{\mathbf{W}} = \left( -\sqrt{\frac{G_H}{N_H}} \dot{W}_H, -\sqrt{\frac{G_P}{N_P}} \dot{W}_P \right)^\top$ . Denoting  $S_H, S_P$  and  $S_{HP}$  the components of  $S_{\bar{\mathbf{z}}}$  corresponding to the host power spectrum, parasite power spectrum and host-parasite cross-power spectrum we find

$$\begin{aligned} S_H(\mathbf{k}) &= \frac{B_H^2 G_H^2 \frac{G_P}{N_P} + \frac{G_H}{N_H} [G_P(A_P + B_P) + \frac{1}{2} \sigma_P^2 \|\mathbf{k}\|^2]^2}{\{B_H B_P G_H G_P + [G_H(A_H - B_H) + \frac{1}{2} \sigma_H^2 \|\mathbf{k}\|^2][G_P(A_P + B_P) + \frac{1}{2} \sigma_P^2 \|\mathbf{k}\|^2]\}^2}, \\ S_P(\mathbf{k}) &= \frac{B_P^2 G_P^2 \frac{G_H}{N_H} + \frac{G_P}{N_P} [G_H(A_H - B_H) + \frac{1}{2} \sigma_H^2 \|\mathbf{k}\|^2]^2}{\{B_H B_P G_H G_P + [G_H(A_H - B_H) + \frac{1}{2} \sigma_H^2 \|\mathbf{k}\|^2][G_P(A_P + B_P) + \frac{1}{2} \sigma_P^2 \|\mathbf{k}\|^2]\}^2}, \\ S_{HP}(\mathbf{k}) &= \frac{B_P G_P \frac{G_H}{N_H} [G_P(A_P + B_P) + \frac{1}{2} \sigma_P^2 \|\mathbf{k}\|^2] - B_H G_H \frac{G_P}{N_P} [G_H(A_H - B_H) + \frac{1}{2} \sigma_H^2 \|\mathbf{k}\|^2]}{\{B_H B_P G_H G_P + [G_H(A_H - B_H) + \frac{1}{2} \sigma_H^2 \|\mathbf{k}\|^2][G_P(A_P + B_P) + \frac{1}{2} \sigma_P^2 \|\mathbf{k}\|^2]\}^2}. \end{aligned}$$

Assuming coevolution is weak so that  $B_H^2, B_P^2, B_H B_P \approx 0$ , we obtain the approximations

$$\begin{aligned} S_H(\mathbf{k}) &\approx \frac{G_H/N_H}{\left(G_H(A_H - B_H) + \frac{\sigma_H^2}{2} \|\mathbf{k}\|^2\right)^2}, \quad S_P(\mathbf{k}) \approx \frac{G_P/N_P}{\left(G_P(A_P + B_P) + \frac{\sigma_P^2}{2} \|\mathbf{k}\|^2\right)^2} \\ S_{HP}(\mathbf{k}) &\approx \frac{B_P G_H G_P / N_H}{\left(G_H(A_H - B_H) + \frac{\sigma_H^2}{2} \|\mathbf{k}\|^2\right)^2 \left(G_P(A_P + B_P) + \frac{\sigma_P^2}{2} \|\mathbf{k}\|^2\right)} \\ &\quad - \frac{B_H G_H G_P / N_P}{\left(G_H(A_H - B_H) + \frac{\sigma_H^2}{2} \|\mathbf{k}\|^2\right) \left(G_P(A_P + B_P) + \frac{\sigma_P^2}{2} \|\mathbf{k}\|^2\right)^2}. \end{aligned}$$

In Figure 1, we compare these approximations to the exact power spectra for varying strengths of coevolutionary selection.

To simplify notation, we denote by  $\xi_S$  the characteristic scale of spatial trait covariance within species  $S = H, P$  and by  $V_S$  the marginal variance of the same species. The marginal variance  $V_S$  can be thought of as a measure of uncertainty when observing local mean traits. Setting

$$\begin{aligned} \xi_H &= \frac{\sigma_H}{\sqrt{G_H(A_H - B_H)}}, \quad \xi_P = \frac{\sigma_P}{\sqrt{G_P(A_P + B_P)}}, \\ V_H &= \frac{1}{N_H \sigma_H^2 (A_H - B_H)}, \quad V_P = \frac{1}{N_P \sigma_P^2 (A_P + B_P)}, \end{aligned}$$

