
THE ROLE OF GEOGRAPHY IN PATTERNS OF HOST-PARASITE LOCAL ADAPTATION

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Abstract

Previous work modeling the consequences of interactions between gene-flow, random genetic drift and coevolution on local adaptation in host-parasite systems have made use of metapopulation models where geography is discretized and dispersal is global. These studies generally conclude that an increased rate of gene-flow for the parasite relative to the host yields parasite local adaptation. The classical explanation for this result is that increased dispersal can lead to increased genetic variance and thus promote adaptive capacity. However, this explanation ignores the effect of continuous versus discrete geography on patterns of local adaptation. To close this gap we study a phenotypic model of host-parasite coevolution in continuous space with finite local population densities. We find the parasite is locally adapted to its host when its average dispersal distance is shorter than the average dispersal distance of the host. Performing a similar analysis on two metapopulation models of host-parasite trait coevolution where dispersal is either limited or global, but genetic variance is held constant for both, we recover the classical result described above. This highlights the role of geography and in particular suggests an important distinction between the effects of dispersal rate and dispersal distance on host-parasite local adaptation. Our results also contribute to the field of spatial statistics by providing a novel process-based model of spatial cross-correlation.

Keywords host-parasite coevolution · local adaptation · spatial scale · cross-correlation

1 Introduction

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

To understand patterns of phenotypic variation and host-parasite local adaptation in continuous space, we introduce and analyze a pair of stochastic partial differential equations (SPDE) that account for coevolution between host and parasite, abiotic stabilizing selection and random genetic drift. A brief justification for our model is provided in Appendix C. SPDE models are stochastic generalizations of deterministic PDE which 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 (Senthilnathan and Gavrillets 2021). By assuming additive genetic variances and population densities are constant in space and time, 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 mean traits for each species along with a spatial cross-covariance function between the mean traits of the two species. Each auto-covariance function provides the covariance of mean trait values for a given species

measured at a given distance apart. The cross-covariance function is similar, but returns the covariance of mean traits between species at a given distance apart.

The approach to obtaining spatial covariance functions from SPDE was made popular in the field of spatial statistics by Lindgren et. al. (2011). Under a weak coevolution approximation, the spatial auto-covariance functions found from our SPDE model provide natural notions of scale for intraspecific spatial patterns of phenotypic variation and coincide with results found by Slatkin (1978). Inspecting the cross-covariance function does not lead to an obvious candidate for the notion of cross-scale, or the spatial scale of coevolution. However, inspection of the cross-spectrum (ie, the distribution of harmonic content shared by patterns of phenotypic spatial variation between the two species) does yield a natural notion for the spatial scale of coevolution.

To study the consequences of continuous geography on host-parasite local adaptation, we extend the definition of local adaptation (previously defined for metapopulation models) to continuous space. We find, similarly to the metapopulation predecessors, the key determinant of local adaptation is spatial correlation of mean trait values. In terms of our cross-covariance function this is proportional to the cross-covariance function evaluated zero distance, which has been referred to as the marginal or collocated cross-covariance. Evaluating the collocated cross-covariance under the two limits where one species disperses much further than the other, we find the species with the shorter dispersal distance tends to be locally adapted.

To determine whether our result on local adaptation in continuous space is a consequence of geography, we studied local adaptation in two metapopulation models. In all of our models, we assume the coevolutionary interaction is mediated by a trait-matching mechanism, that each species experiences abiotic stabilizing selection, and that additive genetic variance and population size/density are constant in space and time. The two metapopulation models we consider are the island and two-dimensional stepping-stone models. As far as understanding the role of relative dispersal abilities in determining local adaptation, we find identical the result that the faster dispersing species is locally adapted for both models. This result appears opposite to what we found under our continuous space model, but coincides with findings of previous theoretical studies. However, those previous studies made use of population genetic models where the genetic variance evolved in space and time. The conventional reasoning for this classical result is that migrants from genetically distinct populations can increase local genetic variance and thus the rate of local adaptation. In contrast, our metapopulation models assume spatiotemporal constancy of genetic variance, but found the same result. While this certainly does not dismiss the importance of dynamical genetic variance in determining which species is locally adapted, it does suggest geography plays an important role.

We provide details on our models, extension of local adaptation for continuous space, and analytical approaches used in the **Methods** section. We summarize our results in greater detail in the **Results** section. Finally we discuss the implications of our findings, caveats, and future directions in the **Discussion** section.

2 Methods

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 a classical measure of local adaptation in terms of population growth rates instead of fitness measured as lifetime reproductive output. 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.

2.1 SPDE model

Our model of coevolution in continuous space employs a pair of linear stochastic partial differential equations to track the evolution of mean traits in the host, $\bar{z}_H(\mathbf{x})$, and the parasite, $\bar{z}_P(\mathbf{x})$, as functions of the two-dimensional spatial coordinates $\mathbf{x} = (x_1, x_2)^\top$. We assume geographical space is unbounded so that \mathbf{x} spans the entire plane \mathbb{R}^2 . As with all models studied here, we account for the effects of host-parasite coevolution using a trait-matching mechanism (ref other pprs using this model). This implies fitness of the host is minimized and fitness of the parasite is maximized when traits are matching and induces a local coevolutionary chase, where the parasite evolves to match the host and 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 θ_H, θ_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 $\sigma_H, \sigma_P > 0$ the standard deviations of individual movement in the host and parasite respectively. In our SPDE model, this translates to diffusion with coefficients $\sigma_H^2/2$ and $\sigma_P^2/2$ so that $\sigma_S^2 \Delta \bar{z}_S/2 = \sigma_S^2 (\frac{\partial^2}{\partial x_1^2} \bar{z}_S + \frac{\partial^2}{\partial x_2^2} \bar{z}_S)/2$ is the instantaneous rate of change in \bar{z}_S due to gene flow. For the sake of mathematical tractability, we also assume the additive genetic variances $G_H, G_P > 0$ and population densities $N_H, N_P > 0$ are temporally and spatially homogeneous for the host and parasite respectively. In Table X we provide a summary of model parameters. With this notation, our model can be written as

$$\dot{\bar{z}}_H = G_H B_H (\bar{z}_H - \bar{z}_P) + G_H A_H (\theta_H - \bar{z}_H) + \frac{\sigma_H^2}{2} \Delta \bar{z}_H + \sqrt{\frac{G_H}{N_H}} \dot{W}_H, \quad (1a)$$

$$\dot{\bar{z}}_P = G_P B_P (\bar{z}_H - \bar{z}_P) + G_P A_P (\theta_P - \bar{z}_P) + \frac{\sigma_P^2}{2} \Delta \bar{z}_P + \sqrt{\frac{G_P}{N_P}} \dot{W}_P. \quad (1b)$$

Here \dot{W}_H, \dot{W}_P denote two independent space-time white noise processes, which are Gaussian processes with values that are independent in both space and time. In particular, integrating \dot{W}_S 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, over an interval of unit length and region of unit area, the integral of $\sqrt{G_S/N_S} \dot{W}_S$ is normal with mean zero and variance G_S/N_S in analogy with classical models of random genetic drift used in quantitative genetic theory (refs). Since every parameter of the model is assumed to be spatially and temporally homogeneous, spatial variation under this model is ultimately caused by random genetic drift.

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 thereof. 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 equilibrium solution of model (1) is a bivariate Gaussian random field (refs for GRFs). An example of an equilibrium solution to model (1) 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 $\mathbf{C}(\mathbf{x}, \mathbf{y})$ (refs). While the (intraspecific) auto-covariance functions for each of the p variables occur along the diagonal of $\mathbf{C}(\mathbf{x}, \mathbf{y})$, the (interspecific) cross-covariance functions occur on the off-diagonal entries representing covariance between different variables at potentially different locations. In particular, the i, j th entry of $\mathbf{C}(\mathbf{x}, \mathbf{y})$ measures the covariance between the i th and j th variables sampled at locations $\mathbf{x} = (x_1, x_2)$ and $\mathbf{y} = (y_1, y_2)$ respectively. Taking expectation of our model at equilibrium, we find $\boldsymbol{\mu}(x_1, x_2) = (\mu_H, \mu_P)^\top$ is the vector of expected equilibrium trait values, which are spatially homogeneous and are determined by a balance between biotic and abiotic selection (expressions and derivation are provided in Appendix A).

Obtaining the spatial auto/cross-covariance matrix $\mathbf{C}(\mathbf{x}, \mathbf{y})$ is more challenging. However, since we assume all model parameters are spatio-temporally homogeneous, we can use known results on linear SPDE to conclude that $\mathbf{C}(\mathbf{x}, \mathbf{y})$ is stationary which implies that it only depends on the distance between \mathbf{x} and \mathbf{y} (refs). Hence, from hereon we write $\mathbf{C}(h)$ for some distance $h \geq 0$ between sampled locations. Linearity of the SPDE model (1) and stationarity of the auto/cross-covariance matrix allow us to employ spectral methods and capitalize on the relationship between spatial auto-covariance functions and power spectra of stationary Gaussian random fields. In particular, the power spectrum of a stationary Gaussian random field (where stationarity here implies spatial homogeneity of mean vector and stationarity of auto-covariance function) is the Fourier transform of the spatial auto-covariance function. Denote by $(\hat{z}_H(\mathbf{k}), \hat{z}_P(\mathbf{k}))^\top = \mathcal{F}[(\bar{z}_H(\mathbf{x}), \bar{z}_P(\mathbf{x}))^\top]$ the Fourier transformed equilibrium solution to model (1), where $\mathbf{k} = (k_1, k_2)$ correspond to spatial frequencies in each direction. The power spectra of the stationary solution to our model can then be computed as $S_H(\mathbf{k}) = \mathbb{E}(\hat{z}_H^2(\mathbf{k}))$, $S_P(\mathbf{k}) = \mathbb{E}(\hat{z}_P^2(\mathbf{k}))$ and $S_{HP}(\mathbf{k}) = \mathbb{E}(\hat{z}_H(\mathbf{k})\hat{z}_P(\mathbf{k}))$, where \mathbb{E} denotes expectation across all possible outcomes. Then, by setting $C_H(h), C_P(h)$ equal to the respective spatial auto-covariance functions

of the host and parasite mean traits and $C_{HP}(h)$ equal to the spatial cross-covariance function between host and parasite mean traits at distance h , we have

$$C_H = \mathcal{F}^{-1}[S_H], \quad C_P = \mathcal{F}^{-1}[S_P], \quad C_{HP} = \mathcal{F}^{-1}[S_{HP}], \quad (2)$$

where \mathcal{F}^{-1} denotes inverse Fourier transformation. In Appendix A we use a weak coevolution approximation to simplify expressions of power spectra and calculate analytical expressions for the spatial (intraspecific) auto-covariance and (interspecific) cross-covariance functions of host and parasite mean traits. In the next section, we make use of the spatial cross-covariance function $C_{HP}(h)$ to define a measure of local adaptation for species distributed continuously in space.

