

Supplementary Material (SM)

Throughout this supplement, we set use dot notation for time derivatives so that $\dot{f}(x, t) = \frac{\partial}{\partial t} f(x, t)$ and set $\Delta = \sum_{i=1}^d \frac{\partial^2}{\partial x_i^2}$ the Laplace operator on \mathbb{R}^d , except in §10.1.3 where Δ represents a random variable.

1 Sufficient conditions for finite mean, variance and total abundance in the deterministic case

Recall that $m(\nu, x)$ is shorthand for $m((K\nu)(x, t), x)$. That is, $m : [0, +\infty) \times \mathbb{R} \rightarrow \mathbb{R}$. Following our assumptions of the main text, we have that $m(h, x)$ is differentiable with respect to both x and h and there exists $r \in \mathbb{R}$ such that $m(h, x) \leq r$ across all $h \geq 0$ and $x \in \mathbb{R}$. As in the main text, we also assume the initial condition $u(x)$ is continuous and integrable in x and satisfies

$$0 \leq \int_{\mathbb{R}} (|x| + x^2) u(x) dx < +\infty \quad (1)$$

and consider the Cauchy problem

$$\begin{cases} \dot{\nu}(x, t) = m(\nu, x)\nu(x, t) + \frac{\mu}{2}\Delta\nu(x, t) & t > 0 \\ \nu(x, 0) = u(x) & t = 0. \end{cases} \quad (2)$$

According to Theorem 2.5.6 of Zheng (2004), if the operator F defined by $\nu(x, t) \rightarrow m(\nu, x)\nu(x, t)$ is locally Lipschitz, corresponding to equation (8) of the main text, then for some maximal $T > 0$ problem (2) admits a unique local classical solution $\nu(x, t)$ for $t \in [0, T)$. Furthermore, either $T = +\infty$ or $T < +\infty$ and $\lim_{t \uparrow T} \int_{\mathbb{R}} |\nu(x, t)| dx = +\infty$. In this section we show that our assumption $m(h, x) \leq r$ for all $h \geq 0$ and $x \in \mathbb{R}$ implies $T = +\infty$. Replacing m with it's upper bound $r \in \mathbb{R}$, equation (2) reduces to a simple parabolic equation that can be solved using elementary techniques (Farlow 1993). In particular, when $m(\nu, x) \equiv 0$ denote the solution to (2) by $\nu_0(x, t)$. Then, denoting

$$\Phi(x, t) = \frac{\exp(-x^2/2\mu t)}{\sqrt{2\pi\mu t}}, \quad (3)$$

we have

$$\nu_0(x, t) = \int_{\mathbb{R}} \Phi(x - y, t) \nu(y, 0) dy. \quad (4)$$

In the more general case, when $m(\nu, x) \equiv r \in \mathbb{R}$, equation (2) has the solution $\nu_r(x, t) = e^{rt} \nu_0(x, t)$. Hence, $\nu_r(x, t) \geq 0$ for all $x \in \mathbb{R}$ and $\int_{\mathbb{R}} \nu_r(x, t) dx = e^{rt} N(0) < +\infty$ for all $t \geq 0$. Furthermore, denoting

$$\begin{aligned} N_r(t) &= \int_{\mathbb{R}} \nu_r(x, t) dx, \\ p_r(x, t) &= \nu_r(x, t) / N_r(t), \\ \bar{x}_r(t) &= \int_{\mathbb{R}} x p_r(x, t) dx, \\ \sigma_r^2(t) &= \int_{\mathbb{R}} (x - \bar{x}_r(t))^2 p_r(x, t) dx, \end{aligned} \quad (5)$$

we have

$$\bar{x}_r(t) = \int_{\mathbb{R}} x \int_{\mathbb{R}} \Phi(x - y, t) p(y, 0) dy dx = \int_{\mathbb{R}} y p(y, 0) dy = \bar{x}(0), \quad (6)$$

$$\sigma_r^2(t) = \int_{\mathbb{R}} (x - \bar{x}_r(t))^2 \int_{\mathbb{R}} \Phi(x - y, t) p(y, 0) dy dx = \int_{\mathbb{R}} ((y - \bar{x}(0))^2 + \mu t) p(y, 0) dy = \sigma^2(0) + \mu t. \quad (7)$$

Hence, $|\bar{x}_r(t)|, \sigma_r^2(t) < +\infty$ for all $t \geq 0$. For the sake of contradiction, suppose there exists $x \in \mathbb{R}$ and $t \geq 0$ such that $\nu(x, t) > \nu_r(x, t)$. Then

$$\nu(x, t) - \nu(x, 0) = \int_0^t m(\nu, x) \nu(x, s) ds + \frac{\mu}{2} \Delta \nu(x, s) ds > \int_0^t r \nu_r(x, s) ds + \frac{\mu}{2} \Delta \nu_r(x, s) ds = \nu_r(x, t) - \nu(x, 0) \quad (8)$$

which implies there exists $h \geq 0$ and $x \in \mathbb{R}$ such that $m(h, x) > r$. But this contradicts our assumption $m(h, x) \leq r$ for all $h \geq 0$ and $x \in \mathbb{R}$. So we have $\nu(x, t) \leq \nu_r(x, t)$ for each $x \in \mathbb{R}$ and $t \geq 0$. This implies that $N(t) = \int_{\mathbb{R}} \nu(x, t) dx < +\infty$,

$$0 \leq \int_{\mathbb{R}} x^2 \nu(x, t) dx \leq \int_{\mathbb{R}} x^2 \nu_r(x, t) dx < +\infty \quad (9)$$

and in particular

$$0 \leq \sigma^2(t) + \bar{x}^2(t) = \frac{1}{N(t)} \int_{\mathbb{R}} x^2 \nu(x, t) dx < +\infty \quad (10)$$

for each $t \geq 0$.

2 Equilibrium moments for a deterministic population experiencing logistic growth and stabilizing selection

Here we set out to show, given the initial conditions $\nu(\cdot, 0) \in L^1(\mathbb{R})$ such that $\bar{x}(0) \in \mathbb{R}$, $\sigma^2(0) \in [0, +\infty)$ and $N(0) \in (0, +\infty)$, and given the growth rate

$$m(\nu, x) = r - \frac{a}{2}(\theta - x)^2 - c \int_{\mathbb{R}} \nu(y, t) dy \quad (11)$$

such that $\theta \in \mathbb{R}$, $a, c, \mu > 0$ and $r > \frac{1}{2}\sqrt{\mu a}$, we have the following stable equilibrium $N_{\infty} = \lim_{t \rightarrow \infty} N(t) = \frac{1}{c}(r - \frac{1}{2}\sqrt{\mu a})$, $\bar{x}_{\infty} = \lim_{t \rightarrow \infty} \bar{x}(t) = \theta$ and $\sigma_{\infty}^2 = \lim_{t \rightarrow \infty} \sigma^2(t) = \sqrt{\frac{\mu}{a}}$.