the approximated power spectra can be rewritten as

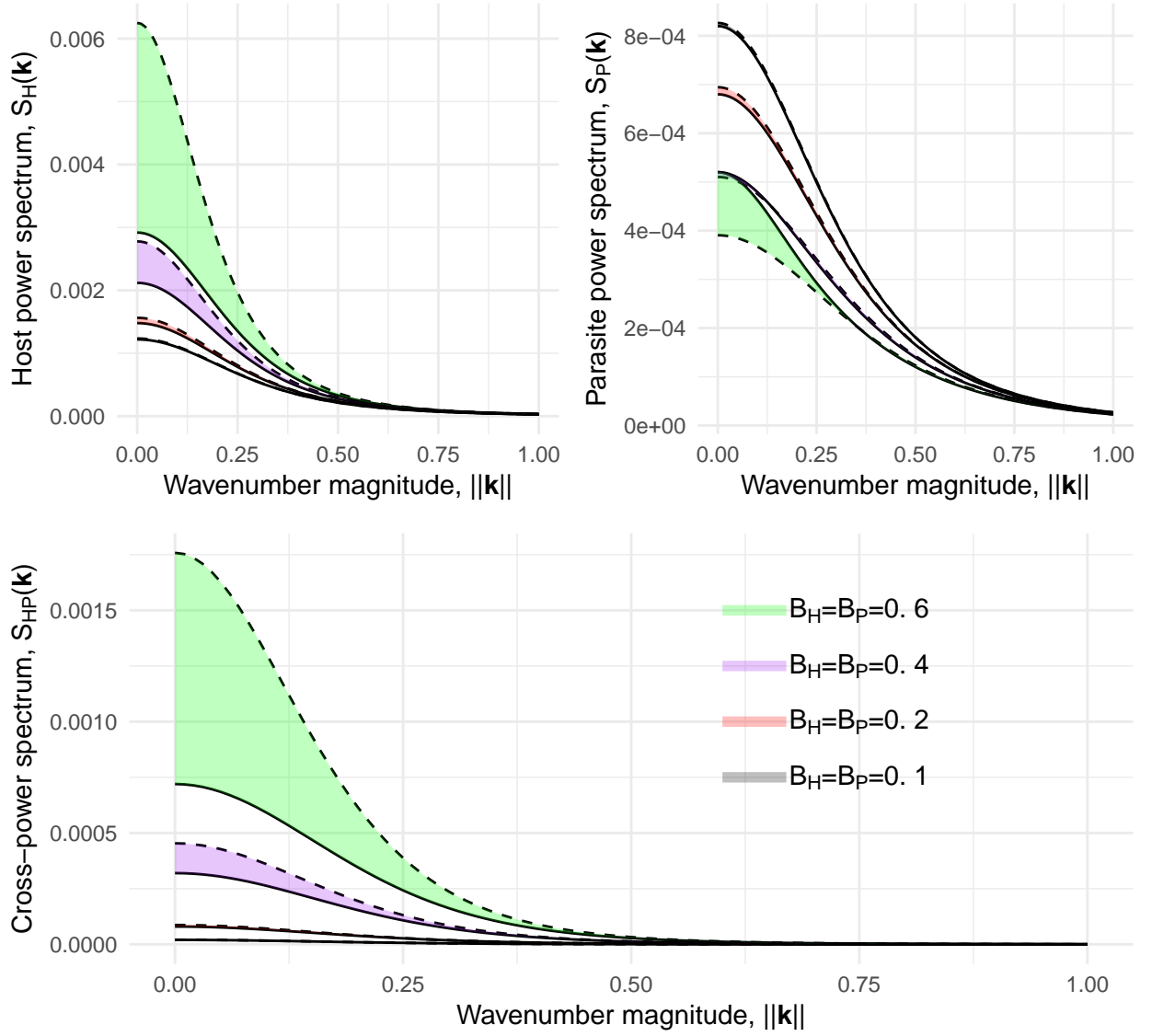


Figure 1: Comparisons of approximated power spectra (dashed lines) to exact power spectra (solid lines) for four different strengths of biotic (coevolutionary) selection  $B = 0.1, 0.2, 0.4, 0.6$ . For simplicity, biotic selection on host and parasite are set equal ( $B_H = B_P = B$ ). Background parameters are set to  $A_H = A_P = 1$ ,  $G_H = G_P = 10$ ,  $\sigma_H = \sigma_P = 10$  and  $N_H = N_P = 100$ . Our model only is defined for  $B_H < A_H$ . Hence, the behaviour of power spectra as  $B$  increases reflects what happens when the host comes closer to being able to overcome abiotic stabilizing selection and escape parasitism. In this limit, we see that our approximations over estimate the magnitudes of low frequency content in the host spatial covariance and host-parasite cross-covariance. This implies that our approximations over estimate the spatial scale of phenotypic covariance of the host and phenotypic cross-covariance of the host and parasite when coevolution is strong. In contrast, we see that our approximations under estimate the amount of low frequency content in the spatial covariance of parasite traits. This implies that our approximations under estimate the spatial scale of phenotypic covariance of the parasite when coevolution is strong. However, when coevolution is relatively weak, say one-tenth the strength of abiotic selection, we see our approximation matches closely the exact power spectra.

