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Online Supplement:

Host-Parasite Coevolution in Continuous Space Leads to Variation in Local Adaptation Across Spatial Scales

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S1 Technical Description of the Model

In this section we provide further mathematical details of our model. Justification for our model is provided in §S4 below. The presentation of our model in the main text made use of a simplified notation to minimize the complexity of its expression. Here we present our model using more accurate notation. For species S, we denote by G_S the additive genetic variance at any given location and by N_S the effective population density at any given location. We assume both parameters are constant in space and time (justification for which provided in §S4). In this more accurate notation, the strengths of selection presented in the main text are replaced with products of selection strengths and additive genetic variances. That is, A_S is replaced with $G_S A_S$ and B_S is replaced with $G_S B_S$. Here, we do not make the assumption that stabilizing selection occurs around zero. Instead, we denote the abiotic optimum for species S by θ_S. We also denote by ∇^2 the sum of second spatial derivatives (i.e., the Laplacian operator). With this notation, our model can be written more formally as

$$\frac{\partial}{\partial t}\bar{z}_H(\boldsymbol{x},t) = G_H A_H(\theta_H - \bar{z}_H(\boldsymbol{x},t)) - G_H B_H(\bar{z}_P(\boldsymbol{x},t) - \bar{z}_H(\boldsymbol{x},t)) + \frac{\sigma_H^2}{2}\nabla^2\bar{z}_H(\boldsymbol{x},t) + \sqrt{\frac{G_H}{N_H}}\xi_H(\boldsymbol{x},t), \tag{S1a}$$

$$\frac{\partial}{\partial t}\bar{z}_P(\boldsymbol{x},t) = G_P A_P(\theta_P - \bar{z}_P(\boldsymbol{x},t)) + G_P B_P(\bar{z}_H(\boldsymbol{x},t) - \bar{z}_P(\boldsymbol{x},t)) + \frac{\sigma_P^2}{2}\nabla^2\bar{z}_P(\boldsymbol{x},t) + \sqrt{\frac{G_P}{N_P}}\xi_P(\boldsymbol{x},t), \tag{S1b}$$

where ξ_H, ξ_P are space-time white noise processes (see the example in §S2 below). In general, neither $\bar{z}_H$ nor $\bar{z}_P$ will be differentiable with respect to their spatial arguments for any time t. Hence, ∇^2 must be taken in the weak sense (Evans 2010). Additionally, neither $\bar{z}_H$ nor $\bar{z}_P$ will be differentiable with respect to time in general. Thus, a formal understanding of our model requires technical prerequisites from infinite-dimensional stochastic calculus (Walsh 1986; Da Prato and Zabczyk 2014). Fortunately, such prerequisites are not required to understand the equilibrium solutions to our model, background for which has been collected below in §S2. All symbols involved with the technical description of our model are summarized in Table S1.

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Table S1: Model Parameters & Symbols

Symbol	Description	Class
$\bar{z}_H(\boldsymbol{x}, t)$	Host Mean Trait at Location $\boldsymbol{x} \in \mathbb{R}^2$ at Time $t \geq 0$	Stochastic Process
$\bar{z}_P(\boldsymbol{x}, t)$	Parasite Mean Trait at Location $\boldsymbol{x} \in \mathbb{R}^2$ at Time $t \geq 0$	Stochastic Process
G_H	Local Host Additive Genetic Variance	Parameter
G_P	Local Parasite Additive Genetic Variance	Parameter
N_H	Local Host Population Density	Parameter
N_P	Local Parasite Population Density	Parameter
θ_H	Host Abiotic Optimal Phenotype	Parameter
θ_P	Parasite Abiotic Optimal Phenotype	Parameter
A_H	Host Abiotic Stabilizing Selection	Parameter
A_P	Parasite Abiotic Stabilizing Selection	Parameter
B_H	Host Biotic Selection	Parameter
B_P	Parasite Biotic Selection	Parameter
σ_H	Host Dispersal Distance	Parameter
σ_P	Parasite Dispersal Distance	Parameter
∇^2	Dispersal (Laplacian) Operator	Mathematical Operation
$\xi_H(\boldsymbol{x}, t)$	Space-Time White Noise due to Host Genetic Drift	Stochastic Process
$\xi_P(\boldsymbol{x}, t)$	Space-Time White Noise due to Parasite Genetic Drift	Stochastic Process

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S2 Gaussian Random Fields and Spatial Covariance Functions

As our results are obtained from spatial covariance functions associated with Gaussian random fields (GRFs), we provide some relevant definitions here for the sake of self-containment. Our primary reference is Rue and Held (2005). We begin by defining univariate GRFs before proceeding to multivariate GRFs.