2.2 Local adaptation in continuous space

Measures of local adaptation quantify the difference in average fitness of individuals reared in local environmental conditions versus average fitness of individuals reared in foreign environmental conditions (refs). When individual fitness tends to be greater in local conditions in comparison to foreign conditions, the species is considered to be locally adapted. In this section we introduce a definition of local adaptation for species distributed continuously in space. However, before doing so, we briefly review a classical measure of local adaptation for species distributed in a finite number of discrete locations to motivate our continuous space analog.

Classically, measures of local adaptation are defined for finite, spatially discrete habitats in terms of expected lifetime reproductive output for an average individual transplanted from some locality i to some other locality j , denoted here by $\bar{w}_S(i, j)$ for species $S = H, P$. The bar above w_S signifies that we are averaging across trait values of individuals in species S found at location i . Then, assuming a finite number K of discrete habitats, average fitness of individuals reared in their local environmental conditions can be captured by $\bar{\bar{w}}_S = \sum_i \bar{w}_S(i, i)/K$ and average fitness of individuals transplanted to a randomly selected location can be captured by $\hat{\bar{w}}_S = \sum_{i,j} \bar{w}_S(i, j)/K^2$, where the sums are taken over $i = 1, \dots, K$ and $i, j = 1, \dots, K$ respectively. Then, a commonly used definition of local adaptation is given by $\mathcal{L}_S = \bar{\bar{w}}_S - \hat{\bar{w}}_S$ (refs). In turn, \mathcal{L}_S can be written in terms of the spatial covariance of host and parasite genotype frequencies (refs) or of host and parasite phenotypic distributions (see Appendix ??). In particular, this definition implies the parasite species is locally adapted when genotype or phenotype frequencies between host and parasite positively covary across locations. Conversely, the host is locally adapted when this covariance is negative.

To obtain an analogous measure of local adaptation to \mathcal{L}_S for species distributed continuously in space, we consider the difference in Malthusian growth rates for individuals reared in local conditions versus those reared in randomly drawn locations. In particular, we denote by $m_H(z_H, z_P)$ the Malthusian growth rate of host individuals having trait z_H encountering parasite individuals with trait z_P . Similarly, $m_P(z_P, z_H)$ is the growth rate of parasite individuals with trait z_P encountering host individuals with trait z_H . Setting $\varphi_S(z_S, \mathbf{x})$ the frequency of trait value z_S in species S at location \mathbf{x} , the Malthusian growth rate of hosts transplanted from location \mathbf{x} to location \mathbf{y} is given by

$$\bar{m}_H(\mathbf{x}, \mathbf{y}) = \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} m_H(z_H, z_P) \varphi_H(z_H, \mathbf{x}) \varphi_P(z_P, \mathbf{y}) dz_H dz_P. \quad (3)$$

The analogous quantity for the parasite species, $\bar{m}_P(\mathbf{x}, \mathbf{y})$, can be defined in a similar fashion. Since under our model (1) mean traits are random variables, the Malthusian growth rates $\bar{m}_H(\mathbf{x}, \mathbf{y})$, $\bar{m}_P(\mathbf{x}, \mathbf{y})$ are also random variables. We therefore define local adaptation in terms of expectations of these growth rates. In particular, we define a geographically specific measure of local adaptation for individuals of species S drawn from location \mathbf{x} and transplanted to location \mathbf{y} as

$$\Delta_S(\mathbf{x}, \mathbf{y}) = \mathbb{E}[\bar{m}_S(\mathbf{x}, \mathbf{x}) - \bar{m}_S(\mathbf{x}, \mathbf{y})]. \quad (4)$$

Since our model of mean trait evolution described in section 2.1 implies $(\bar{z}_H(\mathbf{x}), \bar{z}_P(\mathbf{x}))^\top$ is a stationary, isotropic Gaussian random field, $\bar{m}_S(\mathbf{x}, \mathbf{y})$ and $\Delta_S(\mathbf{x}, \mathbf{y})$ depend only on the distance $h \geq 0$ between locations \mathbf{x} and \mathbf{y} for both host and parasite. We therefore write $\bar{m}_S(h) = \bar{m}_S(\mathbf{x}, \mathbf{y})$ and $\Delta_S(h) = \Delta_S(\mathbf{x}, \mathbf{y})$ when the distance between \mathbf{x} and \mathbf{y} is h . Furthermore, since we model host and parasite species as being distributed continuously across the entire plane \mathbb{R}^2 , the assumption that the location transplanted to is drawn uniformly

at random (consistent with the classical measure \mathcal{L}_S) implies the distance transplanted will almost surely be infinite. We therefore define our continuous space analog of local adaptation for species S distributed in unbounded habitats as

$$\ell_S^\infty = \lim_{h \rightarrow \infty} \Delta_S(h). \quad (5)$$

In section ?? we present results found by combining our definition of local adaptation in continuous space with our model of host-parasite coevolution.

3 Results

3.1 Spatial covariances and characteristic lengths of phenotypic turnover

Using a weak coevolution approximation to simplify expressions for the power spectra (see Appendix A), we were able to employ an inverse Fourier transform to obtain analytic expressions for the (intraspecific) spatial auto-covariance and (interspecific) spatial cross-covariance functions of host and parasite mean trait values. In particular, we find spatial auto-covariance functions for the host and parasite respectively taking the forms

$$C_H(d) \approx \sqrt{2}V_H \frac{d}{\xi_H} K_1 \left(\sqrt{2} \frac{d}{\xi_H} \right), \quad (6a)$$

$$C_P(d) \approx \sqrt{2}V_P \frac{d}{\xi_P} K_1 \left(\sqrt{2} \frac{d}{\xi_P} \right), \quad (6b)$$

where V_H, V_P are the collocated variances (i.e., $C_S(0) = V_S$ for $S = H, P$), ξ_H, ξ_P are the characteristic lengths of phenotypic turnover across geographic space in each species and $K_\nu(d)$ is a modified Bessel function of second order, degree ν (ref aboromitz). These spatial covariance functions belong to the class of Matérn covariance functions which have been widely employed in the fields of spatial statistics (refs) and machine learning (refs).

The collocated variances V_H, V_P represent uncertainty in mean trait value at any particular location as opposed to variance of trait values among individuals at that location. Since solutions to our model are spatially homogeneous random fields (i.e., they have the same statistical properties at any given spatial location), mean traits of species S (where $S = H$ or $S = P$) at locations separated by distances much greater than the characteristic length ξ_S return essentially independent and identically distributed random variables with variances equal to the collocated variance V_S . Thus, the collocated variances also provide measures of global diversity of mean traits across space. In terms of our model parameters, the collocated variances can be expressed as

$$V_H = \frac{1}{N_H \sigma_H^2 A_H}, \quad V_P = \frac{1}{N_P \sigma_P^2 A_P}. \quad (7)$$

From the expressions for V_H and V_P we see population density N_S , dispersal distance σ_S and strength of abiotic stabilizing selection A_S all tend to decrease the overall diversity of mean traits of species S across space. Since our model assumes the ultimate source of spatial variation in mean traits is random genetic drift, this explains why increased population density erodes spatial diversity. Similarly, since we assume space extends across the entire plane \mathbb{R}^2 , in the limit of infinite dispersal distance we arrive at a panmictic population of infinite size, explaining why increased σ_S decreases V_S . These two results mirror those found in studies of continuous space population genetics using Wright's neighborhood size $\mathcal{N}_S = 4\pi N_S \sigma_S$, which is a continuous space analog of effective population size (refs). Since the abiotic optima θ_H, θ_P are assumed to be spatially homogeneous, abiotic stabilizing selection around these optima erodes spatial variation of mean traits in both species. In contrast, biotic selection has opposing effects on the degree of spatial variation in host and parasite mean traits. In particular, while increased biotic selection erodes spatial diversity of mean traits for the parasite species since it is stabilizing under the trait-matching model, increased biotic selection on the host promotes spatial variation because it is disruptive under the trait-matching model. However, since we require abiotic stabilizing selection on the host to outweigh biotic disruptive selection (i.e., $A_H > B_H$) for the existence of equilibrium solutions, selection will be overall stabilizing for both species around augmented optima that strike a balance between biotic and abiotic selection (see Appendix A). In

turn, since these augmented optima are spatially homogeneous, the overall stabilizing effect of selection diminishes the magnitude of spatial variation in mean traits for both species.

The characteristic lengths of phenotypic turnover across space in the host and parasite can be expressed in terms of model parameters respectively as

$$\xi_H = \frac{\sigma_H}{\sqrt{G_H A_H}}, \quad \xi_P = \frac{\sigma_P}{\sqrt{G_P A_P}}. \quad (8)$$

From these expressions, we see that characteristic spatial scales of phenotypic variation are proportional to the standard deviations of dispersal distances in the respective species. Hence, the further individuals tend to move, the larger the spatial scales one must observe to see significant phenotypic variation. We also see that increased additive genetic variance and abiotic stabilizing selection tends to decrease these spatial scales in each species. This reduction in spatial scale by additive genetic variance can be explained by the fact that additive genetic variation inflates the effects of random genetic drift, here assumed to be the ultimate source of spatial variation. With increased spatial variation, one can observe significant changes in mean trait values over shorter spatial scales. However, since stabilizing selection homogenizes mean trait values across space, it is less obvious why increased strength of abiotic selection should decrease spatial scales of phenotypic turnover.

