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

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abstract: Previous host-parasite coevolutionary theory has focused on understanding the determinants of local adaptation using spatially discrete models. However, these studies fall short of describing patterns of host-parasite local adaptation across spatial scales. In contrast, empirical work demonstrates that patterns of adaptation depend on the scale at which they are measured. Here, we propose a mathematical model of host-parasite coevolution in continuous space that naturally leads to a scale-dependent definition of local adaptation. In agreement with empirical research, we find that patterns of adaptation vary across spatial scales. In some cases, not only the magnitude of local adaptation but also the identity of the locally adapted species will depend on the spatial scale at which measurements are taken. Building on our results, we suggest a way to consistently measure parasite local adaptation when continuous space is the driver of cross-scale variation. We also describe a way to test whether continuous space is driving cross-scale variation. Taken together, our results provide a new perspective that can be used to understand empirical observations previously unexplained by theoretical expectations and deepens our understanding of the mechanics of host-parasite local adaptation.

Keywords: host-parasite coevolution, local adaptation, continuous space, spatial scale.

Introduction

Interactions between hosts and parasites have shaped patterns of diversity across all scales of biological organization. For example, coevolution with parasites can alter epidemiological dynamics (Best et al. 2010; Débarre et al. 2012; Lion and Gandon 2015), promote the evolution of sexual reproduction (Otto and Nuismer 2004; Lively 2010), yield novel mutualisms (Yamamura 1993), and influence patterns of speciation across a broad range of taxa (Agrawal and Zhang 2021). In each of these examples, the geography of the interspecific interactions plays a critical role in determining ecological and evolutionary outcomes. Previous theoretical studies of host-parasite coevolution have incorporated geography using models in which dispersal occurs between spatially discrete locations (Gandon et al. 1996; Boots and Sasaki 1999; Nuismer et al. 2000; Gandon 2002; Gandon and Michalakis 2002; Nuismer 2006; Ridenhour and Nuismer 2007; Gandon and Nuismer 2009; Débarre et al. 2012; Lion and Gandon 2015). However, because most species disperse in continuous space (Nathan et al. 2008) and because the consequences of spatially continuous systems may only be poorly approximated by discrete space models, there is a need for models that help us understand the drivers of host-parasite local adaptation in spatially continuous systems.

A theoretical model of coevolution in continuous space may also explain empirically observed variation in spatial patterns of host-parasite adaptation across spatial scales. Researchers often document a spatial pattern in which greater support for parasite local adaptation is found at larger spatial scales and little to no support is found at shorter spatial scales (Hanks and Denno 1994; Kaltz et al. 1999; Thrall et al. 2002; Schönrogge et al. 2006; Tack et al. 2014). We lack a mechanistic explanation for why this pattern should emerge because previous theory has not explicitly related parasite local adaptation to the geographic distances that measurements are taken at. Furthermore, these studies rely on indices of local adaptation that do not explicitly account for geographic distance. Therefore, there is a need to further integrate theoretical predictions and empirical observations of spatial patterns of coevolution. In this article, we aim to close this gap by analyzing the interaction among host-parasite coevolution, random genetic drift, and gene flow in a continuous two-dimensional habitat by introducing a novel quantitative genetic model and an index of local adaptation that explicitly accounts for the geographic distance measurements are taken at.

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We begin by introducing our model, which is a two-species generalization of Slatkin's (1978) model of quantitative trait evolution in continuous space. We then introduce our novel measure of local adaptation that explicitly accounts for geographic distance. Analysis of our model yields an interspecific spatial covariance function, called the cross-covariance function, that allows us to calculate the covariance of traits for host and parasite populations as a function of the geographic distance separating those populations. In particular, the cross-covariance function accounts for spatial autocorrelation of trait values in each species, which occurs when traits measured at different locations tend to look more similar the closer they are geographically. Combining our model of host-parasite coevolution with our continuous space index of local adaptation, we find that parasite local adaptation can be expressed in terms of the cross-covariance function. Our main finding is that parasite local adaptation depends on the spatial scale measurements are taken at relative to the spatial scales of phenotypic autocorrelation for both species. In some cases, not only the magnitude of local adaptation but also the identity of the locally adapted species can vary across spatial scales because of spatially autocorrelated traits. Building on our theoretical results, we make a suggestion for obtaining a consistent measurement of parasite local adaptation when cross-scale variation is due to spatial autocorrelation. In the discussion section, we also suggest an approach to test whether cross-scale variation is due to spatial autocorrelation and describe two directions for generalizing our model.

Methods

The Model

Our model tracks the evolution of local mean traits for a pair of species codistributed across a continuous two-dimensional geographic landscape. For each species, the genomic architecture of their traits is based on an infinitesimal approximation such that the trait of an individual can be thought of as the sum of an infinite number of allelic effects (with no epistasis or dominance), each of infinitesimal size (reviewed in Barton et al. 2017). The primary components of our model (selection, reproduction, and dispersal) can be thought of as different stages in the life cycle of an individual. We assume the life cycle begins by determining fitness in response to selective forces, including interspecific interactions, followed by the production of offspring that disperse to new locations, inherit trait values that are normally distributed around parental trait values, and repeat the cycle of life. However, instead of explicitly tracking individuals, our model focuses on the dynamics of mean traits averaged across individuals at each location in a two-dimensional geographic landscape.

In this section, we begin by outlining our approach to account for biotic and abiotic selection. We then discuss our model of dispersal and random genetic drift before combining these components into our working model. Model parameters are summarized in table 1. A more thorough and technically detailed introduction to and justification for our model is presented in sections S1 and S2 of the supplemental PDF, respectively.