A univariate GRF F is completely characterized by its mean $\mu(\boldsymbol{x}) = \mathbb{E}[F(\boldsymbol{x})]$ and spatial covariance $C(\boldsymbol{x},\boldsymbol{y}) = \mathbb{E}[(\mu(\boldsymbol{x}) - F(\boldsymbol{x}))(\mu(\boldsymbol{y}) - F(\boldsymbol{y}))]$ functions, where $\boldsymbol{x},\boldsymbol{y}$ are geographical locations. For any set of n locations $\boldsymbol{x}_1,\ldots,\boldsymbol{x}_n$, the n-dimensional random vector $(F(\boldsymbol{x}_1),\ldots,F(\boldsymbol{x}_n))$ has a multivariate normal distribution with mean vector $(\mu(\boldsymbol{x}_1),\ldots,\mu(\boldsymbol{x}_n))$ and covariance matrix

$$\begin{pmatrix} C(\boldsymbol{x}_1,\boldsymbol{x}_1) & \cdots & C(\boldsymbol{x}_1,\boldsymbol{x}_n) \\ \vdots & \ddots & \vdots \\ C(\boldsymbol{x}_n,\boldsymbol{x}_1) & \cdots & C(\boldsymbol{x}_n,\boldsymbol{x}_n) \end{pmatrix}. \tag{S2}$$

The GRF F is called *homogeneous* if its mean is constant across all locations (so that $\mu(\boldsymbol{x}_1) = \mu(\boldsymbol{x}_2)$ for any locations $\boldsymbol{x}_1,\boldsymbol{x}_2$) and if its covariance function depends only on the difference between its arguments (so that $C(\boldsymbol{x}_1,\boldsymbol{y}_1) = C(\boldsymbol{x}_2,\boldsymbol{y}_2)$ whenever $\boldsymbol{x}_1 - \boldsymbol{y}_1 = \boldsymbol{x}_2 - \boldsymbol{y}_2$). GRFs that satisfy these two conditions are also referred to as second-order, wide-sense, or weakly homogeneous/stationary. Just as the name implies, a homogeneous GRF exhibits equivalent statistical properties at any given location. In addition, F is called *isotropic* if it is homogeneous and its covariance function only depends on the distance between its arguments (so that $C(\boldsymbol{x}_1,\boldsymbol{y}_1) = C(\boldsymbol{x}_2,\boldsymbol{y}_2)$ whenever $\|\boldsymbol{x}_1 - \boldsymbol{y}_1\| = \|\boldsymbol{x}_2 - \boldsymbol{y}_2\|$, where $\|\cdot\|$ denotes geographic distance). Whereas a general homogeneous random field allows for the covariance function to depend on the spatial direction between its arguments, an isotropic random field is absent of any such dependency on direction or orientation. When a GRF is isotropic, we write its mean and covariance functions respectively as μ and $C(d)$, where d is the distance between two locations (e.g., $d = \|\boldsymbol{x} - \boldsymbol{y}\|$). As $C(0)$ is the variance of the random variable $F(\boldsymbol{x})$ (for any $\boldsymbol{x}$), we call $V = C(0)$ the *co-located*

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variance of the isotropic GRF F. The spatial correlation function is given by $\rho(d) = C(d)/V$. We therefore say the field F exhibits spatial autocorrelation whenever $\rho(d) \neq 0$ for some $d > 0$.

Example: As an example of a GRF, consider a spatial white noise process W. Heuristically, we can think of W as an isotropic GRF with mean-zero, infinite co-located variance, and no spatial autocorrelation. Rigorously, setting $W(U) = \int_U W(\boldsymbol{x})d\boldsymbol{x}$, we have that $W(U)$ and $W(V)$ are normally distributed random variables with mean-zero, variances equal to the areas of the spatial regions U and V respectively, and covariance equal to the area of the intersection between U and V. Hence, if U and V do not overlap, $W(U)$ and $W(V)$ are independent random variables. The covariance function of a spatial white noise is the Dirac delta function $\delta(d)$ for which $\delta(d) = 0$ and $\int_0^d \delta(s)ds = 1$ for all $d > 0$. In relation to the *space-time* white noise processes $\xi_H(\boldsymbol{x}, t), \xi_P(\boldsymbol{x}, t)$ that appear in our model, we have $\int_t^{t+1} \xi_S(\boldsymbol{x}, \tau)d\tau$ is a spatial white noise for both $S = H, P$.

An isotropic k-variate GRF $\boldsymbol{F}$ is composed of k isotropic univariate GRFs $F_1, \ldots, F_k$. $\boldsymbol{F}$ is then completely characterized by means $\mu_1, \ldots, \mu_k$ and covariance functions $C_1, \ldots, C_k$ of the respective univariate fields $F_1, \ldots, F_k$ along with the *cross*-covariance functions

$$C_{ij}(\boldsymbol{x}) = \mathbb{E}[(\mu_i - F_i(\boldsymbol{0}))(\mu_j - F_j(\boldsymbol{x}))],\ i, j = 1, \ldots, d,\ i \neq j. \tag{S3}$$

Similar to the co-located variance, we call $C_{ij}(0)$ the *co-located covariance* of F_i and F_j because it is the covariance of the random variables $F_i(\boldsymbol{x}), F_j(\boldsymbol{x})$ (for any location $\boldsymbol{x}$). Additionally, we call $\rho_{ij} = C_{ij}(0)/\sqrt{V_i V_j}$ the *co-located correlation* of F_i and F_j, where $V_i = C_i(0)$ is the co-located variance of F_i.

S3 Computing Spatial Covariance Functions

Here we briefly describe our analytical approach to obtaining spatial covariance functions from our continuous-space model of host-parasite coevolution. Essentially, our approach is to compute a spectral representation of our model (i.e., a representation in terms of spatial frequencies), make some simplifications using our assumption that biotic selection is weak relative to abiotic stabilizing selection, then take an inverse transform to obtain the spatial covariance functions. We use

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the vector $\boldsymbol{k} = (k_1, k_2)^\top$ to denote spatial frequencies in the two directions (called the wavevector) as opposed to $\boldsymbol{x} = (x_1, x_2)^\top$, which represents geographic location or displacement. One advantage of this approach is that the spatial derivatives appearing in our model become algebraic expressions in terms of spatial frequencies. Another important advantage is the relationship between the spatial covariance function associated with a spatial process and the distribution of harmonic content in that process. The distribution of harmonic content in a spatial process across wavevectors $\boldsymbol{k}$ is called the power spectrum and can be computed from the spectral representation (i.e., the Fourier transform) of the process. In turn, the spatial covariance function can then be obtained by taking the inverse Fourier transform of the power spectrum.