In contrast to the relatively simple expressions for the intraspecific auto-covariance functions, the expression for the interspecific cross-covariance function is rather cumbersome. In particular, $C_{HP}(d)$ can be approximated as the difference of two convolutions when coevolution is weak, the expression for which is provided in Appendix A. However, our measure of local adaptation (eqn. 13) requires only the collocated covariance $C_{HP}(0)$. We can therefore sidestep calculating the cross-covariance $C_{HP}(d)$ for $d > 0$. The collocated covariance $C_{HP}(0)$ can be obtained via spectral methods and the calculations for which are provided in Appendix A. In particular, we find

$$C_{HP}(0) \approx \frac{G_H G_P}{\sigma_H^2 \sigma_P^2} \frac{\xi_H^2 \xi_P^2}{(\xi_H^2 - \xi_P^2)^2} \left[\frac{B_P}{N_H \sigma_H^2} \left(\xi_H^4 + \xi_H^2 \xi_P^2 (\ln \xi_P^2 - \ln \xi_H^2 - 1) \right) - \frac{B_H}{N_P \sigma_P^2} \left(\xi_P^4 + \xi_H^2 \xi_P^2 (\ln \xi_H^2 - \ln \xi_P^2 - 1) \right) \right]. \quad (9)$$

In analogy to how the collocated variances V_H, V_P provide global measures of mean trait variation across space within each species, the collocated covariance $C_{HP}(0)$ provides a global measure of mean trait co-variation across space between the two species. Expression (9) implies that, when hosts and parasites exhibit approximately equal spatial scales of phenotypic turnover (i.e., when $\xi_H \approx \xi$ and $\xi_P \approx \xi$ for some $\xi > 0$), the collocated covariance is approximately

$$C_{HP}^{(\xi_H \approx \xi_P)}(0) \approx \frac{\xi^4}{2} G_H G_P \left(\frac{B_P}{N_H \sigma_H^4 \sigma_P^2} - \frac{B_H}{N_P \sigma_H^2 \sigma_P^4} \right). \quad (10)$$

Hence, in this limiting case, we see that increased biotic selection on the parasite over the host ($B_P > B_H$) tends to increase spatial covariance of host and parasite mean traits. We also see spatial covariance increases when the parasite population density is greater than the host population density ($N_P > N_H$) and when parasite dispersal distance exceeds host dispersal distance ($\sigma_P > \sigma_H$) under the condition that $\sigma_H, \sigma_P > 1$.

We can also investigate the collocated covariance under two other extremes; when the spatial scale of phenotypic turnover for the host is much less than the scale of phenotypic turnover in the parasite, so that $\xi_H \ll \xi_P$, and when this relationship is reversed so that $\xi_P \ll \xi_H$. For $\xi_H \ll \xi_P$ and $\xi_P \ll \xi_H$ respectively, second order Taylor expansion yields

$$C_{HP}^{(\xi_H \ll \xi_P)}(0) \approx -\frac{B_H}{A_H} V_P, \quad C_{HP}^{(\xi_P \ll \xi_H)}(0) \approx \frac{B_P}{A_P} V_H. \quad (11)$$

From these two limiting cases we see the collocated spatial covariance is always negative when $\xi_H \ll \xi_P$ and always positive when $\xi_P \ll \xi_H$. The collocated spatial correlation is given by $C_{HP}(0)/\sqrt{V_H V_P}$ and can therefore be approximated by combining expressions (7) and (11). In the next section we capitalize on these results to understand patterns of host and parasite local adaptation.

3.1.1 When one species disperses much further than the other

Consider here the two complementary cases where 1) the host disperses much further than the parasite so that $\sigma_P/\sigma_H \approx 0$ and 2) the parasite disperses much further than the host so that $\sigma_H/\sigma_P \approx 0$. We can study these cases at the spatial scale of the shorter and longer dispersing species separately. At the spatial scale of the longer disperser, we analyze our model in the limit where dispersal distance of the shorter dispersing species tends to zero. Similarly, at the scale of the shorter dispersing species, we consider the limit where the dispersal distance of the longer disperser tends to infinity.

Let us first consider the spatial scale of the longer disperser. From this perspective the intraspecific spatial covariance structure of the shorter dispersing species collapses. In fact, from this perspective the random field describing the spatial distribution of mean trait values for the shorter dispersing species is described by a spatial white-noise process (which is uncorrelated in space). However, this mis-match of scales does not prevent coevolution and interspecific spatial correlations of trait values. Indeed the interspecific spatial cross-covariance function becomes proportional to the intraspecific spatial covariance function of the longer dispersing species when traits are measured at distinct locations for the two species. When traits are measured at the same locations, there is an additional term that can either increase or decrease interspecific correlation. This is due to the shorter disperser evolving only in response to the conditions at spatially microscopic regions when considered from the scale of the longer disperser. This discontinuity suggests the spatial scale of interspecific cross-correlation due to coevolution is a bivariate quantity when coevolving species disperse on different orders of magnitude and the components of this quantity are just the spatial scales phenotypic variation for each species. In particular, it seems the notion of scale for spatial cross-correlation between species will not yield a suitable definition for the spatial scale of coevolution.

Aside from the suggestion that spatial scale of cross-correlation is a bivariate quantity, a few other results follow. In particular, the signage of the interspecific covariance between mean traits measured at distinct locations is determined by the shorter dispersing species (negative when the host dispersal distance is much less than parasite dispersal distance and positive otherwise). Hence, while the longer disperser determines the spatial scale of cross-covariance between distinct locations, the shorter disperser determines the signage.

We make use of this result below in our analysis of local adaptation. Interestingly, when there is no biotic selection on the shorter disperser the interspecific covariance between traits measured at distinct locations is also zero. However, when traits of the two species are measured at the same locations, there is correlation between them so long as at least one of the species experiences biotic selection just as predicted by previous models.

At the scale of the shorter disperser patterns of spatial covariation appear drastically different. To obtain this perspective from our model, we take the limit as the dispersal distance of the longer disperser tends to infinity. At this scale there are no observable spatial patterns in the trait of the longer disperser. Hence, the intraspecific spatial covariance function of the greater disperser collapses to zero. This implies no spatial variance for the greater disperser and thus no spatial cross-covariance between the species. This result holds when either the host or parasite is assumed to be the longer disperser. From this we conclude that, when interacting species disperse at different orders of magnitude, the signal of coevolution in spatial patterns of covariation tends to resonate at the spatial scale of the longer disperser.

3.2 Local adaptation

Recall that $\Delta_S(d)$ is the differences in fitness (measured as population growth rates) for individuals of species $S = H, P$ reared in their local environment versus individuals transplanted at some distance d . In Appendix ?? we show that the trait-matching model of fitness used to obtain the mean trait dynamics described by equation (1) implies that $\Delta_H(d)$ and $\Delta_P(d)$, the difference in growth rates for respective host or parasite individuals reared in local environment versus those transplanted a distance d , can be simplified to

$$\Delta_H(d) = B_H(C_{HP}(d) - C_{HP}(0)) \quad (12a)$$

$$\Delta_P(d) = B_P(C_{HP}(0) - C_{HP}(d)). \quad (12b)$$

Finally, since under our model of host-parasite coevolution the cross-covariance function $C_{HP}(d)$ decays to zero as $d \rightarrow \infty$, our measure of local adaptation for each species simplifies to

$$\ell_H = -B_H C_{HP}(0), \quad (13a)$$

$$\ell_P = B_P C_{HP}(0). \quad (13b)$$

From equations (13), we see that the host is locally adapted ($\ell_H > 0$) when host and parasite mean traits are negatively correlated across sufficiently long distances (i.e., when $C_{HP}(0) < 0$) and that the parasite is locally adapted when mean traits are positively correlated across sufficiently long distances, where sufficiently long distances here correspond to distances at which intraspecific spatial autocorrelations of mean trait values are negligible. Hence, this definition is consistent with the classical measure \mathcal{L}_S defined for species distributed across discrete patches.

4 Discussion

In the absence of biotic selection, our expressions for the characteristic lengths of phenotypic turnover across space (eqns. 8) coincide with the characteristic length found by Slatkin (1978) in his pioneering work on the evolution of quantitative traits in continuous space. Notably, while Slatkin assumed one-dimensional space and discrete time, we assume two-dimensional space and continuous time. Furthermore, while Slatkin assumed spatial variation in mean traits were the result of spatially varying abiotic stabilizing selection, we assume the ultimate source of spatial variation is due to the effects of random genetic drift. Whether or not this coincidence sheds light on some universal property of phenotypic variation across space or is merely a mathematical artifact due to the approximation schemes employed remains unclear.

Limitations of our approach include the assumption of weakly coevolving hosts and parasites, spatially homogeneous abiotic trait optima, strengths of selection, additive genetic variances and abundance densities. Furthermore, in order for our model to have equilibrium solutions, we require abiotic selection to be greater than biotic selection (i.e., $A_H > B_H$).