The mean fitness can be calculated as

$$\bar{m}(t) = r - \frac{a}{2}((\theta - \bar{x}(t))^2 + \sigma^2(t)) - cN(t). \quad (12)$$

Recalling the ODE derived for $N(t)$,

$$\frac{d}{dt}N(t) = \bar{m}(t)N(t) = (r - \frac{a}{2}((\theta - \bar{x}(t))^2 + \sigma^2(t)) - cN(t))N(t), \quad (13)$$

solving for equilibrium total abundance \hat{N} amounts to setting $\frac{d}{dt}N(t) = 0$ and solving for $N(t)$. Ignoring the equilibrium $N(t) = 0$, this reduces to solving $\bar{m}(t) = 0$ for $N(t)$, which returns

$$\hat{N} = \frac{1}{c} \left(r - \frac{a}{2}((\theta - \hat{x})^2 - \hat{\sigma}^2) \right). \quad (14)$$

Unfortunately, deriving ODE for $\bar{x}(t)$ and $\sigma^2(t)$ leads to expressions involving higher moments and finding ODE for these higher moments will lead to expressions involving yet even higher moments. To avoid this infinite regression, we find the equilibrium abundance density $\hat{\nu}(x)$ by solving $\frac{\partial}{\partial t} \nu(x, t) = 0$ for $\nu(x, t)$. This implies the following ordinary differential equation

$$\frac{d^2}{dx^2} \hat{\nu}(x) = \left(\frac{2c}{\mu} \hat{N} + \frac{a}{\mu}(\theta - x)^2 - \frac{2r}{\mu} \right) \hat{\nu}(x) \quad (15)$$

which has the solution

$$\hat{\nu}(x) = \frac{\hat{N}}{\sqrt{2\pi}} \left(\frac{a}{\mu} \right)^{\frac{1}{4}} \exp \left(-\sqrt{\frac{a}{\mu}} \frac{(\theta - x)^2}{2} \right). \quad (16)$$

From this expression we infer $\hat{x} = \theta$ and $\hat{\sigma}^2 = \sqrt{\frac{\mu}{a}}$. Hence $\hat{N} = \frac{1}{c} (r - \frac{1}{2}\sqrt{a\mu})$. To show that $N_\infty = \hat{N}$, $\bar{x}_\infty = \hat{x}$ and $\sigma_\infty^2 = \hat{\sigma}^2$, we linearize ODE for $N(t)$, $\bar{x}(t)$ and $\sigma^2(t)$ using the equilibrium $\hat{\nu}(x)$. In particular, since $\hat{\nu}(x)$ is Gaussian, we do not run into the same issue with higher moments as above. Assuming the equilibrium $\hat{\nu}(x)$ does not change the ODE for $N(t)$, but the ODE for $\bar{x}(t)$ and $\sigma^2(t)$ can now be expressed as

$$\frac{d}{dt}\bar{x}(t) = \sigma^2(t) \left(\frac{\partial \bar{m}(t)}{\partial \bar{x}(t)} - \frac{\partial \bar{m}(t)}{\partial \bar{x}(t)} \right) = a\sigma^2(t)(\theta - \bar{x}(t)), \quad (17)$$

$$\frac{d}{dt}\sigma^2(t) = 2\sigma^4(t) \left(\frac{\partial \bar{m}(t)}{\partial \sigma^2(t)} - \frac{\partial \bar{m}(t)}{\partial \sigma^2(t)} \right) + \mu = \mu - a\sigma^4(t), \quad (18)$$

where $\hat{\rho}(x) = \hat{\nu}(x)/\hat{N}$. These expressions confirm our findings that $\hat{x} = \theta$ and $\hat{\sigma}^2 = \sqrt{\frac{\mu}{a}}$. Furthermore, calculating

$$\frac{\partial}{\partial \sigma^2(t)} \frac{d}{dt}\sigma^2(t) = -2a\sigma^2(t) \quad (19)$$

and evaluating at $\sigma^2(t) = \hat{\sigma}^2$ demonstrates the equilibrium phenotypic variance is stable when $a, \mu > 0$. Hence, calculating

$$\frac{\partial}{\partial \bar{x}(t)} \frac{d}{dt}\bar{x}(t) = -a\sigma^2(t) \quad (20)$$

and evaluating at $\sigma^2(t) = \hat{\sigma}^2$ and $\bar{x}(t) = \hat{x}$ demonstrates the equilibrium phenotypic mean is stable when $a, \mu > 0$. Finally, calculating

$$\frac{\partial}{\partial N(t)} \frac{d}{dt}N(t) = r - \frac{a}{2}((\theta - \bar{x}(t))^2 + \sigma^2(t)) - 2cN(t) \quad (21)$$

and evaluating at $\sigma^2(t) = \hat{\sigma}^2$, $\bar{x}(t) = \hat{x}$ and $N(t) = \hat{N}$ demonstrates the equilibrium total abundance is stable when $a, c, \mu > 0$, and $r > \frac{1}{2}\sqrt{a\mu}$.

3 The relation between diffusion and convolution with a Gaussian kernel

For continuous $g : \mathbb{R}^d \rightarrow \mathbb{R}$, consider the deterministic Cauchy problem

$$\begin{cases} \dot{f}(x, t) = \Delta f(x, t), & (x, t) \in \mathbb{R}^d \times (0, \infty) \\ f(x, t) = g(x), & (x, t) \in \mathbb{R}^d \times \{0\}. \end{cases} \quad (22)$$

According to Evans (2010), the fundamental solution of (22) is

$$\Phi(x, t) = \frac{1}{(4\pi t)^{d/2}} \exp\left(-\frac{|x|^2}{4t}\right), \quad (x, t) \in (0, \infty) \times \mathbb{R}^d, \quad (23)$$

where $|x| = \sqrt{\sum_i x_i^2}$. The solution $f(x, t)$ of PDE (22) is then given by the convolution

$$f(x, t) = \int_{\mathbb{R}^d} \Phi(x - y, t)g(y)dy, \quad (x, t) \in (0, \infty) \times \mathbb{R}^d. \quad (24)$$