Selection. We assume that fitness consequences for interactions between hosts and parasites are mediated by the difference in quantitative traits $z_H - z_P$, where z_S is the trait value of an individual in species $S = H, P$ for host and parasite, respectively. More precisely, we assume that the probability of infection increases the more similar traits are and decreases with trait mismatch. Given a successful infection, we assume that the host incurs a fitness cost and the parasite receives a fitness benefit. As a consequence, the host trait will evolve to evade the parasite trait in response to biotic selection, while the parasite trait evolves to match the host trait.

To draw biologically meaningful conclusions, we analyze our model at equilibrium. Then, to ensure our model has an equilibrium, we also account for abiotic selection that is stabilizing with strengths A_H, A_P. As our equilibrium analysis of the model is agnostic to globally averaged trait values, without loss of generality we assume that stabilizing selection pulls both traits toward zero. Additionally, our approach to computing spatial covariance functions (outlined in sec. S3 of the supplemental PDF) requires that biotic selection be weak relative to abiotic stabilizing selection for both species ($B_S \ll A_S$, $S = H, P$).

Following classical quantitative genetics, we assume that trait distributions of local populations are normal with mean $\bar{z}_S(\boldsymbol{x})$ for species S at the two-coordinate location $\boldsymbol{x} = (x_1, x_2)$. Although this assumption may be violated as dispersal can lead to skewed trait distributions (Débarre et al. 2015), this effect does not occur when dispersal distance is short relative to the spatial scale of trait variation. As will be shown in the results section, we find that dispersal distances are always short relative to spatial scales of trait variation when selection is weak.

Table 1: Model parameters

Symbol	Description
A_H	Host abiotic stabilizing selection
A_P	Parasite abiotic stabilizing selection
B_H	Host biotic selection
B_P	Parasite biotic selection
σ_H	Host dispersal distance
σ_P	Parasite dispersal distance
D_H	Rate of host (phenotypic) drift
D_P	Rate of parasite (phenotypic) drift

Drift. Random genetic drift can lead to variation in evolutionary trajectories across spatial locations. In our model, drift provides the ultimate source of geographic variation in phenotypes; this geographic variation then interacts with gene flow and selection to yield distinct spatial patterns. The classic model for the response of a quantitative character to random genetic drift is given by Lande (1976). This model states that the change in mean trait in response to drift between consecutive, nonoverlapping generations follows a normal distribution with variance equal to the ratio of additive genetic variance to effective population size. The continuous time analog of this model is trait evolution following Brownian motion, which has been widely applied as a phenomenological model in the field of phylogenetic comparative methods (Felsenstein 1973; Manceau et al. 2016). Mechanistically, this result has been formalized in continuous time by Week et al. (2021). In our continuous space setting, we extend this model so that different locations experience uncorrelated effects of drift (see sec. S1 of the supplemental PDF for mathematical details), with rate D_S for species S. We denote the spatial noise process capturing drift for species S by $\xi_S(\boldsymbol{x})$, which is normalized to have unit rate. That is, $D_S\xi_S(\boldsymbol{x})$ is the instantaneous evolutionary response to drift for species S at location $\boldsymbol{x}$.

Dispersal. We assume that displacement between parental and offspring birthplaces follows a bivariate Gaussian distribution centered on zero with displacement in each direction drawn independently. These assumptions prevent any net directionality in dispersal. For species S, we assume that displacements in the two directions are drawn with a standard deviation σ_S, which we refer to as the dispersal distance.

Gaussian dispersal leads to change in $\bar{z}_S(\boldsymbol{x})$ toward a local average, where the scale of "local" is determined by σ_S. The local mean trait will increase or decrease depending on the concavity of the spatial mean trait surface. As the concavity of a surface is quantified by a second spatial derivative, the effect of Gaussian dispersal on the instantaneous rate of change in local mean trait value is related to the second spatial derivative.

Selection, Dispersal, and Drift. We combine the evolutionary forces described in the previous sections to obtain our working model as

$$
\frac{\partial \bar{z}_H}{\partial t} = -\overbrace{A_H\bar{z}_H}^{\substack{\text{abiotic}\\\text{selection}}} - \overbrace{B_H(\bar{z}_P - \bar{z}_H)}^{\substack{\text{biotic}\\\text{selection}}}
$$
$$
+ \underbrace{\frac{\sigma_H^2}{2}\left(\frac{\partial^2 \bar{z}_H}{\partial x_1^2} + \frac{\partial^2 \bar{z}_H}{\partial x_2^2}\right)}_{\text{dispersal}} + \overbrace{D_H\xi_H}^{\text{drift}}, \tag{1a}
$$

$$
\frac{\partial \bar{z}_P}{\partial t} = -A_P\bar{z}_P + B_P(\bar{z}_H - \bar{z}_P)
$$
$$
+ \frac{\sigma_P^2}{2}\left(\frac{\partial^2 \bar{z}_P}{\partial x_1^2} + \frac{\partial^2 \bar{z}_P}{\partial x_2^2}\right) + D_P\xi_P, \tag{1b}
$$

where A_S is the strength of abiotic stabilizing selection, B_S is the strength of biotic selection, σ_S is the dispersal distance, and D_S is the rate of random genetic drift for species S.

A full technical description of our model can be found in section S1 of the supplemental PDF. The system of equations (1) forms a pair of linear stochastic partial differential equations (Khoshnevisan 2008; Hairer 2009). In the absence of coevolution, the well-studied equilibrium solution to this model is a Gaussian random field (Whittle 1954; Whittle 1963; Lindgren et al. 2011; Lindgren 2012). Background on Gaussian random fields is provided in section S2 of the supplemental PDF. As our model of coevolution implies a linear interaction between two fields, the methods used by Whittle (1954, 1963) to study the case of no interaction can be extended to show that the equilibrium solution of equations (1) is also a Gaussian random field. To illustrate our model, a single realization of mean trait values across space for the two species is provided in figure 1.