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 $\int_{\mathbb{R}^2} S_{\mathbf{F}}(\mathbf{k}) d\mathbf{k} = C_{\mathbf{F}}(\mathbf{0})$. 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 $B_H^2, B_P^2, B_H B_P \approx 0$ and that abiotic selection is relatively strong so that $A_H B_H, A_P B_P \approx 0$, we obtain the approximations

$$\begin{aligned} S_H(\mathbf{k}) &\approx \frac{G_H/N_H}{\left(G_H A_H + \frac{\sigma_H^2}{2} \|\mathbf{k}\|^2\right)^2}, \quad S_P(\mathbf{k}) \approx \frac{G_P/N_P}{\left(G_P A_P + \frac{\sigma_P^2}{2} \|\mathbf{k}\|^2\right)^2} \\ S_{HP}(\mathbf{k}) &\approx \frac{B_P G_P G_H/N_H}{\left(G_H A_H + \frac{\sigma_H^2}{2} \|\mathbf{k}\|^2\right)^2 \left(G_P A_P + \frac{\sigma_P^2}{2} \|\mathbf{k}\|^2\right)} \\ &\quad - \frac{B_H G_H G_P/N_P}{\left(G_H A_H + \frac{\sigma_H^2}{2} \|\mathbf{k}\|^2\right) \left(G_P A_P + \frac{\sigma_P^2}{2} \|\mathbf{k}\|^2\right)^2} \\ &\approx \frac{B_P G_P}{G_P A_P + \frac{1}{2} \sigma_P^2 \|\mathbf{k}\|^2} S_H(\mathbf{k}) - \frac{B_H G_H}{G_H A_H + \frac{1}{2} \sigma_H^2 \|\mathbf{k}\|^2} S_P(\mathbf{k}) \end{aligned}$$

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

Using common notation for describing covariance structures of random fields, we denote by ξ_S the characteristic scale of spatial trait covariance for 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 as well as the expected sample variance for mean traits sampled far enough apart. Setting

$$\xi_H = \frac{\sigma_H}{\sqrt{G_H A_H}}, \quad \xi_P = \frac{\sigma_P}{\sqrt{G_P A_P}},$$

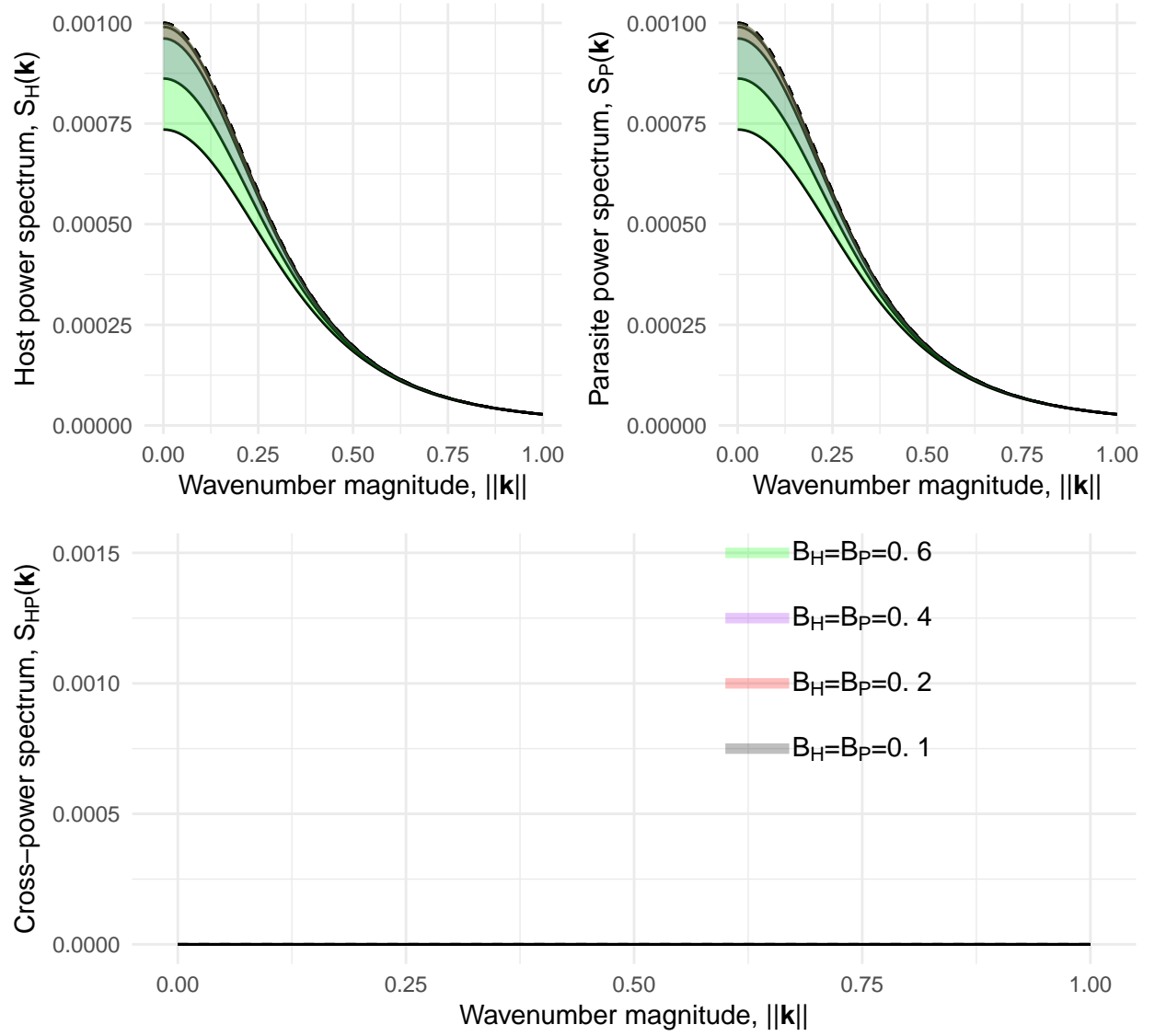


Figure 1: Comparisons of approximated power spectra (dashed lines) to exact power spectra (solid lines) for four different strengths of biotic (coevolutionary) selection $B = 0.1, 0.2, 0.4, 0.6$. For simplicity, biotic selection on host and parasite are set equal ($B_H = B_P = B$). Background parameters 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.

$$V_H = \frac{1}{N_H \sigma_H^2 A_H}, \quad V_P = \frac{1}{N_P \sigma_P^2 A_P},$$

the approximated power spectra can be rewritten as

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

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

The cross-spectrum can be simplified in few special cases. First, in the case where $\xi_H = \xi_P = \xi$ we have

$$S_{HP}^{\{\xi_H = \xi_P = \xi\}}(\mathbf{k}) \approx \left(V_H \frac{B_P}{A_P} - V_P \frac{B_H}{A_H} \right) \frac{\xi^2}{(1 + \frac{1}{2} \xi^2 \|\mathbf{k}\|^2)^3}.$$

Since the cases where $\xi_P \rightarrow 0$ and $\xi_H \rightarrow 0$ respectively imply $\sigma_P \rightarrow 0$ and $\sigma_H \rightarrow 0$ (assuming finite additive genetic variances and selection strengths), we consider the power spectra in terms of the biological parameters above. In these two cases we see the intraspecific power spectra become

$$S_H^{\{\sigma_H \rightarrow 0\}}(\mathbf{k}) \approx \frac{1}{N_H A_H}, \quad S_P^{\{\sigma_P \rightarrow 0\}}(\mathbf{k}) \approx \frac{1}{N_P A_P}.$$

Then it follows the interspecific cross-spectrum becomes

$$S_{HP}^{\{\sigma_P \rightarrow 0\}}(\mathbf{k}) \approx \frac{B_P}{A_P} S_H(\mathbf{k}) - \frac{B_H}{N_P A_H A_P},$$

$$S_{HP}^{\{\sigma_H \rightarrow 0\}}(\mathbf{k}) \approx \frac{B_P}{N_H A_H A_P} - \frac{B_H}{A_H} S_P(\mathbf{k}).$$

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_ν is a modified Bessel function of the second kind, order ν . Conveniently, the approximated spatial covariance functions take the form of a Matérn covariance functions, which are widely applied in the fields of spatial statistics (refs) and machine learning (ref). In general, the 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

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

- $K_0(\|\mathbf{x}\|)$ is positive integrable and square integrable function of \mathbf{x} , which suggests the convolution with $M_1(\mathbf{x}|\xi, V)$ produces a legit covariance function.

- Still need to check that this cross-covariance function is copacetic with the intraspp cov fcts. how to check?

$$\mathcal{F}\{C_{HP}/\sqrt{C_H C_P}\} = \hat{C}_{HP} * \mathcal{F}\{1/\sqrt{C_H}\} * \mathcal{F}\{1/\sqrt{C_P}\}$$

In general, this cross-covariance function is not Matérn. However, under the special cases listed above, this cross-covariance function does take the form of a Matérn function. In particular, under the respective special cases we get

$$C_{HP}^{\{\xi_H=\xi_P=\xi\}}(\mathbf{x}) \approx \left(V_H \frac{B_P}{A_P} - V_P \frac{B_H}{A_H} \right) 2 \frac{\|\mathbf{x}\|^2}{\xi^2} K_2 \left(2 \frac{\|\mathbf{x}\|}{\xi} \right),$$

$$C_{HP}^{\{\xi_P \ll \xi_H\}}(\mathbf{x}) \approx \frac{B_P}{A_P} V_H \sqrt{2} \frac{\|\mathbf{x}\|}{\xi_H} K_1 \left(\sqrt{2} \frac{\|\mathbf{x}\|}{\xi_H} \right),$$

$$C_{HP}^{\{\xi_H \ll \xi_P\}}(\mathbf{x}) \approx -\frac{B_H}{A_H} V_P \sqrt{2} \frac{\|\mathbf{x}\|}{\xi_P} K_1 \left(\sqrt{2} \frac{\|\mathbf{x}\|}{\xi_P} \right).$$

In each of these special cases the notions of spatial scale for cross-covariance, which provides a notion of spatial scale of coevolution, are trivially defined respectively by ξ , ξ_H and ξ_P . Research on the spatial dynamics of host-parasite coevolution has focused on cases of differential migration patterns and selection strengths, resulting here in distinct spatial scales of intraspecific variation. Since our SPDE model predicts Matérn functions that describe spatial cross-covariation between coevolving species require equivalent intraspecific spatial scales, we see that they fall short of capturing the more realistic and interesting biological scenarios.