Hence, by the fundamental theorem of calculus,

$$\begin{aligned} f(x, t) + \int_t^{t+1} \dot{f}(x, s)ds &= f(x, t+1) \\ &= \int_{\mathbb{R}^d} \Phi(x - y, t+1)g(y)dy = \int_{\mathbb{R}^d} \int_{\mathbb{R}^d} \Phi(x - y, 1)\Phi(y - z, t)g(z)dzdy \\ &= \int_{\mathbb{R}^d} \Phi(x - y, 1)f(t, y)dy. \end{aligned} \quad (25)$$

65 In particular,

$$f(x, t) + \int_t^{t+1} \Delta f(x, s) ds = \int_{\mathbb{R}^d} \Phi(1, x - y) f(y, t) dy. \quad (26)$$

66 4 Deterministic dynamics of $\sigma^2(t)$

67 Picking up from the main text §2.1,

$$\begin{aligned} \frac{d}{dt} \sigma^2(t) &= \frac{d}{dt} \int_{\mathbb{R}} (x - \bar{x}(t))^2 p(x, t) dx = \int_{\mathbb{R}} 2(x - \bar{x}(t)) \frac{d}{dt} \bar{x}(t) + (x - \bar{x}(t))^2 \frac{\partial}{\partial t} p(x, t) dx \\ &= \int_{\mathbb{R}} (x - \bar{x}(t))^2 \left((m(\nu, x) - \bar{m}(t)) p(x, t) + \frac{\mu}{2} \frac{\partial^2}{\partial x^2} p(x, t) \right) dx \\ &= \int_{\mathbb{R}} ((x - \bar{x}(t))^2 - \sigma^2(t) + \sigma^2(t)) (m(\nu, x) - \bar{m}(t)) p(x, t) + (x - \bar{x}(t))^2 \frac{\mu}{2} \frac{\partial^2}{\partial x^2} p(x, t) dx \\ &= \text{Cov}_t((x - \bar{x}(t))^2, m(\nu, x)) + \frac{\mu}{2} \int_{\mathbb{R}} (x - \bar{x}(t))^2 \frac{\partial^2}{\partial x^2} p(x, t) dx. \end{aligned} \quad (27)$$

68 Applying integration by parts twice yields

$$\int_{-\infty}^{+\infty} (x - \bar{x}(t))^2 \frac{\partial^2}{\partial x^2} p(x, t) dx = 2. \quad (28)$$

69 4.1 Simplifying covariances with fitness under the assumption of a Gaussian density

70 By assuming

$$p(x, t) = \frac{\exp\left(-\frac{(x - \bar{x}(t))^2}{2\sigma^2(t)}\right)}{\sqrt{2\pi\sigma^2(t)}} \quad (29)$$

72 we have

$$\begin{aligned} \sigma^2 \left(\frac{\partial \bar{m}}{\partial \bar{x}} - \overline{\frac{\partial m}{\partial \bar{x}}} \right) &= \sigma^2 \left(\frac{\partial}{\partial \bar{x}} \int_{\mathbb{R}} m(\nu, x) p(x, t) dx - \int_{\mathbb{R}} p(x, t) \frac{\partial}{\partial \bar{x}} m(\nu, x) dx \right) \\ &= \sigma^2 \int_{\mathbb{R}} m(\nu, x) \frac{\partial}{\partial \bar{x}} p(x, t) dx = \sigma^2 \int_{\mathbb{R}} \frac{x - \bar{x}(t)}{\sigma^2} m(\nu, x) p(x, t) dx \\ &= \int_{\mathbb{R}} (x - \bar{x})(m(\nu, x) - \bar{m}) p(x, t) dx = \text{Cov}_t(m, x), \end{aligned} \quad (30)$$

73 and

$$\begin{aligned} 2\sigma^4 \left(\frac{\partial \bar{m}}{\partial \sigma^2} - \overline{\frac{\partial m}{\partial \sigma^2}} \right) &= 2\sigma^4 \left(\frac{\partial}{\partial \sigma^2} \int_{\mathbb{R}} m(\nu, x) p(x, t) dx - \int_{\mathbb{R}} p(x, t) \frac{\partial}{\partial \sigma^2} m(\nu, x) dx \right) \\ &= 2\sigma^4 \int_{\mathbb{R}} \frac{(x - \bar{x})^2 - \sigma^2}{2\sigma^4} m(\nu, x) p(x, t) dx = \int_{\mathbb{R}} ((x - \bar{x})^2 - \sigma^2) (m(\nu, x) - \bar{m}) p(x, t) dx \\ &= \text{Cov}_t((x - \bar{x})^2, m). \end{aligned} \quad (31)$$

5 Comparing our treatment of white noise to Da Prato and Zabczyk (2014)

Our approach in the main text is inspired by the treatment provided in §4.2 of Da Prato and Zabczyk (2014). Here the authors develop a stochastic integral of operator-valued processes. In particular, they consider processes indexed by time $t \geq 0$ valued as Hilbert-Schmidt operators $\Phi(t)$ and define the norm

$$\|\Phi\|_t = \sqrt{\mathbb{E} \left(\int_0^t \text{Tr}[\Phi(s)\Phi^*(s)]ds \right)}, \quad t \geq 0. \quad (32)$$

In our case we only consider the so-called multiplication operators. That is, processes that consist of operators $\Phi(t)$ having the form $\Phi(t)g(x) = \varphi(x, t)g(x)$ such that $\varphi(\cdot, t) \in L^2(\mathbb{R})$ a.s. for each $t \geq 0$. In this case $\Phi(t) = \Phi^*(t)$ and

$$\|\Phi\|_t = \|\varphi\|_t = \sqrt{\mathbb{E} \left(\int_0^t \int_{\mathbb{R}} \varphi^2(x, s) dx ds \right)}, \quad t \geq 0. \quad (33)$$

Da Prato and Zabczyk (2014) form the space $\mathcal{N}_W^2(0, T)$ of Hilbert-Schmidt operator-valued predictable processes $\Phi(t)$ that satisfy $\|\Phi\|_T < +\infty$ for some $T > 0$. This corresponds to our more specialized space \mathcal{N}_2 that consists of $L^2(\mathbb{R})$ valued processes $\varphi(x, t)$ such that $\|\varphi\|_t < +\infty$ for all $t \geq 0$. In their treatment, $W(t)$ plays a similar role to our generalized process \mathbf{W}_t . For $\Phi \in \mathcal{N}_W^2(0, T)$, they denote the stochastic integral for $t \in [0, T]$ by $\Phi \cdot W(t)$. Hence, for $\Phi(t)g(x) = \varphi(x, t)g(x)$ as above, $\mathbf{W}_t(\varphi) = \Phi \cdot W(t)$. The authors then prove the following:

Proposition 4.28 *Assume that $\Phi_1, \Phi_2 \in \mathcal{N}_W^2(0, T)$. Then*

$$\mathbb{E}(\Phi_i \cdot W(t)) = 0, \quad \mathbb{E}(\|\Phi_i \cdot W(t)\|^2) < +\infty, \quad \forall t \in [0, T].$$

Corollary 4.29 *Under the same assumptions as Proposition 4.28,*

$$\mathbb{C}(\Phi_1 \cdot W(t), \Phi_2 \cdot W(s)) = \mathbb{E} \left(\int_0^{t \wedge s} \text{Tr}[\Phi_2(r)\Phi_1^*(r)]dr \right), \quad \forall t, s \in [0, T].$$

Simplifying these expressions for the multiplication operators described above returns equations (23) and (24) of the main text.

6 Simulating the rescaled process

Here we provide a detailed description of the branching random walk and how we have chosen to rescale it. We focus on the case

$$m(\nu, x) = r - \frac{a}{2}(\theta - x)^2 - c \int_{\mathbb{R}} \nu(x, t) dx. \quad (34)$$

6.1 Description of simulation

We begin by describing the branching random walk before introducing our scheme to rescale it. Our branching random walk follows closely the description of branching Brownian motion in the main text. However, we replace exponentially distributed lifetimes with deterministic unit time steps for easier implementation. Hence, we restrict time to $t = 0, 1, 2, \dots$, and so on. Furthermore, we allow individual fitness to depend on both trait value and the state of the entire population. For time t we write $\{\xi_1(t), \dots, \xi_{N(t)}(t)\}$ as the set of trait values across all $N(t)$ individuals alive in the population. Since our simulation follows discrete individuals instead of continuous distributions of trait values, we can write

$$\nu(x, t) = \sum_{i=1}^{N(t)} \delta(x - \xi_i(t)), \quad (35)$$

where $\delta(x - \xi_i(t))$ denotes the point mass located at $\xi_i(t)$. For simplicity we assume perfect heritability. At each iteration we draw, for each individual, a random number of offspring from a Negative-Binomial distribution. Recall the Negative-Binomial distribution models the number of failed Bernoulli trials that occur before a given number of successful trials. Denoting q the probability of success for each trial and s the number of successes, the mean and variance is given respectively by

$$\frac{s(1-q)}{q}, \frac{s(1-q)}{q^2}. \quad (36)$$

Then if we require the i th individual to have mean number offspring $\mathcal{W}(\nu, \xi_i)$ and variance equal to V , the parameters of the associated Negative-Binomial distribution become

$$q(\nu, \xi_i) = \frac{\mathcal{W}(\nu, \xi_i)}{V}, \quad s(\nu, \xi_i) = \frac{\mathcal{W}^2(\nu, \xi_i)}{V - \mathcal{W}(\nu, \xi_i)}. \quad (37)$$

This imposes the restriction $V > \mathcal{W}(\nu, \xi_i)$. For each offspring produced by the individual with trait value $\xi_i(t)$, we assign indepently drawn trait values normally distributed around $\xi_i(t)$ with variance μ . This summarizes the basic structure of our simulation. To impose selection and density dependent growth rates, we set

$$\mathcal{W}(\nu, \xi_i) = \exp \left(r - \frac{a}{2}(\theta - \xi_i)^2 - c \int_{\mathbb{R}} \nu(x, t) dx \right), \quad (38)$$

where the above integral becomes $\int_{\mathbb{R}} \nu(x, t) dx = \sum_{i=1}^{N(t)} 1 = N(t)$.

6.2 Rescaling

To rescale the branching random walk by a positive integer n , we rescale mutational variance by $\mu \rightarrow \mu/n$, time by $t \rightarrow t/n$ and the reproductive law by $V \rightarrow V$ and

$$\mathcal{W}(\nu, \xi_i) \rightarrow \mathcal{W}^{(n)}(\nu, \xi_i) = \exp \left(\frac{r}{n} - \frac{a}{2n}(\theta - \xi_i)^2 - \frac{c}{n^2}N(t) \right) = \exp \left(\frac{r}{n} - \frac{a}{2n}(\theta - \xi_i)^2 - \frac{c}{n}N^{(n)}(t) \right). \quad (39)$$

We also replace individual mass with $\frac{1}{n}$ and write rescaled abundance as $N^{(n)}(t) = \frac{1}{n}N(nt)$. When it exists, we denote by $N^{(\infty)}(t)$ the limiting process of $N^{(n)}(t)$. Then

$$\lim_{n \rightarrow \infty} n \left(\mathcal{W}^{(n)}(\nu, \xi_i) - 1 \right) = r - \frac{a}{2}(\theta - \xi_i)^2 - cN^{(\infty)}(t). \quad (40)$$

Note that, since the limiting fitness function is bounded above and decreases linearly with respect to $N^{(\infty)}(t)$, it satisfies the hypotheses of Champagnat, Ferrière and Méléard (2006). We have implemented this simulation in the programming language Julia. A copy can be found at the url:

<https://github.com/bobweek/branching.brownian.motion.and.spde>

For the sake of illustration, we simulated the unscaled process ($n = 1$) and the rescaled process with $n = 5$ and $n = 20$ for 50 units of time. Results are shown in Figure 2 of the main text.