Equilibrium solutions to our model are completely characterized by five quantities: (1) the expected host mean trait at each location μ_H, (2) the expected parasite mean trait at each location μ_P, (3) the covariance between host mean traits sampled at any displacement $C_H(\boldsymbol{x})$, (4) the covariance between parasite mean traits sampled at any displacement $C_P(\boldsymbol{x})$, and (5) the cross-covariance between host and parasite mean traits sampled at any displacement $C_{HP}(\boldsymbol{x})$. As our primary interest is in the spatial covariances of mean traits, we ignore the expected values μ_H, μ_P. In fact, the key quantity derived from our model for drawing conclusions on host-parasite local adaptation is the interspecific cross-covariance between traits $C_{HP}(\boldsymbol{x})$. We describe our analytical approach to approximating this cross-covariance function in section S3 of the supplemental PDF. To make use of this cross-covariance function for understanding cross-scale variation in patterns of local adaptation, we introduce a new index of local adaptation in the following section that explicitly accounts for the effects of geographic scale.

Local Adaptation in Continuous Space

There are two popular definitions of local adaptation at the population level (Kawecki and Ebert 2004; Blanquart et al. 2013; but for a third definition, see Nuismer and Gandon 2008). The first, known as "home versus away," is the mean fitness of a population (where mean fitness of a population is defined as the average fitness among
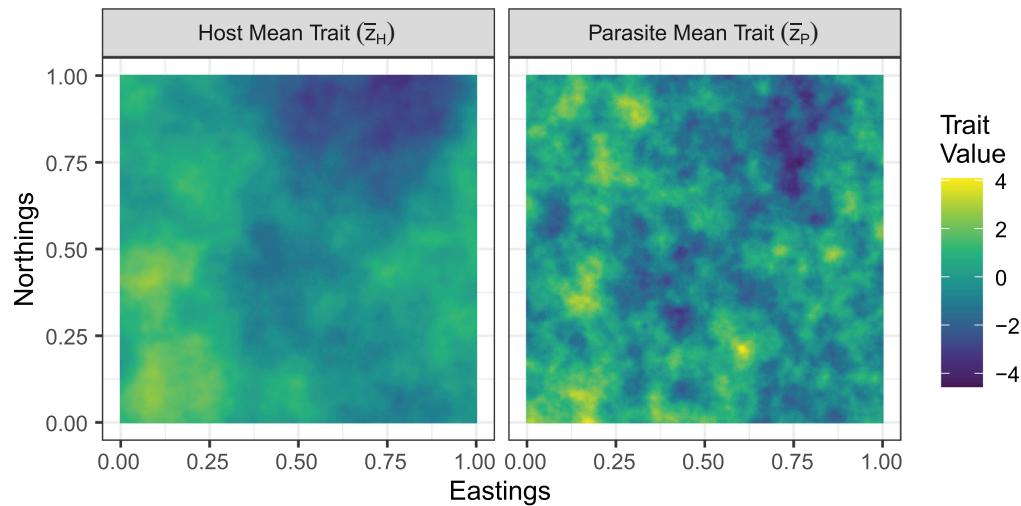
Figure 1: A single realization of our model. Shown are local mean trait values $\bar{z}_H(\boldsymbol{x})$, $\bar{z}_P(\boldsymbol{x})$, given by equations (1a) and (1b), respectively, across geographic space $\boldsymbol{x} = (x_1, x_2)$, where x_1 quantifies eastings and x_2 quantifies northings, for the host (*left*) and parasite (*right*). Local mean trait values are colored according to the scale on the right. Here we have made the dispersal distance of the host to be five times that of the parasite, with all other pairs of parameters equal.

all individuals in that population) in its local environment minus the average mean fitness of that population when transplanted to any other location. An alternative definition, known as "local versus foreign," is the mean fitness of a population in its local environment minus the average mean fitness of populations transplanted from any other location to that local environment. These definitions are particularly well suited for metapopulations, composed of a finite number K of discrete locations, because a randomly drawn foreign location (for home versus away) or population (for local versus foreign, but from here on we simply write location) occurs with probability $1/K$. However, this definition fails to account for the effects of geographic scale on measurements of local adaptation. Therefore, we introduce a definition that explicitly accounts for the geographic scale at which measurements are taken.

To obtain an index of local adaptation for species distributed continuously in space that accounts for geographic scale, we compute the population growth rate (referred to as a Malthusian growth rate in Crow and Kimura 1970) for a population in its local environment (say at location $\boldsymbol{x}$) minus the growth rate for the focal population when transplanted to a different location $\boldsymbol{y}$. This definition corresponds to a home versus away definition of local adaptation, as described above. Although classical indices of local adaptation are defined in terms of fitness as lifetime expected number of offspring, we chose population growth rate because it leads to relatively simple mathematical expressions. However, given the close correspondence between growth rate and fitness, conclusions drawn using either one should be qualitatively similar.

We denote by $m_H(z, \boldsymbol{x})$ the population growth rate of hosts with trait z encountering parasites located at $\boldsymbol{x}$. Similarly, $m_P(z, \boldsymbol{x})$ is the growth rate of parasites with trait z encountering hosts located at $\boldsymbol{x}$. Expressions for these growth rates are given by equations (S33) in section S4 of the supplemental PDF. The population growth rate for individuals of species S transplanted from location $\boldsymbol{x}$ to location $\boldsymbol{y}$, written $\bar{m}_S(\boldsymbol{x}, \boldsymbol{y})$, is then the average of $m_S(z, \boldsymbol{y})$ across trait values of individuals in species S at location $\boldsymbol{x}$.