The general cross-covariance function above is rather unwieldy, making its direct study difficult. An alternative quantity to consider is the so-called *coherence function*, which describes linear relationships between two random fields at each frequency in their spectral representations. In particular, interspecific coherence is defined by

$$\kappa_{HP}(\mathbf{k}) = \frac{S_{HP}(\mathbf{k})}{\sqrt{S_H(\mathbf{k})S_P(\mathbf{k})}}.$$

This function can be used to compute frequencies of maximal coherency, which provides information about the spatial scale of interspecific covariance (and thus a notion for the spatial scale of interspecific coevolution). Before examining the general case, we consider the special cases where the cross-covariance function is Matérn. In general, for a pair of random fields having Matérn covariance functions with smoothness ν_i and scale ξ_i for the i th field and ν_{12}, ξ_{12} for the cross-smoothness and cross-scale, the frequencies $\|\mathbf{k}\|^2$ that maximize the square coherency function $|\kappa_{12}(\mathbf{k})|^2$ are known to solve

$$\frac{\nu_1 + d/2}{2\nu_1/\xi_1^2 + \|\mathbf{k}\|^2} + \frac{\nu_2 + d/2}{2\nu_2/\xi_2^2 + \|\mathbf{k}\|^2} - \frac{2\nu_{12} + d}{2\nu_{12}/\xi_{12}^2 + \|\mathbf{k}\|^2} = 0.$$

Following our results above, in the special case of $\xi_H = \xi_P = \xi$ we obtain maximum square coherence at frequency $\|\mathbf{k}\| = \sqrt{2}/\xi$. This suggests that the frequency of maximum square coherence is inversely proportional to the spatial scale of coevolution. In both cases where one species disperses a much greater distance than the other and we take the perspective of the greater disperser (so that the dispersal distance of the shorter disperser is sent to zero) the square coherence is maximized at $\|\mathbf{k}\| = +\infty$ which, by the same reasoning, would suggest the spatial scale of coevolution is zero. In general, coherence under our model takes the form

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

The square of this coherence function is maximized at

$$\|\mathbf{k}^*\|^2 = 2 \frac{V_P B_H A_P \xi_H^{-2} - V_H B_P A_H \xi_P^{-2} \pm \sqrt{V_H V_P B_H B_P A_H A_P} |\xi_P^{-2} - \xi_H^{-2}|}{V_P B_P A_H - V_H B_H A_P}.$$

It can be verified that the three special cases treated above can be derived from this general solution. A unique solution exists when

$$\left(\frac{V_H B_P A_H}{V_P B_H A_P} - 1 \right) \xi_H^4 < \left(1 - \frac{V_P B_H A_P}{V_H B_P A_H} \right) \xi_P^4.$$

Under these conditions we can define the spatial scale of coevolution as $\xi_{HP} = \sqrt{2}/\|\mathbf{k}^*\|$. When these conditions are not met either no solution exists or two solutions exist. In the case of two solutions, denote them by $\|\mathbf{k}_1^*\|^2$ and $\|\mathbf{k}_2^*\|^2$, we can extend the definition of the spatial scale of coevolution to $\xi_{HP} = 2/\sqrt{\|\mathbf{k}_1^*\|^2 + \|\mathbf{k}_2^*\|^2}$ which returns the original definition when $\|\mathbf{k}_1^*\| = \|\mathbf{k}_2^*\|$. Lastly, we note that when one species disperses much greater than the other and we take the perspective of the shorter disperser (so that either $\sigma_H \rightarrow +\infty$ or $\sigma_P \rightarrow +\infty$), we obtain $\|\mathbf{k}^*\| = 0$ which implies the spatial scale of coevolution is infinite in these cases. Since the cross-covariance is zero in these cases we had no way to define this scale previously. Pairing with our results above where we considered the scale of the greater disperser, we see that whether the spatial scale of coevolution is zero or infinity depends on whether we take the perspective of the longer or shorter disperser respectively.

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

$$\begin{aligned} C_{HP}(\mathbf{0}) &= \frac{1}{2\pi} \int_{\mathbb{R}^2} S_{HP}(\mathbf{k}) d\mathbf{k} \\ &\approx \frac{G_H G_P}{\sigma_H^2 \sigma_P^2} \frac{\xi_H^2 \xi_P^2}{(\xi_H^2 - \xi_P^2)^2} \left[\frac{B_P}{N_H \sigma_H^2} \left(\xi_H^4 + \xi_H^2 \xi_P^2 (\ln \xi_P^2 - \ln \xi_H^2 - 1) \right) \right. \\ &\quad \left. - \frac{B_H}{N_P \sigma_P^2} \left(\xi_P^4 + \xi_H^2 \xi_P^2 (\ln \xi_H^2 - \ln \xi_P^2 - 1) \right) \right]. \end{aligned}$$

This marginal covariance turns out to be central to our definition of local adaptation in continuous space. However, below we consider alternative definitions of local adaptation and they depend on different functionals of the spatial cross-covariance function. Hence, we list here the needed results for our alternative definitions of local adaptation.

The integral of $C_{HP}(\mathbf{x})$ is approximated via

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

Note that 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 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

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

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

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

We therefore conclude

$$\begin{aligned} \int_0^\infty C_{HP}(r) dr &\approx \frac{1}{4\sqrt{2}} \left(\frac{B_P}{A_P} \xi_H V_H - \frac{B_H}{A_H} \xi_P V_P \right) \\ &= \frac{1}{4\sqrt{2}} \left(\frac{B_P}{A_P} \frac{\xi_H}{\sqrt{2}} V_H - \frac{B_H}{A_H} \left(A_P^{3/2} N_P \sigma_P \sqrt{G_P} \right)^{-1} \right). \end{aligned}$$

Using the same trick to compute the integral lengths of intraspecific phenotypic variation, we find

$$\int_0^\infty C_S(r) dr = \frac{1}{2\pi} \lim_{\mathbf{k} \rightarrow \mathbf{0}} \mathcal{F} \left\{ \frac{C_S(\mathbf{x})}{\|\mathbf{x}\|} \right\} \approx \frac{V_S \xi_S}{4\sqrt{2}}.$$

The quantity $\mathcal{I}_S = \int_0^\infty C_S(r) dr$ has been referred to as the integral length of spatial covariance (here the integral length of intraspecific spatial covariance). Then, an integral length of interspecific spatial covariance may be computed as

$$\mathcal{I}_{HP} := \int_0^\infty |C_{HP}(r)| dr.$$

Assuming $C_{HP}(r)$ is either always positive or always negative allows us to move the absolute value outside of the integral. Then, under our model, we find

$$\begin{aligned} \mathcal{I}_{HP} &\approx \frac{1}{4\sqrt{2}} \left| \frac{B_P}{A_P} V_H \xi_H - \frac{B_H}{A_H} V_P \xi_P \right| \\ &= \frac{1}{4\sqrt{2}} \left| \frac{B_P}{A_P A_H^{3/2}} \frac{1}{\sigma_H N_H \sqrt{G_H}} - \frac{B_H}{A_H A_P^{3/2}} \frac{1}{\sigma_P N_P \sqrt{G_P}} \right|. \end{aligned}$$

B Measures of local adaptation

- use \mathcal{L} for measures in terms of mean fitness and ℓ 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 $\mathcal{L}_P = \tilde{\alpha} - \tilde{\alpha}_0$. Using a slightly different definition, parasite local adaptation simplifies to $\ell_P = \widetilde{\ln \alpha} - \widetilde{\ln \alpha_0} = B_P C_{HP}(0)$.

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

$$\Delta_H(\mathbf{y}) = \mathbb{E} \left[\frac{B_H}{2} (\bar{z}_H(\mathbf{x}) - \bar{z}_P(\mathbf{x}))^2 - \frac{B_H}{2} (\bar{z}_H(\mathbf{x}) - \bar{z}_P(\mathbf{x} + \mathbf{y}))^2 \right] = B_H (C_{HP}(\|\mathbf{y}\|) - C_{HP}(0)),$$

where $\|\mathbf{y}\| = \sqrt{y_1^2 + y_2^2}$. Similarly, we obtain $\Delta_P(\mathbf{y}) = B_P(C_{HP}(0) - C_{HP}(\|\mathbf{y}\|))$ for the parasite. Now, if we consider picking \mathbf{y} at random from a disc of radius h centered on the origin (ie, $U_h = \{\mathbf{x} : \|\mathbf{x}\| < h\}$), the probability that $h/2 < \|\mathbf{y}\| < h$ is $3/4$. Hence, there is a greater probability that $\|\mathbf{y}\|$ will be closer to h than to zero. Then, considering uniform random sampling of the plane \mathbb{R}^2 as the limit of sampling from U_h as $h \rightarrow \infty$, we can expect any \mathbf{y} randomly sampled from the plane to have infinite length. This sampling process is analogous to the global random sampling process used in definitions of local adaptation for metapopulation models. Then, to define a comparable measure of local adaptation for continuously distributed populations we set

$$\ell_S^\infty := \lim_{\|\mathbf{y}\| \rightarrow \infty} \Delta_S(\mathbf{y}).$$

There are alternative notions of local adaptation we can consider that provide different perspectives. For example, we could consider integrating $\Delta_S(\mathbf{y})$ across the entire plane to obtain a different global measure of local adaptation. The idea here is to account for fitness differences measured at all possible distances instead of a random distance. We define this measure as $\hat{\ell}_S := \int_{\mathbb{R}^2} \Delta_S(\mathbf{y}) d\mathbf{y}$. Using our results from section A, we obtain

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

This measure of local adaptation depends on the effective densities N_H, N_P which suggests it provides some indication for the role of random genetic drift in determining global patterns of local adaptation. However, it does not dependent on dispersal distances because of the extra weight given to larger distances implicit in this definition. Hence, it provides no information on the role of gene-flow in determining global patterns of local adaptation. To circumvent this issue, we define another index that explicitly integrates across distances. In particular, we define $\tilde{\ell}_S = \int_0^\infty \tilde{\Delta}_S(h\mathbf{e}) dh$ where $\mathbf{e} = (1/\sqrt{2}, 1/\sqrt{2})^\top$. Using our results from above, we find

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

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 $\bar{\ell}_H, \bar{\ell}_P$ do not capture the effects of random genetic drift. Hence, the two sets of indices $(\bar{\ell}_H, \bar{\ell}_P)$ and $(\hat{\ell}_H, \hat{\ell}_P)$ capture complementary aspects of global patterns of local adaptation driven by interactions between gene-flow, drift, abiotic stabilizing selection, and host-parasite coevolution.

B.1 A local measure of local adaptation

The global measure of local adaptation defined above considered the difference in fitness at two points in space drawn uniformly at random. Hence, the global measure captures the idea of comparing host fitness when confronted with a local parasite to host fitness when confronted to a parasite drawn at random from any location. Since the expected distance between random locations drawn from an infinite plane is infinite, this global measure ignores the effects of spatial autocorrelation. However, the range sizes of empirical host-parasite systems may not be large enough to ignore spatial autocorrelation. Hence, a local measure of local adaptation is needed.