The Fourier transform of a function $f(\boldsymbol{x})$ can be written $\hat{f}(\boldsymbol{k}) = \int_{\mathbb{R}^2} f(\boldsymbol{x}) e^{i\boldsymbol{x}^\top \boldsymbol{k}} d\boldsymbol{x}$. Taking $\bar{\boldsymbol{z}}(\boldsymbol{x}) = (\bar{z}_H(\boldsymbol{x}), \bar{z}_P(\boldsymbol{x}))^\top$ as the equilibrium solution to our model, and $\bar{\boldsymbol{z}}^* = (\bar{z}_H^*, \bar{z}_P^*)^\top$ the deterministic equilibrium of our model (i.e., the equilibrium after taking the limits $N_H, N_P \to \infty$), we first make the change of variables $\tilde{\boldsymbol{z}}(\boldsymbol{x}) = \bar{\boldsymbol{z}} - \bar{\boldsymbol{z}}^*$ so that $\tilde{\boldsymbol{z}}$ has mean zero. Under our model, this is equivalent to setting $\theta_H = \theta_P = 0$. We then denote the frequency space representation of our model by $\hat{\boldsymbol{z}} = \mathcal{F}(\tilde{\boldsymbol{z}})$, where $\mathcal{F}$ denotes Fourier transform. The power spectrum for each species is given by $S_H(\boldsymbol{k}) = \mathbb{E}[\hat{z}_H^2(\boldsymbol{k})]$, $S_P(\boldsymbol{k}) = \mathbb{E}[\hat{z}_P^2(\boldsymbol{k})]$, and the cross-spectrum is $S_{HP}(\boldsymbol{k}) = \mathbb{E}[\hat{z}_H(\boldsymbol{k})\hat{z}_P(\boldsymbol{k})]$. The spatial covariance and spatial cross-covariance functions are then given by

$$C_H = \mathcal{F}^{-1}(S_H),\ C_P = \mathcal{F}^{-1}(S_P),\ C_{HP} = \mathcal{F}^{-1}(S_{HP}), \tag{S4}$$

where $\mathcal{F}^{-1}$ denotes the inverse of the Fourier transform (this is a corollary of Theorems 7.3 and 7.4 in Lindgren 2012).

The frequency space representation of our model at equilibrium under the change of variables mentioned above is given by

$$-G_H A_H \hat{z}_H - G_H B_H(\hat{z}_P - \hat{z}_H) - \frac{\sigma_H^2}{2}\|\boldsymbol{k}\|^2 \hat{z}_H = \sqrt{\frac{G_H}{N_H}}\hat{\xi}_H, \tag{S5a}$$

$$-G_P A_P \hat{z}_P + G_P B_P(\hat{z}_H - \hat{z}_P) - \frac{\sigma_P^2}{2}\|\boldsymbol{k}\|^2 \hat{z}_P = \sqrt{\frac{G_P}{N_P}}\hat{\xi}_P. \tag{S5b}$$

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Writing $\hat{\boldsymbol{\xi}} = (\sqrt{G_H/N_H}\hat{\xi}_H, \sqrt{G_P/N_P}\hat{\xi}_P)^\top$ and

$$\mathcal{H} = \begin{pmatrix} G_H(B_H - A_H) + \sigma_H^2\|\boldsymbol{k}\|^2/2 & -G_H B_H \\ G_P B_P & -G_P(B_P + A_P) + \sigma_P^2\|\boldsymbol{k}\|/2 \end{pmatrix}, \tag{S6}$$

the frequency space representation becomes $\mathcal{H}\,\hat{\boldsymbol{z}} = \hat{\boldsymbol{\xi}}$. Matrix algebra yields

$$\hat{\boldsymbol{z}}\hat{\boldsymbol{z}}^\top = \mathcal{H}^{-1}\hat{\boldsymbol{\xi}}\hat{\boldsymbol{\xi}}^\top\mathcal{H}^{-\top}. \tag{S7}$$

The power spectra of the noise processes are given by

$$S_{\boldsymbol{\xi}} = \mathbb{E}[\hat{\boldsymbol{\xi}}\hat{\boldsymbol{\xi}}^\top] = \begin{pmatrix} G_H/N_H & 0 \\ 0 & G_P/N_P \end{pmatrix}. \tag{S8}$$

Denoting $S_{\boldsymbol{z}}$ the matrix of spectra of our equilibrium solution and taking expectation of equation (S7) provides

$$S_{\boldsymbol{z}} = \mathcal{H}^{-1}S_{\boldsymbol{\xi}}\mathcal{H}^{-\top}. \tag{S9}$$

Power Spectra:

To obtain analytically tractable results, we assume coevolution is weak relative to abiotic stabilizing selection so that $B_H - A_H \approx -A_H, B_P + A_P \approx A_P$ and $B_H^2, B_P^2, B_H B_P \approx 0$. With this approximation, we arrive at

$$S_H(\boldsymbol{k}) = \frac{G_H/N_H}{(G_H A_H + \frac{\sigma_H^2}{2}\|\boldsymbol{k}\|^2)^2}, \tag{S10a}$$

$$S_P(\boldsymbol{k}) = \frac{G_P/N_P}{(G_P A_P + \frac{\sigma_P^2}{2}\|\boldsymbol{k}\|^2)^2}, \tag{S10b}$$

$$S_{HP}(\boldsymbol{k}) = \frac{G_P B_P}{G_P A_P + \frac{\sigma_P^2}{2}\|\boldsymbol{k}\|^2}S_H(\boldsymbol{k}) - \frac{G_H B_H}{G_H A_H + \frac{\sigma_H^2}{2}\|\boldsymbol{k}\|^2}S_P(\boldsymbol{k}). \tag{S10c}$$

We can also parameterize these spectra in terms of the co-located variances $V_S = 1/A_S N_A \sigma_S^2$ and intraspecific spatial scales $\lambda_S = \sigma_S/\sqrt{G_S A_S}$. Doing so yields

$$S_H(\boldsymbol{k}) = \frac{\lambda_H^2 V_H}{(1 + \frac{\lambda_H^2}{2}\|\boldsymbol{k}\|^2)^2}, \tag{S11a}$$

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$$S_P(\boldsymbol{k}) = \frac{\lambda_P^2 V_P}{(1+\frac{\lambda_P^2}{2}\|\boldsymbol{k}\|^2)^2}, \tag{S11b}$$

$$S_{HP}(\boldsymbol{k}) = \frac{B_P/A_P}{1+\frac{\lambda_P^2}{2}\|\boldsymbol{k}\|^2} S_H(\boldsymbol{k}) - \frac{B_H/A_H}{1+\frac{\lambda_H^2}{2}\|\boldsymbol{k}\|^2} S_P(\boldsymbol{k}). \tag{S11c}$$

For the sake of reproducibility, we provide a Mathematica notebook (`freq-sp.nb`) to compute these expressions in the Zenodo repository associated with this manuscript (Week and Bradburd 2023).

Co-located Interspecific Covariance

Our index of parasite local adaptation ℓ_P is proportional to the co-located interspecific covariance $C_{HP}(\mathbf{0})$ for sufficiently large distances. Using the cross-spectrum of our model, this co-located covariance is given by

$$C_{HP}(0) = \int_{\mathbb{R}^2} S_{HP}(\boldsymbol{k}) d\boldsymbol{k}. \tag{S12}$$

In terms of the model parameters used in the main text, this evaluates to

$$C_{HP}(0) = \varrho_1 \left(\frac{\sigma_H^2}{A_H} - \frac{\sigma_P^2}{A_P} \right) + \varrho_2 \left(\log\left(\frac{\sigma_P^2}{A_P}\right) - \log\left(\frac{\sigma_H^2}{A_H}\right) \right), \tag{S13}$$

where

$$\varrho_1 = (A_H B_H D_P^2 + A_P B_P D_H^2)/(A_P\sigma_H^2 - A_H\sigma_P^2)^2 \tag{S14a}$$

$$\varrho_2 = (B_H D_P^2 \sigma_H^2 + B_P D_H^2 \sigma_P^2)/(A_P\sigma_H^2 - A_H\sigma_P^2)^2. \tag{S14b}$$

For the sake of reproducibility, we provide a Mathematica notebook (`Chp0.nb`) to compute these expressions in the Zenodo repository associated with this manuscript (Week and Bradburd 2023).

S4 Model Justification

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 geographic location $\boldsymbol{x} \in \mathbb{R}^2$. Assuming semelparous life-cycles, we model mortality and reproduction simultaneously so that individuals replace themselves with a Poisson number of offspring between unit intervals of time. The lifetime expected number of offspring (i.e., fitness) is determined by the geographical location

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and trait value of a focal individual along with the locations and traits of other individuals the focal individual interacts with. This is similar to the starting points taken by Week et al. (2021) in the derivation of a diffuse-coevolution model and by Week and Nuismer (2021) 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 ($S = H, P$). We decompose the effects of biotic selection into sources due to intraspecific competition $\mathcal{B}_S^c$ (which we require to justify our assumption of spatially homogeneous abundance densities in the main text) and interspecific parasitism $\mathcal{B}_S^p$ so that $\mathcal{B}_S = \mathcal{B}_S^c \mathcal{B}_S^p$. We assume the biotic and abiotic effects multiply to produce the net fitness of an individual, written $w_S = \mathcal{A}_S \mathcal{B}_S$. Denote by $w_{0,S}$ the maximum fitness possible for species S in the absence of interspecific interactions, θ_S the abiotic optimal trait value, and A_S the strength of abiotic selection. Then, for either species, the multiplicative component of fitness due to abiotic stabilizing selection for an individual with trait z at any geographic location is

$$\mathcal{A}_S(z) = w_{0,S} \exp\left(-\frac{A_S}{2}(\theta_S - z)^2\right). \tag{S15}$$