$$S_H(\mathbf{k}) \approx \frac{V_H \xi_H^2}{(1 + \frac{1}{2} \xi_H^2 \|\mathbf{k}\|^2)^2}, \quad S_P(\mathbf{k}) \approx \frac{V_P \xi_P^2}{(1 + \frac{1}{2} \xi_P^2 \|\mathbf{k}\|^2)^2}$$

$$S_{HP}(\mathbf{k}) \approx \frac{B_P}{A_P + B_P} \frac{1}{1 + \frac{1}{2} \xi_P^2 \|\mathbf{k}\|^2} \frac{V_H \xi_H^2}{(1 + \frac{1}{2} \xi_H^2 \|\mathbf{k}\|^2)^2} - \frac{B_H}{A_H - B_H} \frac{1}{1 + \frac{1}{2} \xi_H^2 \|\mathbf{k}\|^2} \frac{V_P \xi_P^2}{(1 + \frac{1}{2} \xi_P^2 \|\mathbf{k}\|^2)^2}.$$

The spatial covariance functions, equal to the inverse Fourier transforms of the power spectra  $S_H(\mathbf{k}), S_P(\mathbf{k}), S_{HP}(\mathbf{k})$ , can then be approximated as

$$C_H(\mathbf{x}) \approx V_H \sqrt{2} \frac{\|\mathbf{x}\|}{\xi_H} K_1 \left( \sqrt{2} \frac{\|\mathbf{x}\|}{\xi_H} \right),$$

$$C_P(\mathbf{x}) \approx V_P \sqrt{2} \frac{\|\mathbf{x}\|}{\xi_P} K_1 \left( \sqrt{2} \frac{\|\mathbf{x}\|}{\xi_P} \right),$$

where  $K_\nu$  is a modified Bessel function of the second kind, order  $\nu$ . Conveniently, the approximated spatial covariance functions take the form of Whittle-Matérn covariance functions, which are widely applied in the fields of spatial statistics (refs) and machine learning (ref). In general, the Whittle-Matérn covariance function takes the form

$$M_\nu(\mathbf{x}|\xi, V) = V \frac{2^{1-\nu}}{\Gamma(\nu)} \left( \sqrt{2\nu} \frac{\|\mathbf{x}\|}{\xi} \right)^\nu K_\nu \left( \sqrt{2\nu} \frac{\|\mathbf{x}\|}{\xi} \right).$$

Hence,  $C_S(\mathbf{x}) = M_1(\mathbf{x}|\xi_S, V_S)$  for both  $S = H, P$ . With this notation, the interspecific spatial cross-covariance function can be approximated by

$$C_{HP}(\mathbf{x}) \approx \int_{\mathbb{R}^2} \frac{2B_P}{A_P + B_P} \frac{K_0(\|\mathbf{y}\|/\xi_P)}{\xi_P^2} M_1(\mathbf{x} - \mathbf{y}|\xi_H, V_H) - \frac{2B_H}{A_H - B_H} \frac{K_0(\|\mathbf{y}\|/\xi_H)}{\xi_H^2} M_1(\mathbf{x} - \mathbf{y}|\xi_P, V_P) d\mathbf{y}.$$

### A.1 Marginal values and integrals of spatial covariance and cross-covariance functions

Following results from section A, the marginal covariance of species mean traits can be approximated via

$$C_{HP}(\mathbf{0}) = \frac{1}{2\pi} \int_{\mathbb{R}^2} S_{HP}(\mathbf{k}) d\mathbf{k}$$

$$\approx \frac{G_H G_P}{\sigma_H^2 \sigma_P^2} \frac{\xi_H^2 \xi_P^2}{(\xi_H^2 - \xi_P^2)^2} \left[ \frac{B_P}{N_H \sigma_H^2} \left( \xi_H^4 + \xi_H^2 \xi_P^2 (\ln \xi_P^2 - \ln \xi_H^2 - 1) \right) \right.$$

$$\left. - \frac{B_H}{N_P \sigma_P^2} \left( \xi_P^4 + \xi_H^2 \xi_P^2 (\ln \xi_H^2 - \ln \xi_P^2 - 1) \right) \right].$$