Writing $D_S(\mathbf{y})$ as the dispersal kernel for species S , we can compute the average spatial fitness difference with respect to this dispersal kernel as $\bar{\Delta}_S := \int_{\mathbb{R}^2} \Delta_S(\mathbf{y}) D_S(\mathbf{y}) d\mathbf{y}$. To compute this average we use the relation $\int_{\mathbb{R}^2} \Delta_S(\mathbf{y}) D_S(\mathbf{y}) d\mathbf{y} = \int_{\mathbb{R}^2} \hat{\Delta}_S(\mathbf{k}) \hat{D}_S(\mathbf{k}) d\mathbf{k}$, where $\hat{\Delta}_S(\mathbf{k})$ and $\hat{D}_S(\mathbf{k})$ are respectively the Fourier transforms of $\Delta_S(\mathbf{x})$ and $D_S(\mathbf{x})$.

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) σ_H, σ_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

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

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

$$\begin{aligned} \mathbb{E}[\bar{m}_H(\mathbf{x}, \mathbf{x})] = r_H - \frac{A_H}{2} [(\theta_H - \mu_H)^2 + v_H + V_H] + \frac{B_H}{2} [(\mu_H - \mu_P)^2 + v_H + v_P + V_H + V_P] \\ - B_H C_{HP}(0), \end{aligned} \quad (14)$$

$$\begin{aligned} \mathbb{E} \left[\int_{\mathbb{R}^2} \bar{m}_H(\mathbf{x}, \mathbf{y}) D(\mathbf{y}) d\mathbf{y} \right] &= r_H - \frac{A_H}{2} [(\theta_H - \mu_H)^2 + v_H + V_H] \\ &\quad + \frac{B_H}{2} [(\mu_H - \mu_P)^2 + v_H + v_P + V_H + V_P] - B_H \int_{\mathbb{R}^2} C_{HP}(\mathbf{y}) D(\mathbf{y}) d\mathbf{y}, \end{aligned} \quad (15)$$

$$\begin{aligned} \mathbb{E}[\bar{m}_P(\mathbf{x}, \mathbf{x})] &= r_P - \frac{A_P}{2} [(\theta_P - \mu_P)^2 + v_P + V_P] - \frac{B_P}{2} [(\mu_P - \mu_H)^2 + v_P + v_H + V_P + V_H] \\ &\quad + B_P C_{HP}(0), \end{aligned} \quad (16)$$

$$\begin{aligned} \mathbb{E} \left[\int_{\mathbb{R}^2} \bar{m}_P(\mathbf{x}, \mathbf{y}) D(\mathbf{y}) d\mathbf{y} \right] &= r_P - \frac{A_P}{2} [(\theta_P - \mu_P)^2 + v_P + V_P] \\ &\quad - \frac{B_P}{2} [(\mu_P - \mu_H)^2 + v_P + v_H + V_P + V_H] + B_P \int_{\mathbb{R}^2} C_{HP}(\mathbf{y}) D(\mathbf{y}) d\mathbf{y}, \end{aligned} \quad (17)$$

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

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

where \bar{m}^0 is the spatial average of growth rate in the absence of biotic selection. Setting \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

$$\begin{aligned} a_P &= B_P (C_{HP} - C_{HP}^{P,0}) - \frac{B_P}{2} [(\bar{z}_H - \bar{z}_P)^2 + V_H + V_P + v_H + v_P] \\ &\quad - \frac{A_P}{2} [(\theta_P - \bar{z}_P)^2 - (\theta_P - \bar{z}_P^0)^2 + V_P - V_P^0], \end{aligned} \quad (18)$$

$$\begin{aligned} a_H &= -B_P (C_{HP} - C_{HP}^{H,0}) + \frac{B_H}{2} [(\bar{z}_P - \bar{z}_H)^2 + V_H + V_P + v_H + v_P] \\ &\quad - \frac{A_H}{2} [(\theta_H - \bar{z}_H)^2 - (\theta_H - \bar{z}_H^0)^2 + V_H - V_H^0]. \end{aligned} \quad (19)$$

- 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 The discrete geography models

B.3.1 Global dispersal

To study the role of geography, we consider an extreme alternative to our continuous space model. In particular, we assume dispersal is global and follows a metapopulation model with n locations. Individuals

move between locations at a fixed rate for each species. We denote these migration rates by $\omega_H, \omega_P \geq 0$. Then, denoting $\mu_S(t)$ the average of $\bar{z}_S(t)$ across locations, our discrete geography model is

$$\dot{\bar{z}}_H = G_H A_H (\theta_H - \bar{z}_H) - G_H B_H (\bar{z}_P - \bar{z}_H) + \omega_H (\mu_H - \bar{z}_H) + \sqrt{\frac{G_H}{N_H}} \dot{W}_H,$$

$$\dot{\bar{z}}_P = G_P A_P (\theta_P - \bar{z}_P) + G_P B_P (\bar{z}_H - \bar{z}_P) + \omega_P (\mu_P - \bar{z}_P) + \sqrt{\frac{G_P}{N_P}} \dot{W}_P.$$

Here N_S is no longer a spatial density of abundance, but the measure of abundance at any location in this discrete geography. Since our goal is to compute $C_{HP} = \frac{1}{n} \sum_{i=1}^n (\bar{z}_H(i) - \mu_H)(\bar{z}_P(i) - \mu_P)$ at equilibrium we can set $\theta_H = \theta_P = \mu_H = \mu_P = 0$ without loss of generality. In addition, using our assumption that $A_S \gg B_S$ the discrete space model simplifies to

$$\dot{\bar{z}}_H = -(G_H A_H + \omega_H) \bar{z}_H - G_H B_H \bar{z}_P + \sqrt{\frac{G_H}{N_H}} \dot{W}_H,$$

$$\dot{\bar{z}}_P = -(G_P A_P + \omega_P) \bar{z}_P + G_P B_P \bar{z}_H + \sqrt{\frac{G_P}{N_P}} \dot{W}_P.$$

We use the Ito product rule to get

$$\dot{C}_{HP} = \frac{1}{n} \sum_{i=1}^n \bar{z}_H \dot{\bar{z}}_P + \bar{z}_P \dot{\bar{z}}_H.$$

Expanding and taking the limit $n \rightarrow \infty$ provides

$$\dot{C}_{HP} = -(G_P A_P + \omega_P) C_{HP} + G_P B_P V_H - (G_H A_H + \omega_H) C_{HP} - G_H B_H V_P,$$

where $V_S = \lim_{n \rightarrow \infty} \frac{1}{n} \sum_{i=1}^n \bar{z}_S^2(i)$. At equilibrium we have

$$C_{HP} = \frac{B_P G_P V_H - B_H G_H V_P}{A_H G_H + A_P G_P + \omega_H + \omega_P}.$$

Assuming V_H, V_P remain fixed while adjusting ω_H, ω_P , the only effect of dispersal is to decrease the magnitude of C_{HP} . However, to get the full story we need expressions for V_H, V_P at equilibrium. Using the same trick as for \dot{C}_{HP} we get

$$\dot{V}_H = -2(G_H A_H + \omega_H) V_H - 2G_H B_H C_{HP} + \frac{G_H}{N_H},$$

$$\dot{V}_P = -2(G_P A_P + \omega_P) V_P + 2G_P B_P C_{HP} + \frac{G_P}{N_P}.$$

With this information we can compute the interspecific spatial correlation of local mean trait values at equilibrium. Assuming parameters are equal except for dispersal rates, the numerator of the interspecific spatial correlation coefficient is proportional to $\omega_P - \omega_H$. The denominator of the correlation is always positive under the same symmetry assumptions, so the identity of the locally adapted species is completely determined by the signage of the above expression. In particular, this tells use the species that disperses at a faster rate is locally adapted, all else being equal.

B.3.2 Local dispersal

Here we consider the consequences of local dispersal on local adaptation in a discrete space stepping model. In particular we assume spatial localities are arranged on an infinite two-dimensional lattice with locations identified by (i, j) where $i, j \in \mathbb{Z}$. Movement occurs only between adjacent locations for each species. That is, for a given location (i, j) , the only possible origins of incoming migrants are $(i+1, j)$, $(i-1, j)$, $(i, j+1)$, $(i, j-1)$. Conversely, these locations are the only possible destinations for individuals emigrating from (i, j) . Just as in the island model of global dispersal, we denote by ω_H, ω_P the migration rates for host and parasite respectively. To obtain the instantaneous rate of change in a mean trait $\bar{z}(i, j)$ due to this form of dispersal, first consider the discrete time case over an interval of time Δt . Denoting $\bar{z}'(i, j)$ the mean trait after dispersal has occurred over the interval Δt and assuming $\Delta t \ll 1$, we have

$$\bar{z}'(i, j) = \frac{(1 - \omega\Delta t)\bar{z}(i, j) + 4\omega\Delta t\mu(i, j)}{(1 - \omega\Delta t) + 4\omega\Delta t}$$

where $\mu(i, j) = (\bar{z}(i+1, j) + \bar{z}(i-1, j) + \bar{z}(i, j+1) + \bar{z}(i, j-1))/4$. Dropping the (i, j) , we have

$$\frac{\bar{z}' - \bar{z}}{\Delta t} = \frac{4\omega(\mu - \bar{z})}{1 + 3\omega\Delta t},$$

which yields the instantaneous contribution of local dispersal: $d\bar{z}/dt = 4\omega(\mu - \bar{z})$. Inheriting all other aspects of the island model above (including intent), we can describe the evolution of mean traits by the stochastic differential equations

$$\dot{\bar{z}}_H = -G_H A_H \bar{z}_H - G_H B_H \bar{z}_P - 4\omega_H(\mu_H - \bar{z}_H) + \sqrt{\frac{G_H}{N_H}} \dot{W}_H,$$

$$\dot{\bar{z}}_P = -G_P A_P \bar{z}_P + G_P B_P \bar{z}_H + 4\omega_P(\mu_P - \bar{z}_P) + \sqrt{\frac{G_P}{N_P}} \dot{W}_P.$$