7 Derivation of SDE for \bar{x} and σ^2

Picking up from §2.2.2 of the main text, we have

$$\tilde{x}(t) = \int_{\mathbb{R}} x \nu(x, t) dx, \quad \tilde{\sigma}^2(t) = \int_{\mathbb{R}} x^2 \nu(x, t) dx \quad (41)$$

and

$$\tilde{x}(t) = \tilde{x}(0) + \int_0^t \int_{\mathbb{R}} \nu(x, s) m(\nu, x) x + x \sqrt{V \nu(x, s)} \dot{W}(x, s) dx ds, \quad (42)$$

$$\tilde{\sigma}^2(t) = \tilde{\sigma}^2(0) + \int_0^t \int_{\mathbb{R}} \nu(x, s) (m(\nu, x) x^2 + \mu) + x^2 \sqrt{V \nu(x, s)} \dot{W}(x, s) dx ds. \quad (43)$$

7.1 Derivation for trait mean

We make use of the notation

$$\begin{cases} \|N\|_2 = \sqrt{V \int_{\mathbb{R}} \nu(x, t) dx} = \sqrt{VN} \\ \|\tilde{x}\|_2 = \sqrt{V \int_{\mathbb{R}} x^2 \nu(x, t) dx} \\ \langle \tilde{x}, N \rangle = V \int_{\mathbb{R}} x \nu(x, t) dx = \bar{x}VN. \end{cases} \quad (44)$$

Rewriting formula (42) as an SDE provides

$$d\tilde{x} = \left(\bar{x}mN + \frac{\mu}{2} \int_{\mathbb{R}} x \Delta \nu(x, t) dx \right) dt + \|\tilde{x}\|_2 d\tilde{W}_2, \quad (45)$$

where,

$$d\tilde{W}_2 = d\hat{\mathbf{W}}_t(\sqrt{Vx^2\nu}) = \frac{1}{\|\tilde{x}\|_2} \int_{\mathbb{R}} x \sqrt{V\nu(x, t)} \dot{W}(x, t) dx dt. \quad (46)$$

Using Itô's quotient rule on $\bar{x} = \tilde{x}/N$, we obtain

$$d\bar{x} = d\left(\frac{\tilde{x}}{N}\right) = \frac{\tilde{x}}{N} \left(\frac{d\tilde{x}}{\tilde{x}} - \frac{dN}{N} - \frac{d\tilde{x}}{\tilde{x}} \frac{dN}{N} + \left(\frac{dN}{N}\right)^2 \right) = \frac{d\tilde{x}}{N} - \bar{x} \frac{dN}{N} - \frac{d\tilde{x}}{N} \frac{dN}{N} + \bar{x} \left(\frac{dN}{N}\right)^2. \quad (47)$$

From Table 1 of the main text $d\tilde{x}dN = \langle \tilde{x}, N \rangle$ and $dN^2 = \|N\|_2^2$. Hence,

$$\begin{aligned} d\bar{x} &= \bar{x}m dt + \frac{\|\tilde{x}\|_2}{N} d\tilde{W}_2 - \bar{x} \left(\bar{m} dt + \sqrt{\frac{V}{N}} dW_1 \right) - \frac{\langle \tilde{x}, N \rangle}{N^2} dt + \bar{x} \frac{\|N\|_2^2}{N^2} dt \\ &= (\bar{x}m - \bar{x}\bar{m}) dt + \frac{\|\tilde{x}\|_2}{N} d\tilde{W}_2 - \bar{x} \sqrt{\frac{V}{N}} dW_1 - V \frac{\bar{x}}{N} dt + V \frac{\bar{x}}{N} dt \\ &= \text{Cov}_t(x, m) + \frac{\|\tilde{x}\|_2}{N} d\tilde{W}_2 - \bar{x} \sqrt{\frac{V}{N}} dW_1. \end{aligned} \quad (48)$$

Note that

$$\begin{aligned} \frac{\|\tilde{x}\|_2}{N} d\tilde{W}_2 - \bar{x} \sqrt{\frac{V}{N}} dW_1 &= \frac{1}{N} \int_{\mathbb{R}} x \sqrt{V\nu(x, t)} \dot{W}(x, t) dx - \frac{\bar{x}}{N} \int_{\mathbb{R}} \sqrt{V\nu(x, t)} \dot{W}(x, t) dx \\ &= \int_{\mathbb{R}} \frac{x - \bar{x}}{N} \sqrt{V\nu(x, t)} \dot{W}(x, t) dx \end{aligned} \quad (49)$$

and

$$\mathbb{V} \left(\int_{\mathbb{R}} \frac{x - \bar{x}}{N} \sqrt{V\nu(x, t)} \dot{W}(x, t) dx \right) = \frac{V}{N} \int_{\mathbb{R}} (x - \bar{x})^2 p(x, t) dx = V \frac{\sigma^2}{N}. \quad (50)$$

Hence, by setting

$$dW_2 = \frac{\int_{\mathbb{R}} \frac{(x-\bar{x})}{N} \sqrt{V\nu(x,t)} \dot{W}(x,t) dx}{\sqrt{V\sigma^2/N}} \quad (51)$$

we can write

$$d\bar{x} = \text{Cov}_t(x, m)dt + \sqrt{V \frac{\sigma^2}{N}} dW_2. \quad (52)$$

7.2 Derivation for trait variance

We make use of the notation

$$\begin{cases} \|\tilde{\sigma}^2\|_2 = \sqrt{V \int_{\mathbb{R}} x^4 \nu(x,t) dx} \\ \langle \tilde{\sigma}^2, N \rangle = V \int_{\mathbb{R}} x^2 \nu(x,t) dx = \overline{x^2} V N. \end{cases} \quad (53)$$

Applying formula (43) provides

$$d\tilde{\sigma}^2 = \left(\overline{x^2 m} N + \mu N \right) dt + \|\tilde{\sigma}^2\|_2 d\tilde{W}_3 \quad (54)$$

where

$$d\tilde{W}_3 = d\hat{\mathbf{W}}_t(\sqrt{V x^4 \nu}) = \frac{1}{\|\tilde{\sigma}^2\|_2} \int_{\mathbb{R}} x^2 \sqrt{V \nu(x,t)} \dot{W}(x,t) dx. \quad (55)$$

Using Itô's quotient rule on $\overline{x^2} = \tilde{\sigma}^2/N$, we obtain

$$d\overline{x^2} = d\left(\frac{\tilde{\sigma}^2}{N}\right) = \frac{\tilde{\sigma}^2}{N} \left(\frac{d\tilde{\sigma}^2}{\tilde{\sigma}^2} - \frac{dN}{N} - \frac{d\tilde{\sigma}^2}{\tilde{\sigma}^2} \frac{dN}{N} + \left(\frac{dN}{N}\right)^2 \right) = \frac{d\tilde{\sigma}^2}{N} - \overline{x^2} \frac{dN}{N} - \frac{d\tilde{\sigma}^2}{N} \frac{dN}{N} + \overline{x^2} \left(\frac{dN}{N}\right)^2. \quad (56)$$