Similarly, the integral of  $C_{HP}(\mathbf{x})$  is approximated via

$$\int_{\mathbb{R}^2} C_{HP}(\mathbf{x}) d\mathbf{x} = 2\pi S_{HP}(\mathbf{0}) \approx 2\pi \left( \frac{B_P}{G_H N_H (A_H - B_H)^2 (A_P + B_P)} - \frac{B_H}{G_P N_P (A_H - B_H) (A_P + B_P)^2} \right)$$

$$= 2\pi \left( \frac{B_P V_H \xi_H^2}{A_P + B_P} - \frac{B_H V_H \xi_H^2}{A_H - B_H} \right).$$

However, the integral  $\int_{\mathbb{R}^2} C_{HP}(\mathbf{x}) d\mathbf{x}$  is biased by larger distances. To see this we can change our integration to polar coordinates to find  $\int_{\mathbb{R}^2} C_{HP}(\mathbf{x}) d\mathbf{x} = 2\pi \int_0^\infty C_{HP}(r) r dr$ . To remove this bias, we should like to calculate  $\int_0^\infty C_{HP}(r) dr$ . Switching this integral back to Cartesian coordinates yields

$$\int_0^\infty C_{HP}(r)dr = \frac{1}{2\pi} \int_{\mathbb{R}^2} \frac{1}{\|\mathbf{x}\|} C_{HP}(\mathbf{x}) d\mathbf{x}.$$

To evaluate  $\int_0^\infty C_{HP}(r)dr$ , we can use the relationship

$$\int_{\mathbb{R}^2} \frac{1}{\|\mathbf{x}\|} C_{HP}(\mathbf{x}) d\mathbf{x} = \mathcal{F} \left\{ \frac{C_{HP}(\mathbf{x})}{\|\mathbf{x}\|} \right\}_{\mathbf{k}=\mathbf{0}},$$

where  $\mathcal{F}$  denotes Fourier transformation and the subscript denotes evaluation at  $\mathbf{k} = \mathbf{0} = (0, 0)^\top$ . Taking the Fourier transform of  $C_{HP}(\mathbf{x})/\|\mathbf{x}\|$ , we find

$$\begin{aligned} \mathcal{F} \left\{ \frac{C_{HP}(\mathbf{x})}{\|\mathbf{x}\|} \right\} &\approx \frac{B_P}{A_P + B_P} \frac{1}{1 + \frac{1}{2}\xi_P^2 \|\mathbf{k}\|^2} \frac{V_H \xi_H / \sqrt{2}}{1 + \frac{1}{2}\xi_H^2 \|\mathbf{k}\|^2} E \left( -\frac{1}{2}\xi_H^2 \|\mathbf{k}\|^2 \right) \\ &\quad - \frac{B_H}{A_H - B_H} \frac{1}{1 + \frac{1}{2}\xi_H^2 \|\mathbf{k}\|^2} \frac{V_P \xi_P / \sqrt{2}}{1 + \frac{1}{2}\xi_P^2 \|\mathbf{k}\|^2} E \left( -\frac{1}{2}\xi_P^2 \|\mathbf{k}\|^2 \right), \end{aligned}$$

where  $E(\zeta) = \int_0^{\pi/2} \sqrt{1 - \zeta \sin^2 \theta} d\theta$  is an elliptic integral. In particular, this provides

$$\mathcal{F} \left\{ \frac{C_{HP}(\mathbf{x})}{\|\mathbf{x}\|} \right\}_{\mathbf{k}=\mathbf{0}} \approx \frac{\pi}{2} \left( \frac{B_P}{A_P + B_P} \frac{\xi_H}{\sqrt{2}} - \frac{B_H}{A_H - B_H} \frac{\xi_P}{\sqrt{2}} \right).$$

We therefore conclude

$$\int_0^\infty C_{HP}(r)dr \approx \frac{1}{4} \left( \frac{B_P}{A_P + B_P} \frac{\xi_H}{\sqrt{2}} - \frac{B_H}{A_H - B_H} \frac{\xi_P}{\sqrt{2}} \right).$$

## B Measures of local adaptation

- use  $\mathcal{L}$  for measures in terms of mean fitness and  $\ell$  for measures in terms of log-mean fitness

Local adaptation is commonly measured as the difference in fitness for individuals experiencing their local environment and fitness for individuals experiencing foreign environments (Gandon & Nuismer 2009, Nuismer 2017, etc). In the case of coevolution, the environmental variable is replaced by the trait value of the interacting partner species.

yada yada yada, folks end up with something like  $\mathcal{L}_P = \bar{\alpha} - \bar{\alpha}_0$ . Using a slightly different definition, parasite local adaptation simplifies to  $\ell_P = \ln \bar{\alpha} - \ln \bar{\alpha}_0 = B_P C_{HP}(0)$ .