Just as for the island model, since our concern is with spatial covariance we set $\theta_H = \theta_P = 0$. Since this implies $\mathbb{E}[\mu_S(i, j)] = 0$ for all $i, j \in \mathbb{Z}$ at equilibrium, we set $\mu_H = \mu_P = 0$ without losing any generality in our conclusions on C_{HP} . Setting

$$C_{HP} = \lim_{n \rightarrow \infty} \frac{1}{4n^2} \sum_{i, j = -n, n} \bar{z}_H(i, j) \bar{z}_P(i, j)$$

and for brevity writing $C_{HP} = \overline{\bar{z}_H \bar{z}_P}$, we have

$$\begin{aligned} \dot{C}_{HP} &= \overline{\bar{z}_H \dot{\bar{z}}_P} + \overline{\dot{\bar{z}}_H \bar{z}_P} \\ &= -G_P A_P \overline{\bar{z}_H \bar{z}_P} + G_P B_P \overline{\bar{z}_H^2} - 4\omega_P \overline{\bar{z}_H \bar{z}_P} - G_H A_H \overline{\bar{z}_H \bar{z}_P} - G_H B_H \overline{\bar{z}_P^2} - 4\omega_H \overline{\bar{z}_H \bar{z}_P} \\ &= -(G_H A_H + G_P A_P + 4(\omega_H + \omega_P))C_{HP} + G_P B_P V_H - G_H B_H V_P, \end{aligned}$$

where $V_S = \overline{\bar{z}_S^2} = \lim_{n \rightarrow \infty} \sum_{i, j = -n, n} \bar{z}_S^2(i, j)/4n^2$. Dynamical equations for V_H, V_P are given by

$$\dot{V}_H = 2\overline{\bar{z}_H \dot{\bar{z}}_H} + \frac{G_H}{N_H} = -2(G_H A_H + 4\omega_H)V_H - 2G_H B_H C_{HP} + \frac{G_H}{N_H},$$

$$\dot{V}_P = -2(G_P A_P + 4\omega_P)V_P + 2G_P B_P C_{HP} + \frac{G_P}{N_P}.$$

Since the dynamical equations for V_H, V_P, C_{HP} under the stepping stone model match those of the island model, except with dispersal appearing four times as fast for each species, we obtain the same qualitative conclusions on the role of relative dispersal abilities in determining the identity of the locally adapted species.

C Justification for continuous space model

For the sake of space, we omit any attempt to formally derive our continuous space model from biological first principles. Instead we describe a possible approach that can be taken. The level at which we write is for both the mathematically curious and for the trained probabilist seeking an outline of ideas employed. We make no claim of rigor and no promise of general heuristics that can be employed. Instead, we only provide a schema.

To begin, one may start with a pair of interacting individual-based branching processes where individuals are associated with a trait $z \in \mathbb{R}$ and a location $\mathbf{x} \in \mathbb{R}^2$. Assuming semelparous life-cycles, we model mortality and reproduction simultaneously so that individuals replace themselves with a Poisson number of offspring between exponentially distributed intervals. For simplicity, we assume the rate at which these branching events occur is constant. However, the number of offspring is determined by the trait of the parent along with the traits of other individuals the parent interacts with. This is similar to the starting points taken by Week et. al. (2021a) in the derivation of a diffuse-coevolution model and by Week et. al. (2021b) in the derivation of the offset-matching coevolution model, except neither of those models have a spatial component.

To model fitness, we first consider the effects of abiotic selection \mathcal{A}_S and biotic selection \mathcal{B}_S separately for host and parasite species ($S = H, P$). Furthermore, we decompose the effects of biotic selection into sources due to intraspecific competition \mathcal{B}_S^c and interspecific parasitism \mathcal{B}_S^p so that $\mathcal{B}_S = \mathcal{B}_S^c \mathcal{B}_S^p$. We will assume these effects multiply to produce the net fitness of an individual, $w_S = \mathcal{A}_S \mathcal{B}_S$. For either species, the multiplicative component of fitness due to abiotic stabilizing selection for an individual with trait z at any location is

$$\mathcal{A}_S(z) \propto \exp\left(-\frac{A_S}{2}(\theta_S - z)^2\right).$$

We assume competition occurs locally such that individuals that are geographically closer to each other induce stronger competition on another than individuals that are further apart. This induces a form of local population regulation that prevents run-away population growth. In particular, denoting the distance between two spatial positions \mathbf{x} and \mathbf{y} by $\|\mathbf{x} - \mathbf{y}\|$, \mathbf{x}_i^S the location of the i th individual in species S , and n_S the number of individuals in species S , we model the effect of intraspecific competition on the j th individual as

$$\mathcal{B}_S^c(\mathbf{x}_j, n_S) \propto \exp\left(-c_S \sum_{i \neq j}^{n_S} \exp\left(-\frac{\lambda_S}{2}\|\mathbf{x}_j^S - \mathbf{x}_i^S\|^2\right)\right),$$

where c_S denotes the strength of spatial competition, λ_S is the rate at which competition decays with distance, and n_S denotes the abundance measure for species S . In particular, since $n_S(U, V)$ returns the number of individuals in species S with trait values in $U \subset \mathbb{R}$ spatially located in the region $V \subset \mathbb{R}^2$, n_S determines the total abundance and spatial locations of individuals in species S .

Host-parasite interactions can be modeled by assuming a probability of infection that is a function of trait values given an encounter has occurred. In particular, assuming a host individual with trait z^H encounters a parasite with trait z^P , the probability of infection $\alpha(z^H, z^P)$ can be written as

$$\alpha(z^H, z^P) = \exp\left(-\frac{\gamma}{2}(z^H - z^P)^2\right),$$

where $\gamma \geq 0$ determines the sensitivity of this probability to differences in individual trait values. We will always assume weak sensitivity (ie, $\gamma \ll 1$) so that $\alpha(z^H, z^P) \approx 1 - \gamma(z^H - z^P)^2/2$. We model the probability of encounter ε similarly as a function of the geographical distance between individuals. Denoting $\iota \geq 0$ the sensitivity of ε to distance and \mathbf{x}^S the location of the individual in species S , we model the probability of encounter as

$$\varepsilon(\mathbf{x}^H, \mathbf{x}^P) = \exp\left(-\frac{\iota}{2}\|\mathbf{x}^H - \mathbf{x}^P\|^2\right).$$

Unlike the sensitivity of the infection probability, we do not assume $\iota \ll 1$ so that encounters may strongly depend on distance. Then, assuming the parasite acquires the benefit $s_P \geq 0$ and the host receives the cost $s_H \geq 0$, the multiplicative effects of this single interaction on the fitness' of the respective participants

are proportional to $\exp(s_P \alpha(z^H, z^P) \varepsilon(\mathbf{x}^H, \mathbf{x}^P))$ and $\exp(-s_H \alpha(z^H, z^P) \varepsilon(\mathbf{x}^P, \mathbf{x}^P))$. Then, assuming every parasite could potentially infect every host, the components of biotic selection due to interspecific interactions for each species can be written

$$\mathcal{B}_H^p(z_j^H, \mathbf{x}_j^H, n_P) \propto \exp \left(-s_H \sum_{i=1}^{n_P} \alpha(z_j^H, z_i^P) \varepsilon(\mathbf{x}_j^H, \mathbf{x}_i^P) \right),$$

$$\mathcal{B}_P^p(z_j^P, \mathbf{x}_j^P, n_H) \propto \exp \left(s_P \sum_{i=1}^{n_H} \alpha(z_i^H, z_j^P) \varepsilon(\mathbf{x}_i^H, \mathbf{x}_j^P) \right).$$

To model mutation and spatial movement, we assume offspring trait values are normally distributed around their parental value (technically, this is done with breeding values, see Week et. al. (2021a)) and offspring locations are bivariate normal around their parental locations with no correlations between the displacements in the two spatial dimensions (ie, dispersal is isotropic).

To take a diffusion limit of this individual-base process, we follow Week et. al. (2021a) so that the rate of branching goes to infinity, the number of initial individuals in each species goes to infinity, the effects of mutation and distances of dispersal go to zero and fitness for each individual goes to unity. We also rescale the probability of parasite encounter so that it converges to a delta function. This means parasitism can only occur locally in the diffusion limit. All of these limits occur simultaneously and at specific rates to ensure the rescaled individual-based processes $n_H^{(k)}, n_P^{(k)}$ converge to well-defined population-level processes $\mathcal{N}^H, \mathcal{N}^P$, where $n_S^{(k)}$ denotes the k th stage of rescaling. In this diffusion limit the growth rates associated with trait value z at location \mathbf{x} can be obtained for each species as

$$m_H(z, \mathbf{x}, \mathcal{N}^H, \mathcal{N}^P) = \lim_{k \rightarrow \infty} k \left(w_H^{1/k}(z, \mathbf{x}, n_H^{(k)}, n_P^{(k)}) - 1 \right),$$

$$m_P(z, \mathbf{x}, \mathcal{N}^P, \mathcal{N}^H) = \lim_{k \rightarrow \infty} k \left(w_P^{1/k}(z, \mathbf{x}, n_P^{(k)}, n_H^{(k)}) - 1 \right).$$

For the host this yields

$$m_H(z, \mathbf{x}, \mathcal{N}_H, \mathcal{N}_P) = r_H - \frac{A_H}{2} (\theta_H - z)^2 - c_H \int_{\mathbb{R}^2} K_H(\mathbf{x}, \mathbf{y}) \mathcal{N}_H(\mathbb{R}, d\mathbf{y}) - s_H \int_{\mathbb{R}^2} \int_{\mathbb{R}} \alpha(z, \zeta) \mathcal{N}_P(d\zeta, d\mathbf{x}),$$

where r_H is some real number (the intrinsic growth rate) and we set $K_S(\mathbf{x}, \mathbf{y}) = \exp(-\frac{\lambda_S}{2} \|\mathbf{x} - \mathbf{y}\|^2)$. A similar expression for the parasite is also obtained. We now make the approximation that competition is sufficiently weak and the intrinsic growth rate is sufficiently positive so that local density of abundance is approximately constant in time and space for each species. This implies the population growth rates m_H, m_P are near zero. With this approximation we write N_S as the abundance density for species S so that $\mathcal{N}_S(\mathbb{R}, U) = |U| N_S$ for $U \subset \mathbb{R}^2$ where $|U|$ is the area of U . In this case we have

$$\int_{\mathbb{R}^2} K_S(\mathbf{x}, \mathbf{y}) \mathcal{N}^S(\mathbb{R}, d\mathbf{y}) = N_S \frac{2\pi}{\lambda_S}.$$