Table 1 of the main text implies $d\tilde{W}_3 dW_1 = \langle \tilde{\sigma}^2, N \rangle$ and hence

$$\begin{aligned} d\overline{x^2} &= \left(\overline{x^2 m} + \mu \right) dt + \frac{\|\tilde{\sigma}^2\|_2}{N} d\tilde{W}_3 - \overline{x^2} \left(\bar{m} dt + \sqrt{\frac{V}{N}} dW_1 \right) - \frac{\langle \tilde{\sigma}^2, N \rangle}{N^2} dt + \overline{x^2} \frac{\|N\|_2^2}{N^2} dt \\ &= \left(\overline{x^2 m} - \overline{x^2} \bar{m} dt + \mu \right) dt + \frac{\|\tilde{\sigma}^2\|_2}{N} d\tilde{W}_3 - \overline{x^2} \sqrt{\frac{V}{N}} dW_1 - \overline{x^2} \frac{V}{N} dt + \overline{x^2} \frac{V}{N} dt \\ &= \left(\text{Cov}_t(x^2, m) + \mu \right) dt + \frac{\|\tilde{\sigma}^2\|_2}{N} d\tilde{W}_3 - \overline{x^2} \sqrt{\frac{V}{N}} dW_1. \end{aligned} \quad (57)$$

Setting $F(y, z) = y - z^2$, use Itô's formula on $\sigma^2 = F(\overline{x^2}, \bar{x}) = \overline{x^2} - \bar{x}^2$ to obtain:

$$\begin{aligned}
d\sigma^2 &= d\bar{x}^2 - 2\bar{x}d\bar{x} - (d\bar{x})^2 = \left(\text{Cov}_t(x^2, m) + \mu \right) dt + \frac{\|\tilde{\sigma}^2\|_2}{N} d\tilde{W}_3 - \bar{x}^2 \sqrt{\frac{V}{N}} dW_1 \\
&\quad - 2\bar{x} \left(\text{Cov}_t(x, m) + \mu dt + \sqrt{\frac{V\sigma^2}{N}} dW_2 \right) - \left(\text{Cov}_t(x, m) dt + \mu dt + \sqrt{\frac{V\sigma^2}{N}} dW_2 \right)^2 \\
&= \left(\text{Cov}_t(x^2 - 2\bar{x}x, m) + \mu \right) dt + \frac{\|\tilde{\sigma}^2\|_2}{N} d\tilde{W}_3 - \bar{x}^2 \sqrt{\frac{V}{N}} dW_1 - 2\bar{x} \sqrt{\frac{V\sigma^2}{N}} dW_2 - \left(\frac{V\sigma^2}{N} \right) dt \\
&= \left(\text{Cov}_t(x - \bar{x})^2, m \right) + \mu - \frac{V\sigma^2}{N} \right) dt + \frac{\|\tilde{\sigma}^2\|_2}{N} d\tilde{W}_3 - \bar{x}^2 \sqrt{\frac{V}{N}} dW_1 - 2\bar{x} \sqrt{\frac{V\sigma^2}{N}} dW_2. \quad (58)
\end{aligned}$$

145 In light of

$$\begin{aligned}
\frac{\|\tilde{\sigma}^2\|_2}{N} d\tilde{W}_3 - \bar{x}^2 \sqrt{\frac{V}{N}} dW_1 - 2\bar{x} \sqrt{\frac{V\sigma^2}{N}} dW_2 &= \frac{1}{N} \int_{\mathbb{R}} (x^2 - \bar{\sigma}^2 - 2\bar{x}(x - \bar{x})) \sqrt{V\nu(x, t)} \dot{W}(x, t) dx \\
&= \frac{1}{N} \int_{\mathbb{R}} ((x - \bar{x})^2 - \sigma^2) \sqrt{V\nu(x, t)} \dot{W}(x, t) dx \quad (59)
\end{aligned}$$

146 and

$$\begin{aligned}
\frac{1}{N} \int_{\mathbb{R}} ((x - \bar{x})^2 - \sigma^2) \sqrt{V\nu(x, s)}^2 dx &= \frac{V}{N} \left(\int_{\mathbb{R}} ((x - \bar{x})^4 - 2(x - \bar{x})^2 \sigma^2 + \sigma^4) p(x, t) dx \right) \\
&= \frac{V}{N} \left(\overline{(x - \bar{x})^4} - \sigma^4 \right) \quad (60)
\end{aligned}$$

147 we set

$$dW_3 = \frac{\int_{\mathbb{R}} ((x - \bar{x})^2 - \sigma^2) \sqrt{V\nu(x, t)} \dot{W}(x, t) dx}{V \left(\overline{(x - \bar{x})^4} - \sigma^4 \right)} \quad (61)$$

148 so that

$$d\sigma^2 = \text{Cov}_t((x - \bar{x})^2, m) dt + \left(\mu - V \frac{\sigma^2}{N} \right) dt + \sqrt{V \frac{\overline{(x - \bar{x})^4} - \sigma^4}{N}} dW_3. \quad (62)$$

149 Table 1 of the main text implies

$$dW_1 dW_2 = \frac{\int_{\mathbb{R}} (x - \bar{x}) \nu(x, t) dx}{\sqrt{N\sigma^2}} dt = 0, \quad (63)$$

$$dW_1 dW_3 = \frac{\int_{\mathbb{R}} ((x - \bar{x})^2 - \sigma^2) \nu(x, t) dx}{\sqrt{\overline{(x - \bar{x})^4} - \sigma^4}} dt = 0, \quad (64)$$

$$dW_2 dW_3 = \frac{\int_{\mathbb{R}} (x - \bar{x}) ((x - \bar{x})^2 - \sigma^2) p(x, t) dx}{\sqrt{\sigma^2 ((x - \bar{x})^4 - \sigma^4)}} dt = \frac{N(\bar{x} - \bar{x})^3}{\sqrt{\sigma^2 ((x - \bar{x})^4 - \sigma^4)}} dt. \quad (65)$$

150 In particular, when p is a Gaussian curve $dW_2 dW_3 = 0$.

151 8 Relating fitness of expressed traits to fitness of breeding values

152

153 Following §2.3.2 of the main text, we have $\sigma^2 = G + \eta$ and

$$m^*(\rho, g) = \int_{\mathbb{R}} m(\nu, x) \psi(x, g) dx. \quad (66)$$

154 Hence,

$$\begin{aligned} \frac{\partial m^*}{\partial \bar{x}} &= \int_{\mathbb{R}} \frac{\rho(g, t)}{N(t)} \frac{\partial}{\partial \bar{x}} \int_{\mathbb{R}} m(\nu, x) \psi(x, g) dx dg = \\ &\int_{\mathbb{R}} \int_{\mathbb{R}} \frac{\rho(g, t)}{N(t)} \psi(x, g) dg \frac{\partial}{\partial \bar{x}} m(\nu, x) dx = \int_{\mathbb{R}} p(x, t) \frac{\partial}{\partial \bar{x}} m(\nu, x) dx = \frac{\partial m}{\partial \bar{x}} \end{aligned} \quad (67)$$