To justify our assumption of spatially homogeneous abundance densities in the main text, we require a mechanism of local population regulation. For the sake of simplicity, we chose to model intraspecific competition that occurs locally such that individuals that are geographically closer to each experience stronger competition with one another than individuals that are further apart. The details of our model of competition are similar in spirit to the model introduced by Bolker and Pacala (1997) and further studied by Etheridge (2004). Denoting the distance between two spatial positions $\boldsymbol{x}$ and $\boldsymbol{y}$ by $\|\boldsymbol{x} - \boldsymbol{y}\|$, $\boldsymbol{x}_S^i$ is the location of the ith individual in species S, and n_S the number of individuals in species S, we model the effect of intraspecific competition on the fitness of jth individual in species S as

$$\mathcal{B}_S^c(\boldsymbol{x}_S^j, \mathcal{N}_S) = \exp\left(-c_S \sum_{i \neq j}^{n_S} \exp\left(-\frac{\|\boldsymbol{x}_S^j - \boldsymbol{x}_S^i\|^2}{2\omega_S^2}\right)\right), \tag{S16}$$

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where c_S denotes the strength of spatial competition, ω_S is the spatial scale of competition, and $\mathcal{N}_S$ denotes the abundance measure for species S. As $\mathcal{N}_S(U, V)$ returns the number of individuals in species S with trait values in $U \subset \mathbb{R}$ spatially located in the region $V \subset \mathbb{R}^2$, $\mathcal{N}_S$ describes the trait distribution and abundance in any region of space for species S.

We model host-parasite interactions by assuming a probability of infection that is a function of trait values given an encounter has occurred. 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

$$\alpha(z_H, z_P) = \exp\left(-\frac{\gamma}{2}(z_H - z_P)^2\right), \tag{S17}$$

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 that a particular parasite encounters a particular host, denoted ε, as a function of the geographical distance between individuals. Denoting $\iota \geq 0$ the geographic scale of host-parasite interactions, we model the probability of encounter as

$$\varepsilon(\boldsymbol{x}_H, \boldsymbol{x}_P) = \exp\left(-\frac{\|\boldsymbol{x}_H - \boldsymbol{x}_P\|^2}{2\iota^2}\right). \tag{S18}$$

We allow $\iota \ll 1$ so that encounters may strongly depend on distance. Set E_{ij} the Bernoulli random variable representing whether the ith parasite encounters the jth host and I_{ij} the Bernoulli random variable representing the ith parasite infecting the jth host given their encounter. 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's of the respective participants are $\exp(s_P E_{ij} I_{ij})$ and $\exp(-s_H E_{ij} I_{ij})$. Taking expectations provide

$$\mathbb{E}[\exp(\pm s_S E_{ij} I_{ij}) | E_{ij}] = (1 - \alpha(z_H^j, z_P^i)) + \alpha(z_H^j, z_P^i) \exp(\pm s_S E_{ij}), \tag{S19a}$$

$$\begin{aligned}\mathbb{E}[\exp(\pm s_S E_{ij} I_{ij})] &= \left(1 - \alpha(z_H^j, z_P^i)\right) + \alpha(z_H^j, z_P^i)\left((1 - \varepsilon(\boldsymbol{x}_H^j, \boldsymbol{x}_P^i)) + \varepsilon(\boldsymbol{x}_H^j, \boldsymbol{x}_P^i)\exp(\pm s_S)\right) \\ &= 1 + \alpha(z_H^j, z_P^i)\varepsilon(\boldsymbol{x}_H^j, \boldsymbol{x}_P^i)\left(\exp(\pm s_S) - 1\right) \approx 1 \pm s_S \alpha(z_H^j, z_P^i)\varepsilon(\boldsymbol{x}_H^j, \boldsymbol{x}_P^i),\end{aligned} \tag{S19b}$$

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where the approximation holds when $s_H, s_P \ll 1$, which we assume from hereon. Then, assuming every parasite can potentially infect every host, the components of biotic selection due to interspecific interactions for each species are approximated by

$$\mathcal{B}_H^p(z_H^j, \boldsymbol{x}_H^j, \mathcal{N}_P) \approx \prod_{i=1}^{n_P} 1 - s_H \alpha(z_H^j, z_P^i)\varepsilon(\boldsymbol{x}_H^j, \boldsymbol{x}_P^i), \tag{S20}$$

$$\mathcal{B}_P^p(z_P^j, \boldsymbol{x}_P^j, \mathcal{N}_H) \approx \prod_{i=1}^{n_H} 1 + s_P \alpha(z_H^i, z_P^j)\varepsilon(\boldsymbol{x}_H^i, \boldsymbol{x}_P^j). \tag{S21}$$

Using our weak biotic selection assumption $s_H, s_P \ll 1$, it will be convenient to rewrite these expressions as

$$\begin{aligned}\mathcal{B}_H^p(z_H^j, \boldsymbol{x}_H^j, \mathcal{N}_P) &\approx \exp\left(\int_{\mathbb{R}}\int_{\mathbb{R}^2} \ln\left(1 - s_H \alpha(z_H^j, \zeta)\varepsilon(\boldsymbol{x}_H^j, \boldsymbol{y})\right)\mathcal{N}_P(d\zeta, d\boldsymbol{y})\right) \\ &\approx \exp\left(-s_H \int_{\mathbb{R}}\int_{\mathbb{R}^2} \alpha(z_H^j, \zeta)\varepsilon(\boldsymbol{x}_H^j, \boldsymbol{y})\mathcal{N}_P(d\zeta, d\boldsymbol{y})\right), \end{aligned} \tag{S22}$$

$$\begin{aligned}\mathcal{B}_P^p(z_P^j, \boldsymbol{x}_P^j, \mathcal{N}_H) &\approx \exp\left(\int_{\mathbb{R}}\int_{\mathbb{R}^2} \ln\left(1 + s_P \alpha(\zeta, z_P^j)\varepsilon(\boldsymbol{y}, \boldsymbol{x}_P^j)\right)\mathcal{N}_H(d\zeta, d\boldsymbol{y})\right) \\ &\approx \exp\left(s_P \int_{\mathbb{R}}\int_{\mathbb{R}^2} \alpha(\zeta, z_P^j)\varepsilon(\boldsymbol{y}, \boldsymbol{x}_P^j)\mathcal{N}_H(d\zeta, d\boldsymbol{y})\right). \end{aligned} \tag{S23}$$

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. 2021) and offspring locations are bivariate normal around their parental locations with i.i.d. displacements in the two spatial dimensions.