Here extend this notion of local adaptation to the case of populations distributed continuously in space. In particular, we denote by  $\Delta_H(\mathbf{y})$  the difference in expected population growth rates of the host when confronted with parasites drawn from a spatial lag  $\mathbf{y} = (y_1, y_2)^\top$  away. That is,

$$\Delta_H(\mathbf{y}) = \mathbb{E}[m_H(\bar{z}_H(\mathbf{x}), \bar{z}_P(\mathbf{x})) - m_H(\bar{z}_H(\mathbf{x}), \bar{z}_P(\mathbf{x} + \mathbf{y}))].$$

We define  $\Delta_P(\mathbf{y})$  in a complementary manner for the parasite species. Under our model of trait matching/mismatching,  $\Delta_H(\mathbf{y})$  simplifies to

$$\Delta_H(\mathbf{y}) = \mathbb{E} \left[ \frac{B_H}{2} (\bar{z}_H(\mathbf{x}) - \bar{z}_P(\mathbf{x}))^2 - \frac{B_H}{2} (\bar{z}_H(\mathbf{x}) - \bar{z}_P(\mathbf{x} + \mathbf{y}))^2 \right] = -B_H C_{HP}(\mathbf{y}).$$

Similarly, we obtain  $\Delta_P(\mathbf{y}) = B_P C_{HP}(\mathbf{y})$  for the parasite. To provide a global measure of local adaptation, one that accounts for all spatial distances, we might think  $\hat{\ell}_S = \int_{\mathbb{R}^2} \Delta_S(\mathbf{y}) d\mathbf{y}$  would provide a reasonable definition. Using our results from section A, we obtain



$$\begin{aligned}\hat{\ell}_H &\approx B_H \left( \frac{B_H}{G_P N_P (A_H - B_H)(A_P + B_P)^2} - \frac{B_P}{G_H N_H (A_H - B_H)^2 (A_P + B_P)} \right), \\ \hat{\ell}_P &\approx B_P \left( \frac{B_P}{G_H N_H (A_H - B_H)^2 (A_P + B_P)} - \frac{B_H}{G_P N_P (A_H - B_H)(A_P + B_P)^2} \right).\end{aligned}$$

These measures of local adaptation depend on the effective densities  $N_H, N_P$  which suggests they provide some indication for the role of random genetic drift in determining global patterns of local adaptation. However, they are not dependent on dispersal distances because of the extra weight given to larger distances implicit in this definition (see above). Hence, they provide no information on the role of gene-flow in determining global patterns of local adaptation. To circumvent this issue, we define another index  $\tilde{\ell}_S = \int_0^\infty \tilde{\Delta}_S(r) dr$  where  $\tilde{\Delta}_S(r) = \Delta_S(\mathbf{r})$  and  $\mathbf{r} = (r/\sqrt{2}, r/\sqrt{2})$ . Using our results from above, we find

$$\begin{aligned}\tilde{\ell}_H &\approx \frac{B_H}{4} \left( \frac{B_H}{A_H - B_H} \frac{\xi_P}{\sqrt{2}} - \frac{B_P}{A_P + B_P} \frac{\xi_H}{\sqrt{2}} \right), \\ \tilde{\ell}_P &\approx \frac{B_P}{4} \left( \frac{B_P}{A_P + B_P} \frac{\xi_H}{\sqrt{2}} - \frac{B_H}{A_H - B_H} \frac{\xi_P}{\sqrt{2}} \right).\end{aligned}$$

Since  $\xi_S \propto \sigma_S$  for  $S = H, P$  we see that this alternative global index of local adaptation captures the role of gene-flow. However, the absence effective densities in these expressions suggests  $\tilde{\ell}_H, \tilde{\ell}_P$  do not capture the effects of random genetic drift. Hence, the two sets of indices  $(\hat{\ell}_H, \hat{\ell}_P)$  and  $(\tilde{\ell}_H, \tilde{\ell}_P)$  capture complementary aspects of global patterns of local adaptation in coevolving hosts and parasites.