155 and

$$\begin{aligned} \frac{\partial m^*}{\partial G} &= \int_{\mathbb{R}} \frac{\rho(g, t)}{N(t)} \frac{\partial}{\partial G} \int_{\mathbb{R}} m(\nu, x) \psi(x, g) dx dg = \int_{\mathbb{R}} \int_{\mathbb{R}} \frac{\rho(g, t)}{N(t)} \psi(x, g) dg \frac{\partial m}{\partial G} dx = \\ &\int_{\mathbb{R}} p(x, t) \frac{\partial m}{\partial \sigma^2} \frac{\partial \sigma^2}{\partial G} dx = \frac{\partial m}{\partial \sigma^2}. \end{aligned} \quad (68)$$

156 9 Derivation of diffuse coevolution model

157 In this section we provide a derivation of our model of diffuse coevolution driven by competition. Since
158 most of the work in this derivation has already been completed in Supplementary Material §7, we focus here
159 on deriving the Malthusian fitness m as a function of trait value x . We begin with discrete populations of
160 individuals. In particular, we begin by assuming population size n_i is an integer for each species $i = 1, \dots, S$
161 before passing to the large population size limit.

162 The reduction in fitness for an individual of species i caused by competition is captured multiplicatively
163 by $0 < C_i \leq 1$. Biologically this assumes all competitors affect individuals of a given species equally by
164 consuming the same amount of resources. This is a mean-field interaction since any individual that consumes
165 resources has an effect on the fitness of all other individuals competing for the same resources. Denote by x_{ij}
166 the trait value of the j -th individual belonging to species i . The set of trait values across all individuals in the
167 community at time $t \geq 0$ is written $X = \{x_{ij}\}$. We denote by \mathcal{B}_{ij} a function that maps X to the cumulative
168 effect of all competitive interactions on the fitness of the j -th individual in species i . Since individuals do
169 not compete with themselves the net multiplicative effects on fitness of both interspecific and intraspecific
170 competition on the j -th individual in species i can be summarized by

$$\mathcal{B}_{ij}(X) = C_i^{\sum_{l \neq j} \mathcal{O}_{ii}(x_{ij} - x_{il}) + \sum_{k \neq i} \sum_{l=1}^{n_k} \mathcal{O}_{ik}(x_{ij} - x_{kl})}, \quad (69)$$

where \mathcal{O}_{ij} , defined in the main text, measures the overlap in resource use between individuals of species i and j as a function of their niche-centers. Writing $\mathcal{W}_{ij}(X)$ as the average number of offspring left by the j -th individual of species i , we have

$$\mathcal{W}_{ij}(X) = \mathcal{A}_i(x_{ij})\mathcal{B}_{ij}(X), \quad (70)$$

where $\mathcal{A}_i(x) = \int_{\mathbb{R}} e_i(\zeta)u_i(\zeta, x)d\zeta$ accounts for abiotic selection and e_i has been defined in the main text.

We now turn to a diffusion limit. Since we have more than one population, we take the diffusion limit for each population one at a time starting with population 1. We write $\mathbf{n} = (n_1, \dots, n_S)$. Following Méléard and Roelly (1993, 1992) we rescale generation time and individual mass to $\frac{1}{n_1}$ and mean of the reproductive law to

$$\mathcal{W}_{1j}^{(\mathbf{n})}(X) = \mathcal{A}_1(x_{1j})^{1/n_1} \exp \left(\frac{\ln C_1}{n_1^2} \sum_{l \neq j} \mathcal{O}_{1l}(x_{1j} - x_{1l}) + \frac{\ln C_1}{n_1} \sum_{k \neq i} \frac{1}{n_k} \sum_{l=1}^{n_k} \mathcal{O}_{1k}(x_{1j} - x_{kl}) \right). \quad (71)$$

For large n_1 , we have the approximation

$$\mathcal{W}_{1j}^{(\mathbf{n})}(X) \approx \mathcal{A}_1(x_{1j})^{1/n_1} \left(1 + \frac{\ln C_1}{n_1^2} \sum_{l \neq j} \mathcal{O}_{1l}(x_{1j} - x_{1l}) + \frac{\ln C_1}{n_1} \sum_{k \neq i} \frac{1}{n_k} \sum_{l=1}^{n_k} \mathcal{O}_{1k}(x_{1j} - x_{kl}) \right). \quad (72)$$

Hence

$$\lim_{n_1 \rightarrow \infty} n_1 \left(\mathcal{W}_{1j}^{(\mathbf{n})}(X) - 1 \right) = \ln \mathcal{A}_1(x_{1j}) + \left(\int_{\mathbb{R}} \mathcal{O}_{1l}(x_{1j} - y) \nu_1(y, t) dy + \sum_{k \neq 1} \frac{1}{n_k} \sum_{l=1}^{n_k} \mathcal{O}_{1k}(x_{1j} - x_{kl}) \right) \ln C_1. \quad (73)$$

We write $\lim_{\mathbf{n} \rightarrow \infty}$ for the iterated limit $\lim_{n_S \rightarrow \infty} \dots \lim_{n_1 \rightarrow \infty}$ and, assuming $\nu_i(\cdot, t) \in C_1^+(\mathbb{R})$ for $i = 1, \dots, S$ and $t \in [0, \infty)$, we set $\boldsymbol{\nu} = (\nu_1, \dots, \nu_S)$. Then, for any $\boldsymbol{\nu}$, the the diffusion limits for the remaining populations provides the Malthusian parameter for individuals in species i with trait value x_{1j} as

$$m_1(\boldsymbol{\nu}, x_{1j}) := \lim_{\mathbf{n} \rightarrow \infty} n_1 \left(\mathcal{W}_{1j}^{(\mathbf{n})}(X) - 1 \right) = \ln \mathcal{A}_1(x) + \left(\sum_{k=1}^S \int_{\mathbb{R}} \mathcal{O}_{1k}(x_{1j} - y) \nu_k(y, t) dy \right) \ln C_1. \quad (74)$$