As our model considers mean traits as random variables, the averaged population growth rates $\bar{m}_H(\boldsymbol{x}, \boldsymbol{y})$, $\bar{m}_P(\boldsymbol{x}, \boldsymbol{y})$ are also random variables. We therefore define local adaptation in terms of expectations of these growth rates. The measure of local adaptation we propose, $\ell_S(\boldsymbol{x}, \boldsymbol{y})$, allows us to calculate the expected difference between population growth rates for individuals of species S drawn from location $\boldsymbol{x}$ reared locally compared with individuals transplanted to location $\boldsymbol{y}$. Therefore, this definition explicitly accounts for the spatial distance between locations $\boldsymbol{x}$ and $\boldsymbol{y}$. Mathematically, our definition of local adaptation is expressed as

$$\ell_S(\boldsymbol{x}, \boldsymbol{y}) = \mathbb{E}[\bar{m}_S(\boldsymbol{x}, \boldsymbol{x}) - \bar{m}_S(\boldsymbol{x}, \boldsymbol{y})]. \qquad (2)$$

Following this notation, a local versus foreign definition of local adaptation (as described above) would correspond to $\ell_S(\boldsymbol{x}, \boldsymbol{y}) = \mathbb{E}[\bar{m}_S(\boldsymbol{x}, \boldsymbol{x}) - \bar{m}_S(\boldsymbol{y}, \boldsymbol{x})]$. However, under our model we find $\mathbb{E}[\bar{m}_S(\boldsymbol{y}, \boldsymbol{x})] = \mathbb{E}[\bar{m}_S(\boldsymbol{x}, \boldsymbol{y})]$, and thus the two definitions coincide. This is a consequence of solutions to our model being spatially isotropic, which is defined in section S2 of the supplemental PDF. Although

the index of local adaptation we introduce here can be applied to quantify both host and parasite local adaptation, in practice most empirical researchers focus on measuring parasite local adaptation only. For clarity and brevity, we then discuss only parasite local adaptation below, but note here that this index applies equally well to host local adaptation.

In the results section, we combine this definition of local adaptation with the population growth rates found in section S4 of the supplemental PDF to uncover patterns of local adaptation between hosts and parasites coevolving in continuous space.

Results

Spatial Covariance Functions

Intraspecific Spatial Covariance. Taking our approach outlined in section S3 of the supplemental PDF, we obtain analytic approximations for the (intraspecific) spatial covariance and (interspecific) spatial cross-covariance functions of host and parasite mean trait values at equilibrium.

We find spatial covariance functions for the host and parasite respectively take the forms

$$C_H(\boldsymbol{x}) = \sqrt{2}V_H \frac{\|\boldsymbol{x}\|}{\lambda_H} K_1\left(\sqrt{2}\frac{\|\boldsymbol{x}\|}{\lambda_H}\right), \quad (3a)$$

$$C_P(\boldsymbol{x}) = \sqrt{2}V_P \frac{\|\boldsymbol{x}\|}{\lambda_P} K_1\left(\sqrt{2}\frac{\|\boldsymbol{x}\|}{\lambda_P}\right), \quad (3b)$$

where $\|\boldsymbol{x}\|$ is the geographic distance between sampled locations; V_H, V_P are the colocated variances (i.e., $V_S = C_S(0)$); λ_H, λ_P are the spatial scales of autocorrelation in each species; and K_1 is the modified Bessel function of the second kind, order 1 (Abramowitz and Stegun 1965). These spatial covariance functions belong to the class of Matérn covariance functions that have been widely employed in the fields of spatial statistics (Stein 1999; Lindgren et al. 2011) and machine learning (Rasmussen and Williams 2006). In figure 2, we illustrate the relationship between patterns of phenotypic spatial variation and associated spatial covariance functions.
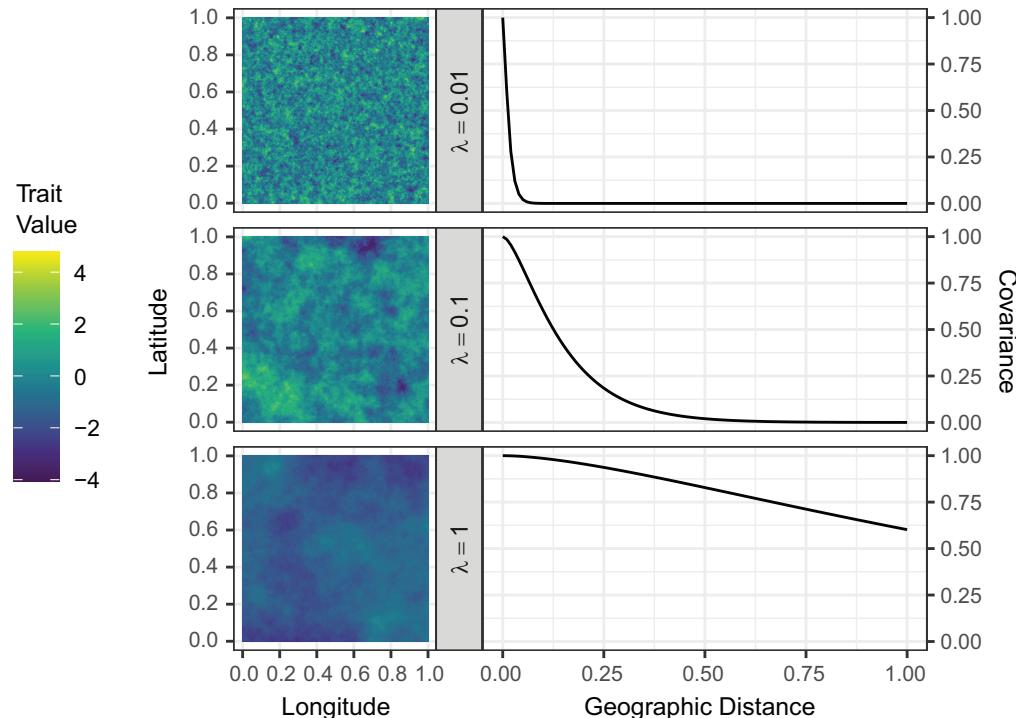