In particular, they both measure adaptation of a host (resp parasite) when confronted with a randomly sampled parasite (resp host) drawn from a randomly chosen location. However, the spatial sampling scheme differs between the two. While  $\hat{\ell}$  samples space uniformly in two-dimensions,  $\tilde{\ell}$  samples space uniformly along a transect. Hence, while  $\hat{\ell}$  captures orientation, it is sensitive to spatial dimension. In contrast,  $\tilde{\ell}$  focuses on the effect of distance and we therefore focus on results for  $\tilde{\ell}$  in the main text.

curious: does  $\hat{\ell}$  match the conditions for winner/loser in the case of stochastic evolution without a spatial component?

### B.1 Modified Index of Local Adaptation Accounting for Limited Dispersal

We denote by  $D(\mathbf{x})$  the probability density that two individuals of opposing species were separated by  $\mathbf{x}$  before dispersal given that they end up at the same location after dispersal. We refer to  $D(\mathbf{x})$  as the separation kernel. Since we assume dispersal for each species is bivariate Gaussian with respective standard deviations (in both coordinates)  $\sigma_H, \sigma_P$ ,  $D(\mathbf{x})$  will also be bivariate Gaussian with standard deviation  $\sqrt{\sigma_H^2 + \sigma_P^2}$ .

Whereas local adaptation is classically measured as the difference between fitness “at home” versus fitness in a randomly selected environment, the limited dispersal analog is fitness “at home” versus fitness in a randomly selected environment weighted by the separation kernel. In particular, for species  $S = H, P$ ,

$$\hat{\mathcal{L}}_S = \mathbb{E}[\bar{w}_S(\mathbf{x}, \mathbf{x})] - \mathbb{E} \left[ \int_{\mathbb{R}^2} \bar{w}_S(\mathbf{x}, \mathbf{x} + \mathbf{y}) D(\mathbf{y}) d\mathbf{y} \right],$$

where  $\bar{w}_H(\mathbf{x}, \mathbf{y})$  and  $\bar{w}_P(\mathbf{x}, \mathbf{y})$  are shorthand for  $\bar{w}_H(\bar{z}_H(\mathbf{x}), \bar{z}_P(\mathbf{y}))$  and  $\bar{w}_P(\bar{z}_P(\mathbf{x}), \bar{z}_H(\mathbf{y}))$  respectively. Applying the trait matching/mis-matching model of fitness, we obtain

$$\hat{\mathcal{L}}_H = \dots$$

$$\hat{\mathcal{L}}_P = \dots$$

For the sake of clarity, we focus on a closely related measure of local adaptation that utilizes the local population growth rate  $\bar{m}_S$  instead of the population mean fitness  $\bar{w}_S$  for species  $S = H, P$ . In particular, we define

$$\hat{\ell}_S = \mathbb{E}[\bar{m}_S(\mathbf{x}, \mathbf{x})] - \mathbb{E} \left[ \int_{\mathbb{R}^2} \bar{m}_S(\mathbf{x}, \mathbf{x} + \mathbf{y}) D(\mathbf{y}) d\mathbf{y} \right],$$

where  $\bar{m}_H(\mathbf{x}, \mathbf{y})$  and  $\bar{m}_P(\mathbf{x}, \mathbf{y})$  are shorthand for  $\bar{m}_H(\bar{z}_H(\mathbf{x}), \bar{z}_P(\mathbf{y}))$  and  $\bar{m}_P(\bar{z}_P(\mathbf{x}), \bar{z}_H(\mathbf{y}))$  respectively. Applying the trait matching/mis-matching model of fitness along with our assumption of spatially homogeneous abiotic stabilizing selection, we obtain

$$\begin{aligned} \mathbb{E}[\bar{m}_H(\mathbf{x}, \mathbf{x})] &= r_H - \frac{A_H}{2} [(\theta_H - \mu_H)^2 + v_H + V_H] + \frac{B_H}{2} [(\mu_H - \mu_P)^2 + v_H + v_P + V_H + V_P] \\ &\quad - B_H C_{HP}(0), \end{aligned} \quad (2)$$

$$\begin{aligned} \mathbb{E} \left[ \int_{\mathbb{R}^2} \bar{m}_H(\mathbf{x}, \mathbf{y}) D(\mathbf{y}) d\mathbf{y} \right] &= r_H - \frac{A_H}{2} [(\theta_H - \mu_H)^2 + v_H + V_H] \\ &\quad + \frac{B_H}{2} [(\mu_H - \mu_P)^2 + v_H + v_P + V_H + V_P] - B_H \int_{\mathbb{R}^2} C_{HP}(\mathbf{y}) D(\mathbf{y}) d\mathbf{y}, \end{aligned} \quad (3)$$