To take a diffusion limit of this individual-based process, we follow Week et al. (2021). In particular, for the kth stage of rescaling, the time interval between generations is divided by k (so it goes to zero as $k \to \infty$), the number of initial individuals $n_S(0)$ in each species $S = H, P$ is multiplied by k (so $n_S(0) \to \infty$ as $k \to \infty$), the variances of mutation and dispersal are divided by k (so both go to zero as $k \to \infty$), fitness for each individual is taken to the $1/k$th power (so individual fitness tends towards unity as $k \to \infty$), and the *mass* of each individual is divided by k (so initial population *mass* remains $n_S(0)$ for all $k \geq 1$). In particular, this last part of our

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rescaling implies

$$\mathcal{N}_S^{(k)}(U,V) = \frac{1}{k}\sum_{i=1}^{kn_S(0)} \delta_{z_i,\boldsymbol{x}_i}(U,V), \tag{S24}$$

where z_i is the trait value of the ith individual, $\boldsymbol{x}_i$ is its geographic location, and $\delta_{z_i,\boldsymbol{x}_i}(U,V) = 1$ if $z_i \in U$ and $\boldsymbol{x}_i \in V$ and zero otherwise. Sufficient conditions under which the rescaled individual-based process $(\mathcal{N}_H^{(k)}, \mathcal{N}_P^{(k)})$ converges to a population-level process $(\mathfrak{N}_H, \mathfrak{N}_P)$ as $k \to \infty$ are provided by Theorem 1 of Méléard and Roelly (1993). In particular, their condition $(\mathscr{H}_1)$ requires the sequence $k\left(w_S^{1/k}(z,\boldsymbol{x},\mathcal{N}_H^{(k)},\mathcal{N}_P^{(k)}) - 1\right)$ to converge to the population growth rate $m_S(z,\boldsymbol{x},\mathfrak{N}_H,\mathfrak{N}_P)$ of the population-level process $\mathfrak{N}_S$ for species S. That is, population growth rates in the diffusion-limit are given by

$$m_H(z,\boldsymbol{x},\mathfrak{N}_H,\mathfrak{N}_P) = \lim_{k\to\infty} k\left(w_H^{1/k}(z,\boldsymbol{x},\mathcal{N}_H^{(k)},\mathcal{N}_P^{(k)}) - 1\right), \tag{S25}$$

$$m_P(z,\boldsymbol{x},\mathfrak{N}_P,\mathfrak{N}_H) = \lim_{k\to\infty} k\left(w_P^{1/k}(z,\boldsymbol{x},\mathcal{N}_H^{(k)},\mathcal{N}_P^{(k)}) - 1\right). \tag{S26}$$

For the host we have

$$k\left(w_H^{1/k}(z,\boldsymbol{x},\mathcal{N}_H^{(k)},\mathcal{N}_P^{(k)}) - 1\right) \approx k\left(w_{0,H}^{1/k}\exp\left(-\frac{A_H}{2k}(z-\theta_H)^2 - \frac{c_H}{k}\int_{\mathbb{R}^2}\chi_H(\boldsymbol{x},\boldsymbol{y})\mathcal{N}_H^{(k)}(\mathbb{R},d\boldsymbol{y})\right.\right.$$
$$\left.\left. -\frac{s_H}{k}\int_{\mathbb{R}}\int_{\mathbb{R}^2}\alpha(z,\zeta)\varepsilon(\boldsymbol{x},\boldsymbol{y})\mathcal{N}_P^{(k)}(d\zeta,d\boldsymbol{y})\right) - 1\right), \tag{S27}$$

where we have set $\chi_S(\boldsymbol{x},\boldsymbol{y}) = \exp\left(-\|\boldsymbol{x}-\boldsymbol{y}\|^2/2\omega_S^2\right)$. For large k, this is approximated by

$$k\left(w_H^{1/k}(z,\boldsymbol{x},\mathcal{N}_H^{(k)},\mathcal{N}_P^{(k)}) - 1\right) \approx kw_{0,H}^{1/k} - 1 - \frac{A_H}{2}(z-\theta_H)^2 - c_H\int_{\mathbb{R}^2}\chi_H(\boldsymbol{x},\boldsymbol{y})\mathcal{N}_H^{(k)}(\mathbb{R},d\boldsymbol{y})$$
$$- s_H\int_{\mathbb{R}}\int_{\mathbb{R}^2}\alpha(z,\zeta)\varepsilon(\boldsymbol{x},\boldsymbol{y})\mathcal{N}_P^{(k)}(d\zeta,d\boldsymbol{y}). \tag{S28}$$