Figure 2: Mean trait surfaces $\bar{z}(\boldsymbol{x})$ (*left*), given by equations (1), and associated intraspecific covariance functions $C(\boldsymbol{x})$ (*right*), given by equations (3), across three different spatial scales of autocorrelation $\lambda = 0.01, 0.1, 1$, with colocated variance $V = 1$. This illustrates the relationship between the spatial scale of phenotypic autocorrelation and the variance of trait values across a fixed region. More precisely, increasing the spatial scale of autocorrelation λ (due to either increased dispersal distance or relaxed selection strengths; see eqq. [4]) leads to decreased trait variation in a fixed region.

Our results also demonstrate that the spatial scales of phenotypic isolation by distance in the host and parasite can be expressed in terms of model parameters respectively as

$$\lambda_H = \frac{\sigma_H}{\sqrt{A_H}}, \tag{4a}$$

$$\lambda_P = \frac{\sigma_P}{\sqrt{A_P}}. \tag{4b}$$

From these expressions, we see that these spatial scales are proportional to the dispersal distances in the respective species; the farther individuals tend to move, the larger the spatial scales one must observe to find significant phenotypic variation. We also see that increased abiotic stabilizing selection decreases these spatial scales in each species. Under the assumption of weak abiotic stabilizing selection (which would imply $A_H, A_P \ll 1$ and which is required in our justification of population growth rates; see section S4 of the supplemental PDF), our expression for the spatial scale of phenotypic variation coincides with that found by Slatkin (1978).

The colocated phenotypic variances, V_H and V_P, represent uncertainty in mean trait value at a particular location due to different possible realizations of drift. This should not be confused with the typical notion of phenotypic variance, which represents the variance of trait values among individuals in a population. As 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 individuals of species S sampled at locations separated by distances much greater than λ_S escape the effects of spatial autocorrelation and return essentially independent and identically distributed random variables with variances equal to the colocated variance V_S. That is, the colocated variances also provide measures of global diversity of mean traits across space. In terms of our model parameters, the colocated variances can be expressed as

$$V_H = \frac{D_H^2}{A_H \sigma_H^2}, \quad V_P = \frac{D_P^2}{A_P \sigma_P^2}. \tag{5}$$

From the expressions for V_H and V_P, we can identify relationships between global diversity of mean traits in each species and the different evolutionary processes of selection, dispersal, and drift. First, increased dispersal distance σ_S decreases V_S because, in the limit of infinite dispersal distance, our model collapses to a panmictic population of infinite size. Additionally, because abiotic selection is stabilizing around spatially homogeneous optima, increased A_S decreases V_S. Last, the variance due to drift D_S, the ultimate

source of spatial differentiation in our model, increases with additive genetic variance and decreases with effective population size (Lande 1976; Week et al. 2021).

Interspecific Spatial Cross-Covariance. In contrast to the intraspecific spatial covariance functions above, the spatial cross-covariance function, which quantifies interspecific trait covariance measured at two potentially different locations, does not yield a closed-form expression. Specifically, we find that the cross-covariance function is approximated by

$$C_{HP}(\boldsymbol{x}) = \int_{\mathbb{R}^2} \frac{B_P}{A_P} \frac{K_0(\|\boldsymbol{y}\|/\lambda_P)}{\lambda_P^2} C_H(\boldsymbol{x} - \boldsymbol{y}) \\ - \frac{B_H}{A_H} \frac{K_0(\|\boldsymbol{y}\|/\lambda_H)}{\lambda_H^2} C_P(\boldsymbol{x} - \boldsymbol{y}) d\boldsymbol{y}. \tag{6}$$

Although the expression for $C_{HP}(\boldsymbol{x})$ is quite technical, we can still draw some basic conclusions. For one, we see that interspecific cross-covariance can occur in the absence of coevolution. For example, in the case where $B_H = 0$ and $B_P > 0$, the host trait evolves only in response to abiotic selection, dispersal, and drift, but the parasite trait continues to evolve in response to the host trait. In this case, interspecific cross-covariance is maintained only by the parasite tracking the host. We can also use this expression to see that interspecific cross-covariance requires intraspecific autocovariance in at least one species (if $C_H(\boldsymbol{x}) = C_P(\boldsymbol{x}) = 0$, then $C_{HP}(\boldsymbol{x}) = 0$). Consequently, because both $C_H(\boldsymbol{x}), C_P(\boldsymbol{x}) \to 0$ in the limit of large geographic distance (i.e., $\|\boldsymbol{x}\| \to \infty$), $C_{HP}(\boldsymbol{x})$ also goes to zero in the limit of large distances. That is, interspecific cross-covariance disappears at distances large enough that intraspecific autocovariance is negligible in both species.