$$\begin{aligned} \mathbb{E}[\bar{m}_P(\mathbf{x}, \mathbf{x})] &= r_P - \frac{A_P}{2} [(\theta_P - \mu_P)^2 + v_P + V_P] - \frac{B_P}{2} [(\mu_P - \mu_H)^2 + v_P + v_H + V_P + V_H] \\ &\quad + B_P C_{HP}(0), \end{aligned} \quad (4)$$

$$\begin{aligned} \mathbb{E} \left[ \int_{\mathbb{R}^2} \bar{m}_P(\mathbf{x}, \mathbf{y}) D(\mathbf{y}) d\mathbf{y} \right] &= r_P - \frac{A_P}{2} [(\theta_P - \mu_P)^2 + v_P + V_P] \\ &\quad - \frac{B_P}{2} [(\mu_P - \mu_H)^2 + v_P + v_H + V_P + V_H] + B_P \int_{\mathbb{R}^2} C_{HP}(\mathbf{y}) D(\mathbf{y}) d\mathbf{y}, \end{aligned} \quad (5)$$

Setting  $\bar{C}_{HP} \int_{\mathbb{R}^2} C_{HP}(\mathbf{y}) D(\mathbf{y}) d\mathbf{y}$ , the expressions for local adaptation accounting for limited dispersal simplify to

$$\hat{\ell}_H = B_H (\bar{C}_{HP} - C_{HP}(0)),$$

$$\hat{\ell}_P = B_P (C_{HP}(0) - \bar{C}_{HP}).$$

## B.2 Scott's measure of coevolutionary advantage

$$a = \bar{\bar{m}} - \bar{\bar{m}}^0$$

where  $\bar{\bar{m}}^0$  is the spatial average of growth rate in the absence of biotic selection. Setting  $\bar{\bar{z}}_S^0, V_S^0$  the spatial mean and variance of local mean traits for species  $S$  and  $C_{HP}^{S,0}$  the covariance of mean traits between species when  $B_S = 0$ , our model assumptions then implies

$$\begin{aligned} a_P &= B_P (C_{HP} - C_{HP}^{P,0}) - \frac{B_P}{2} [(\bar{\bar{z}}_H - \bar{\bar{z}}_P)^2 + V_H + V_P + v_H + v_P] \\ &\quad - \frac{A_P}{2} [(\theta_P - \bar{\bar{z}}_P)^2 - (\theta_P - \bar{\bar{z}}_P^0)^2 + V_P - V_P^0], \end{aligned} \quad (6)$$

$$\begin{aligned} a_H &= -B_P (C_{HP} - C_{HP}^{H,0}) + \frac{B_H}{2} [(\bar{\bar{z}}_P - \bar{\bar{z}}_H)^2 + V_H + V_P + v_H + v_P] \\ &\quad - \frac{A_H}{2} [(\theta_H - \bar{\bar{z}}_H)^2 - (\theta_H - \bar{\bar{z}}_H^0)^2 + V_H - V_H^0]. \end{aligned} \quad (7)$$

- NOTE: Scott defines this measure by comparing the coevolutionary scenario to the no biotic selection for both species scenario. In this case it seems possible that  $a$  can be positive for both species, blurring the distinction of which species is “winning” the coevolutionary race. Alternatively, we can proceed as above and consider the case when just one or the other species incurs zero biotic selection.

### B.3 Relation to results derived without gene-flow

Expressions for the spatial means, variance and covariance of local mean traits across a set of discrete populations without gene-flow between them have been presented by Week & Nuismer (2019). In the model of Week & Nuismer (2019) coevolution was driven by an offset-matching mechanism to capture trait escalation. When a parameter of their model known as the optimal offset is set to zero, the classical trait-matching model is recovered. Here we show how the results of Week & Nuismer (2019) on the spatial moments of a discrete space model with zero optimal offset are recovered as a special case of the SPDE model presented here in the limit of zero gene-flow (that is, in the limit of  $\sigma_H, \sigma_P \rightarrow 0$ ). In this limit our SPDE model becomes

$$\begin{aligned}\dot{\bar{z}}_H &= G_H A_H (\theta_H - \bar{z}_H) - G_H B_H (\bar{z}_P - \bar{z}_H) + \sqrt{\frac{G_H}{N_H}} \dot{W}_H, \\ \dot{\bar{z}}_P &= G_P A_P (\theta_P - \bar{z}_P) + G_P B_P (\bar{z}_H - \bar{z}_P) + \sqrt{\frac{G_P}{N_P}} \dot{W}_P.\end{aligned}$$