Using our assumption that $\gamma \ll 1$, the biotic and abiotic components cumulatively contribute quadratic selection. Hence, given that stabilizing abiotic selection is sufficiently strong relative to disruptive biotic selection on the host, trait distributions at any location will be approximately normal with mean and variance $\bar{z}_S(\mathbf{x}), v_S(\mathbf{x})$ for species S at location \mathbf{x} . In particular, this implies

$$\int_{\mathbb{R}^2} \int_{\mathbb{R}} \alpha(z, \zeta) \mathcal{N}^P(d\zeta, d\mathbf{x}) = N_S \left(1 - \frac{\gamma}{2} (z - \bar{z}_P(\mathbf{x}))^2 + v_P(\mathbf{x}) \right).$$

Furthermore, since selection is quadratic and abundance is constant, selection and drift decay phenotypic variance at a constant rate. From our assumption of Gaussian mutations, phenotypic variance also has a constant rate of input. Hence, we can expect phenotypic variance for each species to fluctuate stochastically

around an equilibrium that is constant in space and time. We thus further approximate by setting the phenotypic variances equal to those constant equilibria. We can therefore approximate the growth rates for each species as

$$m_H(z, \mathbf{x}) \approx R_H - \frac{A_H}{2}(\theta_H - z)^2 + \frac{B_H}{2}(z - \bar{z}_P)^2,$$

$$m_P(z, \mathbf{x}) \approx R_P - \frac{A_P}{2}(\theta_P - z)^2 - \frac{B_P}{2}(z - \bar{z}_P)^2,$$

where $R_H, R_P > 0$, $B_P = s_P N_H \gamma$, $B_H = s_H N_P \gamma$ and we have dropped the dependencies on $\mathcal{N}^H, \mathcal{N}^P$ for brevity.

To obtain the evolutionary dynamics from these fitness functions, we consider a characterization of the population-level processes $\mathcal{N}_t^H, \mathcal{N}_t^P$ as random functions of time. To keep this part of our description as minimal on technical details as possible, we state many propositions without justification. For functions $f(z, \mathbf{x})$ that decay rapidly to zero as $\|\mathbf{x}\| \rightarrow \infty$ and are twice differentiable with respect to space we write

$$\langle \mathcal{N}_t^S, f \rangle = \int_{\mathbb{R}^2} \int_{\mathbb{R}} f(z, \mathbf{x}) \mathcal{N}_t^S(dz, d\mathbf{x}).$$

The characterization we make use of states that for each $f(z, \mathbf{x})$ that is twice differentiable and rapidly decreasing in \mathbf{x} ,

$$M_t(f) = \langle \mathcal{N}_t^S, f \rangle - \langle \mathcal{N}_0^S, f \rangle - \int_0^t \left\langle \mathcal{N}_s^S, \left(m_S + \frac{\sigma_S^2}{2} \Delta \right) f \right\rangle ds$$

is a martingale with so-called increasing process $\int_0^t \langle \mathcal{N}_s^S, f^2 \rangle ds$ (Meleard & Roelly). Martingales are stochastic processes that have expectation zero for each $t \geq 0$ and their increasing processes inform us about their variance around that expectation. Formally, there should be an additional operator to account for mutation, but since we have reasoned phenotypic variance will be constant this detail is unnecessary for our purposes. However, in order for this approach to work, we do need to take back our assumption of constant population size. Hence, we assume the existence of a spatial abundance density so that $\int_{\mathbb{R}} \mathcal{N}_t^S(dz, d\mathbf{x}) = N_S(\mathbf{x}, t) dz d\mathbf{x}$ allow the spatial abundance density $N_S(\mathbf{x}, t)$ to evolve in time and space, but assume it doesn't evolve too much so our approximated growth rates hold. Setting $f(z, \mathbf{x}) = g(\mathbf{x})$ for a rapidly decaying function g , we have

$$\langle \mathcal{N}_t^S, f \rangle = \int_{\mathbb{R}^2} N_S(\mathbf{x}, t) g(\mathbf{x}) d\mathbf{x},$$

and hence the above martingale becomes

$$M_t(g) = \int_{\mathbb{R}^2} N_S(\mathbf{x}, t) g(\mathbf{x}) d\mathbf{x} - \int_{\mathbb{R}^2} N_S(\mathbf{x}, 0) g(\mathbf{x}) d\mathbf{x} - \int_0^t \int_{\mathbb{R}^2} N_S(\mathbf{x}, s) \left(\bar{m}_S(\mathbf{x}, s) g(\mathbf{x}) + \frac{\sigma_S^2}{2} \Delta g(\mathbf{x}) \right) d\mathbf{x} ds$$

where $\bar{m}_S(\mathbf{x}, t) d\mathbf{x} = \int_{\mathbb{R}} m_S(z, \mathbf{x}) \mathcal{N}_t^S(dz, d\mathbf{x}) / N_S(t)$ and the increasing process becomes $\int_0^t N_S(s) ds$. Similar to how the fundamental theorem of calculus states that the integral equation $F(t) - F(0) - \int_0^t f(s) ds = 0$ corresponds to a deterministic differential equation $\dot{F} = f$, the above characterization suggests the process $N_S(\mathbf{x}, t)$ can be described by some sort of stochastic differential equation. In fact, our characterization for the evolution of $N_S(\mathbf{x}, t)$ coincides with the notion of a weak solution to the following stochastic partial differential equation

$$\dot{N}_S = \bar{m}_S N_S + \frac{\sigma_S^2}{2} \Delta N_S + \sqrt{N_S} \dot{W}_{N_S},$$

where \dot{W}_{N_S} is a space-time white noise process. Similarly, we can consider the martingale for $f(z, \mathbf{x}) = zg(\mathbf{x})$

$$\begin{aligned}
 M_t(zg) &= \int_{\mathbb{R}^2} N_S(\mathbf{x}, t) \bar{z}(\mathbf{x}, t) g(\mathbf{x}) d\mathbf{x} - \int_{\mathbb{R}^2} N_S(\mathbf{x}, 0) \bar{z}(\mathbf{x}, 0) g(\mathbf{x}) d\mathbf{x} \\
 &\quad - \int_0^t \int_{\mathbb{R}^2} N_S(\mathbf{x}, s) \left(\bar{m} \bar{z}_S(\mathbf{x}, s) g(\mathbf{x}) + \bar{z}(\mathbf{x}, s) \frac{\sigma_S^2}{2} \Delta g(\mathbf{x}) \right) d\mathbf{x} ds
 \end{aligned}$$

where $\bar{m} \bar{z}_S(\mathbf{x}, t) d\mathbf{x} = \int_{\mathbb{R}} m_S(z, \mathbf{x}) z \mathcal{N}_t^S(dz, d\mathbf{x}) / N_S(\mathbf{x}, t)$. For rapidly decaying g , $\int_{\mathbb{R}^2} N_S(\mathbf{x}, t) g(\mathbf{x}) d\mathbf{x}$ and $\int_{\mathbb{R}^2} N_S(\mathbf{x}, t) \bar{z}_S(\mathbf{x}) g(\mathbf{x}) d\mathbf{x}$ are univariate diffusion processes with noise determined by the increasing processes of $M_t(g)$ and $M_t(zg)$ respectively. Using this, we can apply Ito's quotient rule to compute a stochastic differential equation for $\int_{\mathbb{R}^2} N_S(\mathbf{x}, t) \bar{z}_S(\mathbf{x}) g(\mathbf{x}) d\mathbf{x} / \int_{\mathbb{R}^2} N_S(\mathbf{x}, t) g(\mathbf{x}) d\mathbf{x}$ (taking into account the martingales $M_t(g), M_t(zg)$ are correlated). Then, after some calculations, making some rearrangements, and invoking spatiotemporal constancy of abundance, we find

$$\int_{\mathbb{R}^2} \bar{z}_S(\mathbf{x}, t) g(\mathbf{x}) d\mathbf{x} - \int_{\mathbb{R}^2} \bar{z}_S(\mathbf{x}, 0) g(\mathbf{x}) d\mathbf{x} - \int_0^t \int_{\mathbb{R}^2} \bar{z}_S(\mathbf{x}, s) \left(\text{Cov}_{s, \mathbf{x}}(m_S, z) + \frac{\sigma_S^2}{2} \Delta \right) g(\mathbf{x}) ds$$

is a martingale with increasing process $v_S \int_0^t \int_{\mathbb{R}^2} g^2(\mathbf{x}) d\mathbf{x} ds / N_S$ where

$$\text{Cov}_{t, \mathbf{x}}(m_S, z) d\mathbf{x} = \frac{1}{N_S} \int_{\mathbb{R}} (m(z, \mathbf{x}) - \bar{m}_S(\mathbf{x}, t))(z - \bar{z}_S(\mathbf{x}, t)) \mathcal{N}_t^S(dz, d\mathbf{x}).$$

In particular, this coincides with the definition of the weak solution to the stochastic partial differential equation

$$\dot{\bar{z}}_S = \text{Cov}(m_S, z) + \frac{\sigma_S^2}{2} \Delta \bar{z}_S + \sqrt{\frac{v_S}{N_S}} \dot{W}_S.$$

To finally obtain our continuous space model, rework all the above in terms of breeding values so that the phenotypic variance v_S is replaced with the additive genetic variance G_S (see Week et. al. 2021a) and then use the fact that when traits are normally distributed at each location and m_S does not depend on $\bar{z}_S(\mathbf{x}, t)$, $\text{Cov}_{t, \mathbf{x}}(m_S, z) = G_S \frac{\partial}{\partial \bar{z}(\mathbf{x}, t)} \bar{m}_S(\mathbf{x}, t)$.

$$\mathbb{E} \left[\langle \mu_t, f \rangle - \langle \mu_0, f \rangle - \int_0^t \langle \mu_s, \mathcal{L} f \rangle ds \right] = 0$$

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