Patterns of Local Adaptation across Spatial Scales

Analytical Results. Combining our model with our definition of local adaptation in continuous space (see eq. [2]), we find

$$\ell_H(\boldsymbol{x}, \boldsymbol{y}) = \tilde{B}_H(C_{HP}(\boldsymbol{x} - \boldsymbol{y}) - C_{HP}(\boldsymbol{0})), \tag{7a}$$

$$\ell_P(\boldsymbol{x}, \boldsymbol{y}) = \tilde{B}_P(C_{HP}(\boldsymbol{0}) - C_{HP}(\boldsymbol{x} - \boldsymbol{y})), \tag{7b}$$

where $\tilde{B}_S$ is B_S divided by additive genetic variance in species S (see sec. S1 of the supplemental PDF). As all of the functions involved with this result depend only on spatial distance $d \geq 0$, we simplify our notation by writing $\ell_S(d) = \ell_S(\boldsymbol{x}, \boldsymbol{y})$ when $d = \|\boldsymbol{x} - \boldsymbol{y}\|$. Similarly, we write $C_H(d), C_P(d)$, and $C_{HP}(d)$ for the spatial covariance functions evaluated at geographic distance d. In figure 3, we present our index of parasite local adaptation as a function of geographic distance across nine combinations of λ_H and λ_P, with all other parameter pairs made equal.
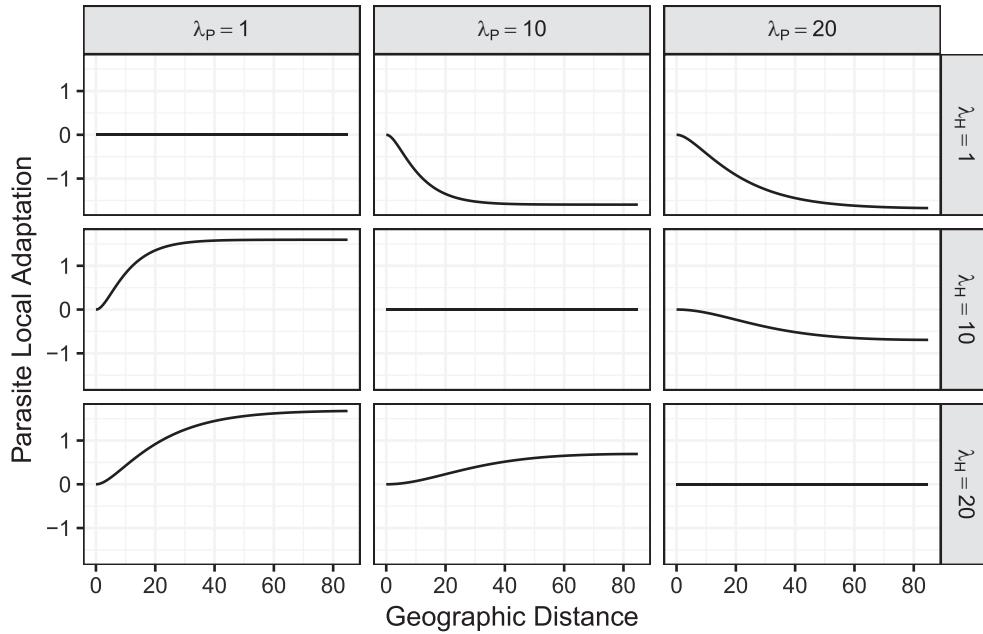
Figure 3: Parasite local adaptation ℓ_P, given by equation (7b), as a function of the geographic distance d between local parasite populations and the populations of hosts they are confronted with, scaled by biotic selection and colocated variances across nine combinations of $\lambda_H, \lambda_P = 1, 10, 20$, with $V_H = V_P = 1$ and $B_H/A_H = B_P/A_P = 1/250$. In the cases where $\lambda_H = \lambda_P$, we have $\ell_H(d) = \ell_P(d) = 0$ for all $d \geq 0$. In general, when all parameters are made equal between the two species, local adaptation does not emerge at any spatial scale.

Spatial Scale Dependency of Local Adaptation. As shown in figure 3, the magnitude of parasite local adaptation depends on the spatial scale measurements are taken at. More precisely, figure 3 suggests that local adaptation will be underestimated for study designs that define allopatric populations to be within the range of spatial autocorrelation for either species. In addition, if we allow for asymmetric background parameter values, which we might expect for realistic systems, our model predicts the potential for not only the magnitude of local adaptation to depend on the spatial scale measurements are taken, but also the identity of the locally adapted species. We present two such cases in figure 4. This result demonstrates that to obtain consistent estimates of local adaptation, measurements need to be taken at sufficiently large spatial scales.

A Consistent Estimate for Parasite Local Adaptation. The most rigorous way to estimate parasite local adaptation would be to confront parasites from a focal population with hosts sampled at populations from many different locations in a large provenance trial (Blanquart et al. 2013). However, such an experiment would be incredibly labor intensive and prone to variable results as predicted by our model. Fortunately, our model suggests an efficient way to consistently measure parasite local adaptation. Namely, when measurements are taken at sufficiently large spatial

scales, $C_{HP}(d) \approx 0$ so that parasite local adaptation $\ell_P(d)$ is proportional to $C_{HP}(0)$ (see eqq. [7]). That is, parasite local adaptation can be consistently measured by computing the interspecific spatial covariance of sympatric mean traits across locations separated by distances that are large relative to both spatial scales of intraspecific autocorrelation λ_H and λ_P. Importantly, this approach, similar to previous approaches based on spatial covariance of allele frequencies (Blanquart et al. 2013), requires only information on host and parasite mean traits sampled across space (rather than the outcome of a manipulative experiment) and is thus much more feasible. Museum and herbarium collections may offer a vital resource for characterizing host/parasite phenotypic diversity across space (e.g., Rabosky et al. 2016). With a geographic map of host and parasite phenotypes in hand, a researcher could determine the spatial scale at which intraspecific phenotypic autocorrelation becomes negligible and thus the spatial scale at which interspecific spatial covariance of mean traits should be calculated to estimate local adaptation.