Then, setting $r_S = \ln w_{0,S}$ (the intrinsic growth rate for species S), we get

$$m_H(z,\boldsymbol{x},\mathfrak{N}_H,\mathfrak{N}_P) =$$
$$r_H - \frac{A_H}{2}(z-\theta_H)^2 - c_H\int_{\mathbb{R}^2}\chi_H(\boldsymbol{x},\boldsymbol{y})\mathfrak{N}_H(\mathbb{R},\boldsymbol{y}) - s_H\int_{\mathbb{R}}\int_{\mathbb{R}^2}\alpha(z,\zeta)\varepsilon(\boldsymbol{x},\boldsymbol{y})\mathfrak{N}_P(d\zeta,d\boldsymbol{y}). \tag{S29}$$

A similar expression for the parasite is also obtained. We now make the approximation that competition and selection are sufficiently weak relative to the intrinsic growth rate (i.e.,

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$c_S, A_S, s_S \ll r_S$) so that spatial fluctuations in local abundance densities due to selection are small relative to average local abundance density for each species when the system has reached stationarity. This implies the population growth rates m_H, m_P are near zero when the system has reached stationarity. With this approximation, we write N_S as the abundance density for species S so that $\mathfrak{N}_S(\mathbb{R}, V) = \int_V \int_{\mathbb{R}} \mathfrak{N}_S(dz, d\boldsymbol{x}) \approx |V| N_S$, where $\mathbb{R}$ is given as the first argument to $\mathfrak{N}_S$ to include individuals with any trait value and $|V|$ is the area of the geographic region $V \subset \mathbb{R}^2$. In this case we have

$$\int_{\mathbb{R}^2} \chi_S(\boldsymbol{x}, \boldsymbol{y}) \mathfrak{N}_S(\mathbb{R}, d\boldsymbol{y}) = 2\pi\omega_S^2 N_S. \tag{S30}$$

The term capturing the effects of the host-parasite interaction has an integral across phenotypic space and an integral across geographic space. To simplify the geographic integral, set

$$\mathfrak{N}_S^{\iota}(U, \boldsymbol{x}) = \frac{\int_{\mathbb{R}^2} \varepsilon(\boldsymbol{x}, \boldsymbol{y}) \mathfrak{N}_S(U, d\boldsymbol{y})}{\int_{\mathbb{R}^2} \varepsilon(\boldsymbol{x}, \boldsymbol{y}) d\boldsymbol{y}} = \sqrt{2\pi\iota^2} \int_{\mathbb{R}^2} \varepsilon(\boldsymbol{x}, \boldsymbol{y}) \mathfrak{N}_S(U, d\boldsymbol{y}). \tag{S31}$$

This notation makes sense because ε is a smooth integrable function and a convolution with such a function yields another smooth function. Furthermore, when $\iota \ll 1$, $\int_V \mathfrak{N}_S^{\iota}(U, \boldsymbol{x}) d\boldsymbol{x} \approx \mathfrak{N}_S(U, V)$. Using our assumption that $\gamma \ll 1$, the biotic and abiotic components cumulatively contribute quadratic selection. 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 $\bar{z}_S(\boldsymbol{x}), v_S(\boldsymbol{x})$ for species S at location $\boldsymbol{x}$ (see §S5 below). Then, assuming $\iota \ll 1$, this implies

$$\int_{\mathbb{R}^2} \int_{\mathbb{R}} \alpha(z, \zeta) \varepsilon(\boldsymbol{x}, \boldsymbol{y}) \mathfrak{N}_P(d\zeta, d\boldsymbol{y}) = \frac{1}{\sqrt{2\pi\iota^2}} \int_{\mathbb{R}} \alpha(z, \zeta) \mathfrak{N}_P^{\iota}(d\zeta, \boldsymbol{x}) \approx \left(1 - \frac{\gamma}{2}(z - \bar{z}_P(\boldsymbol{x}))^2 + v_P(\boldsymbol{x})\right) \frac{N_S}{\sqrt{2\pi\iota^2}}. \tag{S32}$$

As 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. We can therefore expect phenotypic variance for each species to eventually fluctuate stochastically around a spatially constant equilibrium. We thus further approximate by setting the phenotypic variances equal to those constant equilibria. We can

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therefore approximate the growth rates for each species as

$$m_H(z,\boldsymbol{x}) \approx \rho_H - \frac{A_H}{2}(\theta_H - z)^2 + \frac{B_H}{2}(\bar{z}_P(\boldsymbol{x}) - z)^2, \tag{S33a}$$

$$m_P(z,\boldsymbol{x}) \approx \rho_P - \frac{A_P}{2}(\theta_P - z)^2 - \frac{B_P}{2}(\bar{z}_H(\boldsymbol{x}) - z)^2, \tag{S33b}$$

where we have dropped the dependencies on $\mathfrak{N}_H, \mathfrak{N}_P$ for brevity and set $B_S = s_S N_S \gamma / \sqrt{2\pi\iota^2}$ and

$$\rho_H = r_H + B_H v_P/2 - 2\pi\omega_H^2 c_H N_H, \tag{S34a}$$

$$\rho_P = r_P - B_P v_H/2 - 2\pi\omega_P^2 c_P N_P. \tag{S34b}$$

Finally, because we have assumed local trait distributions are Gaussian, and phenotypic variances and abundance densities are spatially homogeneous, we can apply the results of Week et al. (2021) to obtain local mean trait dynamics in response to selection. This part of our model justification does not require $B_H, B_P \ll 1$ (Week et al. 2021). It is possible that our small value assumptions $s_H, s_P, \gamma, \iota \ll 1$ imply $B_H, B_P \ll 1$, but this conclusion requires formal analysis. However, when computing spatial covariance functions, we assume $B_S \ll A_S$ for $S = H, P$ (see §S3 above).