Without the homogenizing action of diffusive movement, solutions to this equation become more technically involved. In particular, we no longer have a function-valued equilibrium solution  $(\bar{z}_H, \bar{z}_P)^\top$ . Instead, we work a more general notion called a measure-valued solution. Whereas the function-valued solution takes points in  $\mathbb{R}^2$  and returns normally distributed random variables, the measure-valued solution takes subsets of  $\mathbb{R}^2$  and returns normally distributed random variables.

To provide intuition for the measure-valued solutions, let us first consider the case where  $\sigma_H, \sigma_P > 0$  so that the equilibrium function-valued solution  $(\bar{z}_H, \bar{z}_P)^\top$  does in fact exist. Then for bounded regions  $U$  of  $\mathbb{R}^2$  we can define

$$\bar{Z}_H(U) = \frac{1}{|U|} \int_U \bar{z}_H(x) dx, \quad \bar{Z}_P(U) = \frac{1}{|U|} \int_U \bar{z}_P(x) dx,$$

where  $|U|$  denotes the area of the region  $U \subset \mathbb{R}^2$ . In this way, both  $\bar{Z}_H$  and  $\bar{Z}_P$  are random measures on subsets of  $\mathbb{R}^2$  and thus constitute an equilibrium measure-valued solution of the SPDE model.

Although the function-valued solution  $(\bar{z}_H, \bar{z}_P)^\top$  fails to exist in the absence of gene-flow ( $\sigma_H, \sigma_P = 0$ ), a measure-valued solution  $(\bar{Z}_H, \bar{Z}_P)^\top$  does exist. In fact, for each fixed  $U \subset \mathbb{R}^2$  such that  $|U| < \infty$ ,  $(\bar{Z}_H(U), \bar{Z}_P(U))^\top$  correspond to equilibrium solutions of a bivariate Ornstein-Uhlenbeck process. Following results presented in Vatiwutipong and Phewchean (2019), the distribution of  $(\bar{Z}_H(U), \bar{Z}_P(U))^\top$  is bivariate normal determined by the mean vector  $\boldsymbol{\mu} = (\mu_H, \mu_P)^\top$  with

$$\begin{aligned}\mu_H &= \frac{(A_P + B_P)A_H\theta_H - B_H A_P \theta_P}{(A_P + B_P)A_H - B_H A_P}, \\ \mu_P &= \frac{(A_H - B_H)A_P \theta_P + B_P A_H \theta_H}{(A_H - B_H)A_P + B_P A_H},\end{aligned}$$

and variance-covariance matrix  $\boldsymbol{\Sigma} = \begin{pmatrix} V_H & C_{HP} \\ C_{HP} & V_P \end{pmatrix}$  with

$$\begin{aligned}V_H &= \frac{\frac{1}{2N_H} - B_H C_{HP}}{A_H - B_H}, \quad V_P = \frac{\frac{1}{2N_P} + B_P C_{HP}}{A_P + B_P} \\ C_{HP} &= \frac{B_P(A_P + B_P)G_P N_P - B_H(A_H - B_H)G_H N_H}{2(A_H A_P + A_H B_P - A_P B_H)((A_H - B_H)G_H + (A_P + B_P)G_P)N_H N_P}.\end{aligned}$$

This results correspond to the results found by Week & Nuismer (2019) when the optimal offset is set to zero. Hence, the statistical model of Week & Nuismer (2019) can be interpreted as a special case of the continuous space model presented here in the limit of zero gene-flow. Assuming weak coevolution so that  $B_H^2, B_P^2, B_H B_P \approx 0$ , we recover the marginal variances of mean trait values found using the SPDE with gene-flow. However, applying the same approximation to the covariance  $C_{HP}$  does not return the marginal covariance found using the SPDE model with gene-flow. Hence, the presence of gene-flow and limited dispersal fundamentally alters patterns of spatial trait covariance between coevolving species.

## **C The individual-based model**

## References

- Vatiwutipong, P., and N. Phewchean. 2019. "Alternative Way to Derive the Distribution of the Multivariate Ornstein-Uhlenbeck Process." *Advances in Difference Equations* 2019 (1). <https://doi.org/10.1186/s13662-019-2214-1>.