Discussion

Here, we have developed a model that tracks the evolution of local mean traits of coevolving species distributed in two-dimensional continuous space. This model accounts
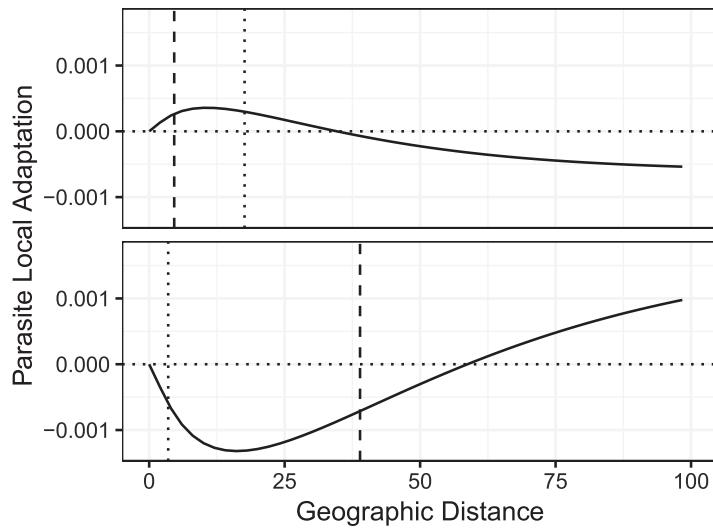
Figure 4: Parasite local adaptation ℓ_P, given by equation (7b), as a function of geographic distance d between local parasite populations and the populations of hosts they are confronted with, for two cases where the identity of the locally adapted species depends on the spatial scale at which measurements are taken. The horizontal dotted line marks a measurement of zero parasite local adaptation. Vertical lines mark spatial scales of intraspecific autocorrelation in the host (dashed vertical lines) and parasite (dotted vertical lines).

for host-parasite interactions mediated by a trait-matching/mismatching mechanism, abiotic stabilizing selection, Gaussian dispersal, and random genetic drift. Solutions to this model are Gaussian random fields that are characterized by two intraspecific spatial autocovariance functions along with an interspecific spatial cross-covariance function. We have also introduced a novel index of local adaptation that explicitly accounts for the geographic distance separating allopatric populations. Combining our novel index of local adaptation in continuous space with the cross-covariance function obtained from our model, we found that variation in measurements of parasite local adaptation across spatial scales can be explained by intraspecific spatial autocorrelation that emerges when species disperse in continuous space. More precisely, figure 3 demonstrates that measurements taken within the range of spatial autocorrelation for either species will underestimate the magnitude of parasite local adaptation or maladaptation. Building on this result, we suggest taking measurements at spatial scales for which intraspecific autocorrelation is negligible for both species to obtain consistent estimates for parasite local adaptation.

The mathematical model we propose may help shed light on several cases where estimates of parasite local adaptation may have been dependent on the spatial scales at which they were measured. For example, Tack et al. (2014) showed that maladaptation of the parasitic powdery mildew *Podosphaera plantaginis* on the invasive weed *Plantago lanceolata* was strong at scales of 6–200 km but weak at scales of less than 6 km. In another study, Thrall et al.

(2002) found evidence of local adaptation of the autoecious rust pathogen *Melampsora lini* on its herbaceous perennial herb host *Linum marginale* to be more apparent at scales of 5–10 km than at scales of 200–400 m. Hanks and Denno (1994) investigated local adaptation of the phytophagous armored scale insect *Pseudaulacaspis pentagon* on individual mulberry trees of the species *Morus alba* and found stronger evidence of local adaptation for insects transplanted to distant trees (≥300 m) than for insects transplanted to nearby trees (<5 m). Schönrogge et al. (2006) found the hoverfly *Microdon mutabilis* to be extremely locally adapted to its host ant *Formica lemani* when confronted with host individuals separated by distances of 3–20 km, moderately locally adapted at distances of 0.1–3 km, and not locally adapted at <100 m. Last, Kaltz et al. (1999) studied local adaptation of the insect-transmitted fungal pathogen *Microbotryum violaceum* to its host plant *Silene latifolia* and found weak parasite local maladaptation when confronted with nearby populations (<10 km), strong parasite maladaptation when confronted with populations at intermediate distances (<30 km), and variation in maladaptation for remote populations (<170 km) ranging from strong to weak maladaptation.

These empirical studies demonstrate the key finding of our model: that there can be variation in the magnitude of local adaptation across spatial scales in naturally occurring systems. For example, in all of the studies referenced in the preceding paragraph, the estimated strength of local adaptation is a function of the geographic distance between the

populations for which it is assessed. A second useful prediction from our model is that because of the phenotypic spatial autocorrelation within each species, measurements of local adaptation taken at larger distances will provide more consistent estimates. Therefore, in each of the cases referenced above (in which local adaptation varies as a function of the spatial scale at which it is measured) we would recommend summarizing local adaptation in the system using comparisons between the most distant population pairs. However, because our model includes stochasticity (due to random genetic drift), it also predicts that there should be some amount of variation in individual measurements of local adaptation, even at large spatial scales. Kaltz et al. (1999) highlight this variation, finding high variance in infection success of the *Microbotryum* parasite on *Silene* hosts at the largest spatial distances. These infection success measurements do appear to increase, on average, with distance, and given the second prediction above, the model would support summarizing these results using the mean measurements at the largest spatial lags.