Denoting $\partial_{sel}\bar{z}_S$ the response to selection for species S in continuous-time, we have

$$\partial_{sel}\bar{z}_S = G_S \left(\frac{\partial \bar{m}_S}{\partial z_S} - \overline{\frac{\partial m_S}{\partial \bar{z}_S}} \right), \tag{S35}$$

where barred symbols are averages across trait values. Applying this formula to the growth rates obtained in equations (S33) returns the abiotic and biotic selection components of our model (equations (1) in the main text).

S5 Gaussian Distribution of Local Traits

To show that local trait distributions can be approximated by Gaussian distributions, we start by considering deterministic dynamics of single species experiencing abiotic stabilizing selection. This leads to a deterministic partial differential equation describing the dynamics of the trait

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distribution and involves diffusion in both trait space and geographic space. The equilibrium solution is spatially homogeneous, allowing us to focus on characterizing the trait distribution at a single location. After confirming the equilibrium trait distribution is Gaussian at all locations for a single species, we move on to incorporate interspecific interactions following our model of host-parasite trait-matching. This leads to a pair of interacting partial differential equations generalizing the single species equation mentioned above. Again, the equilibrium solution is spatially homogeneous, so we focus on a single location. After confirming the trait distribution is Gaussian for the interacting species case, we then argue that, for sufficiently large population sizes in which the diffusion approximation holds, random genetic drift should only slightly perturb the trait distribution. Hence, local trait distributions should be approximately Gaussian.

We begin with the dynamics of the abundance density $\nu(z, \boldsymbol{x})$ (where $N(\boldsymbol{x}) = \int_{\mathbb{R}} \nu(z, \boldsymbol{x}) dz$ is the total abundance at location $\boldsymbol{x}$). We assume Gaussian descendants so that offspring traits are normally distributed around parental traits with variance ς^2. This provides

$$\frac{\partial}{\partial t}\nu = \frac{\varsigma^2}{2}\frac{\partial^2}{\partial z^2}\nu + \frac{\sigma^2}{2}\nabla^2\nu + m\nu. \tag{S36}$$

Following §S4, the growth rate for a single species under our model that is not engaged in an interspecific interaction is given by

$$m(z, \boldsymbol{x}) = r - \frac{A^2}{2}(\theta - z)^2 - cK(\nu), \tag{S37}$$

where

$$K(\nu) = \int_{\mathbb{R}^2}\int_{\mathbb{R}} \nu(z, \boldsymbol{y}) dz \frac{e^{\frac{\|\boldsymbol{x}-\boldsymbol{y}\|^2}{2\omega^2}}}{\sqrt{2\pi\omega^2}} d\boldsymbol{y}. \tag{S38}$$

One can check that $\nu(z, \boldsymbol{x}) = (r - \varsigma A) \exp\left(-\frac{(\theta-z)^2}{2\varsigma/A}\right) / c\sqrt{2\pi\varsigma/A}$ satisfies equation (S36). In particular, this implies the equilibrium trait distribution is spatially homogeneous and Gaussian with mean $\bar{z}(\boldsymbol{x}) \equiv \theta$ and variance $v(\boldsymbol{x}) \equiv \varsigma/A$ along with spatially homogeneous local abundance $N(\boldsymbol{x}) \equiv (r - \varsigma A/2)/c$. Furthermore, at sufficiently large local abundances for which the diffusion approximation outlined in §S4 is valid, demographic stochasticity and random genetic drift will have only small effects on the trait distribution relative to the effects of diffusive mutation and quadratic stabilizing selection so that the trait distribution remains approximately Gaussian.

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For the case of host-parasite interaction mediated by a trait-matching model, we can rewrite the growth rates as

$$m_H(z,\boldsymbol{x}) = \rho_H - \frac{1}{2}(A_H\theta_H^2 - B_H\bar{z}_P^2(\boldsymbol{x})) + \frac{(A_H\theta_H - B_H\bar{z}_P(\boldsymbol{x}))^2}{2(A_H - B_H)} - \frac{A_H - B_H}{2}\left(\frac{A_H\theta_H - B_H\bar{z}_P(\boldsymbol{x})}{A_H - B_H} - z\right)^2 - c_H K_H(\nu_H), \quad \text{(S39a)}$$

$$m_P(z,\boldsymbol{x}) = \rho_P - \frac{1}{2}(A_P\theta_P^2 + B_P\bar{z}_H^2(\boldsymbol{x})) + \frac{(A_P\theta_P + B_P\bar{z}_H(\boldsymbol{x}))^2}{2(A_P + B_P)} - \frac{A_P + B_P}{2}\left(\frac{A_P\theta_P + B_P\bar{z}_H(\boldsymbol{x})}{A_P + B_P} - z\right)^2 - c_P K_P(\nu_P), \quad \text{(S39b)}$$

with ρ_H, ρ_P given by equations (S34). Although these growth rates appear more complicated, they are still quadratic functions of the focal species' trait value. Hence, equilibrium trait distributions will be spatially homogeneous and Gaussian for both species. In particular, these equilibrium trait distributions are free of skew that appears when geographic structure is discrete and abiotic optima are spatially variable (Débarre et al. 2015). In the stochastic case, our assumptions of weak selection and large local abundance prevent significant feedbacks between evolutionary and abundance dynamics and imply phenotypic variation occurs at sufficiently large spatial scales relative to dispersal so that local trait distributions should remain approximately normal.

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