In addition to providing a theoretical explanation for the observation of spatial variation in host-parasite local adaptation, our model predicts that the shorter-dispersing species should be locally adapted to the farther-dispersing species, assuming that all other parameters are equal (see fig. 3). Of the five studies listed above (by no means an exhaustive list), two (Hanks and Denno 1994; Tack et al. 2014) fit this prediction. In Hanks and Denno (1994) the parasite disperses a shorter distance than its host and is locally adapted, and in Tack et al. (2014) the parasite disperses a longer distance than its host and is locally maladapted. Deviations from this prediction may then imply interspecific asymmetry of model parameters other than dispersal distances. Equation (S13) in section S3 of the supplemental PDF shows that the identity of the locally adapted species depends on symmetry of each pair of model parameters (abiotic selection strengths A_H, A_P; biotic selection strengths B_H, B_P; dispersal distances σ_H, σ_P; and rates of drift D_H, D_P). Consequently, our model suggests that the identity of the locally adapted species in the other three studies (Kaltz et al. 1999; Thrall et al. 2002; Schönrogge et al. 2006), in each of which the locally adapted species disperses farther than its partner, is mediated by differential selection strengths or differential rates of drift.

Our suggested approach for obtaining consistent measurements of parasite local adaptation rests on the hypothesis that intraspecific spatial autocorrelation explains variation in measurements of coadaptation across spatial scales. This hypothesis, implied by our theoretical findings, can be tested using geographically referenced phenotypic data. More precisely, standard methods applied in the analysis of spatial data (e.g., Dale and Fortin 2014) may be used to determine the distances for which spatial

autocorrelation is negligible in each species. In turn, these estimates can be compared to the geographical distances between allopatric populations defined in previous empirical studies. Our hypothesis would be rejected if variation in measurements of local adaptation occurs across several spatial scales that are larger than both of the spatial scales of autocorrelation in the host and parasite species. In this case, additional theoretical studies would be required to explain such cross-scale variation.

Additional hypotheses for the cross-scale variation in spatial patterns of adaptation can be developed by extending our model in several directions. For example, heavy-tailed dispersal kernels, which are likely common in nature (Houtan et al. 2007; Bullock et al. 2016; García and Borda-de-Água 2016; Jordano 2016), can be incorporated into our model by replacing the dispersal operator with fractional spatial derivatives (for mathematical details, see Laskin 2000; Bayın 2016). As fractional derivatives are defined in terms of spectral representations, our approach, which recovers covariance functions from spectral representations, is particularly well suited to this generalization of our model. Such a generalization of our model may then be used to predict variation in patterns of adaptation as a consequence of dispersal mode. Another direction this work can be taken is to consider spatial variation of the abiotic environment by modeling abiotic optima as additional Gaussian random fields (making for four random fields in total; one for the host trait, one for the parasite trait, one for the host abiotic optimum, and one for the parasite abiotic optimum). This second direction would allow for theoretical predictions of spatial variation in local adaptation based on spatial scales of abiotic environmental variation. Hu et al. (2013) provides further information on the mathematical details involved with both of these extensions.

Although there is already a large body of theory on geographically structured host-parasite coevolution (e.g., Gandon et al. 1996; Nuismer et al. 2000; Gandon 2002; Gandon and Michalakis 2002; Nuismer et al. 2003; Nuismer 2006; Ridenhour and Nuismer 2007; Gandon and Nuismer 2009; Débarre et al. 2012; Lion and Gandon 2015), these studies are limited in their ability to explain variation in patterns of host-parasite adaptation across spatial scales because they depend on indices of local adaptation that do not explicitly account for geographic distance. In contrast, empirical studies have emphasized that such cross-scale variation is common (Hanks and Denno 1994; Kaltz et al. 1999; Thrall et al. 2002; Schönrogge et al. 2006; Tack et al. 2014). Our model, combined with our novel index of local adaptation, is, to our knowledge, the first to provide a mechanistic explanation for measurements of parasite local adaptation that vary across spatial scales. Furthermore, it is consistent with empirical observations that local adaptation

in host-parasite systems tends to be stronger at larger spatial scales relative to shorter spatial scales.

In addition to the geographically explicit index of local adaptation we have introduced here, our mathematical model of continuous space coevolution has several novel features. In comparison to previous models of coevolution in continuous space (Nuismer et al. 2000, 2003), our model differs in three major ways. First, whereas previous continuous space models have focused on interspecific interactions mediated by allelic variation at genetic loci, our model focuses on coevolution of a pair of quantitative traits that determine the outcomes of interactions. Second, while previous work has focused on a single continuous spatial axis, our model accounts for the more biologically relevant case of two continuous spatial axes. Last, our model accounts for the stochastic dynamics of random genetic drift, which rarely yields tractable evolutionary models in two-dimensional continuous space (Felsenstein 1975; Etheridge 2004; Barton et al. 2010). It is therefore likely that investigations relaxing important assumptions of our model, such as spatially homogeneous abundance densities and weak biotic selection, will require the study of individual-based simulations.

Conclusion

In summary, our work here provides initial steps toward understanding coevolution and local adaptation in continuous space using an analytically tractable mathematical model. Our theoretical findings form testable hypotheses for previously unexplained variation observed in empirical host-parasite systems and suggest an approach to consistently measure parasite local adaptation in the wild. Taken together, this work establishes a novel theoretical approach to model spatial coevolution and lends a new perspective for understanding spatial patterns of interspecific coadaptation.

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Statement of Authorship

B.W. contributed to conceptualization, model development/analysis, visualization, coding simulation, writing—original draft, and writing—review and editing. G.B. contributed to conceptualization, supervision, writing—original draft, writing—review and editing, and funding acquisition.

Data and Code Availability

Data and code for reproducing each of the figures in this article and for deriving some key analytical results have been collected in a Zenodo repository (https://doi.org/10.5281/zenodo.8008017; Week and Bradburd 2023).

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