We compute the average niche overlap of an individual in species i with nich location x across all individuals in species j as

$$\bar{\mathcal{O}}_{ij}(x, t) = \frac{\int_{\mathbb{R}} \mathcal{O}_{ij}(x - y) \nu_j(y, t) dy}{\int_{\mathbb{R}} \nu_j(y, t) dy}. \quad (75)$$

We now assume the resource utilization curves $u_i(\zeta)$ and phenotypic densities $\nu_i(x, t)$ are Gaussian curves for $i = 1, \dots, S$. In this case $\bar{\mathcal{O}}_{ij}(x, t)$ simplifies to

$$\bar{\mathcal{O}}_{ij}(x, t) = \frac{\int_{\mathbb{R}} \mathcal{O}_{ij}(x - y) \nu_j(y, t) dy}{\int_{\mathbb{R}} \nu_j(y, t) dy} = \frac{U_i U_j}{\sqrt{2\pi(w_i + w_j + \sigma_j^2(t))}} \exp \left(-\frac{(x - \bar{x}_j(t))^2}{2(w_i + w_j + \sigma_j^2(t))} \right). \quad (76)$$

187 Setting

$$\sigma_i^2(t) = G_i(t) + \eta_i, \quad (77a)$$

$$R_i = \ln \left(\frac{Q_i U_i}{\sqrt{1 + A_i w_i}} \right), \quad (77b)$$

$$a_i = \frac{A_i}{1 + A_i w_i}, \quad (77c)$$

$$\tilde{b}_{ij}(t) = \frac{1}{w_i + w_j + \sigma_j^2(t)}, \quad (77d)$$

$$c_i = -\ln C_i, \quad (77e)$$

188 we get

$$m_i(\boldsymbol{\nu}, x) = R_i - \frac{a_i}{2}(x - \theta_i)^2 - c_i \sum_{j=1}^S N_j(t) U_i U_j \sqrt{\frac{\tilde{b}_{ij}(t)}{2\pi}} e^{-\frac{\tilde{b}_{ij}(t)}{2}(x - \bar{x}_j(t))^2}. \quad (78)$$

189 Hence, our fitness function is bounded above and decreases linearly with total abundance, as required by the
 190 assumptions of Champagnat, Ferrière and Méléard (2006). For the remainder of the derivation we suppress
 191 notation indicating dependency on $\boldsymbol{\nu}$, x and t . From (78) we calculate

$$\frac{\partial m_i}{\partial \bar{x}_i} = c_i N_i U_i^2 \tilde{b}_{ii}(x - \bar{x}_i) \sqrt{\frac{\tilde{b}_{ii}}{2\pi}} e^{-\frac{\tilde{b}_{ii}}{2}(x - \bar{x}_i)^2} \quad (79)$$

$$\begin{aligned} \frac{\partial m_i}{\partial G_i} &= \frac{c_i N_i U_i^2}{2} \left(\frac{(x - \bar{x}_i)^2 - G_i - \eta_i - 2w_i}{(G_i + \eta_i + 2w_i)^2} \right) \sqrt{\frac{\tilde{b}_{ii}}{2\pi}} e^{-\frac{\tilde{b}_{ii}}{2}(x - \bar{x}_i)^2} \\ &= \frac{c_i N_i U_i^2 \tilde{b}_{ii}^2}{2} ((x - \bar{x}_i)^2 - \sigma_i^2 - 2w_i) \sqrt{\frac{\tilde{b}_{ii}}{2\pi}} e^{-\frac{\tilde{b}_{ii}}{2}(x - \bar{x}_i)^2}. \end{aligned} \quad (80)$$

192 Note that

$$\begin{aligned} &\sqrt{\frac{\tilde{b}_{ii}}{2\pi}} \exp \left(-\frac{\tilde{b}_{ii}}{2}(x - \bar{x}_i)^2 \right) \sqrt{\frac{1}{2\pi\sigma_i^2}} \exp \left(-\frac{(x - \bar{x}_i)^2}{2\sigma_i^2} \right) \\ &= \sqrt{\frac{1}{2\pi(\sigma_i^2 + 1/\tilde{b}_{ii})}} \sqrt{\frac{\sigma_i^2 + 1/\tilde{b}_{ii}}{2\pi\sigma_i^2/\tilde{b}_{ii}}} \exp \left(-\frac{\sigma_i^2 + 1/\tilde{b}_{ii}}{2\sigma_i^2/\tilde{b}_{ii}}(x - \bar{x}_i)^2 \right) \\ &= \sqrt{\frac{1}{4\pi(\sigma_i^2 + w_i)}} \sqrt{\frac{2(\sigma_i^2 + w_i)}{2\pi\sigma_i^2(\sigma_i^2 + 2w_i)}} \exp \left(-\frac{\sigma_i^2(\sigma_i^2 + 2w_i)}{4(\sigma_i^2 + w_i)}(x - \bar{x}_i)^2 \right). \end{aligned} \quad (81)$$

193 Hence,

$$\overline{\frac{\partial m_i}{\partial \bar{x}_i}} = 0, \quad (82)$$

$$\begin{aligned}\frac{\partial \bar{m}_i}{\partial G_i} &= \frac{c_i N_i U_i^2}{2(\sigma_i^2 + 2w_i)^2} \left(\frac{(\sigma_i^2 + 2w_i)\sigma_i^2}{2(w_i + \sigma_i^2)} - \sigma_i^2 - 2w_i \right) \sqrt{\frac{b_{ii}}{2\pi}} \\ &= \frac{c_i N_i U_i^2}{2(\sigma_i^2 + 2w_i)} \left(\frac{\sigma_i^2}{2(\sigma_i^2 + w_i)} - 1 \right) \sqrt{\frac{b_{ii}}{2\pi}} = -\frac{c_i N_i U_i^2 b_{ii}}{2} \sqrt{\frac{b_{ii}}{2\pi}},\end{aligned}\quad (83)$$

194 where

$$b_{ij} = \frac{1}{w_i + w_j + \sigma_i^2 + \sigma_j^2}. \quad (84)$$

195 The average fitness for species i is

$$\bar{m}_i = R_i - \frac{a_i}{2} \left((\bar{x}_i - \theta_i)^2 + G_i + \eta_i \right) - c_i \sum_{j=1}^S N_j U_i U_j \sqrt{\frac{b_{ij}}{2\pi}} e^{-\frac{b_{ij}}{2} (\bar{x}_i - \bar{x}_j)^2}. \quad (85)$$

196 Thus,

$$\frac{\partial \bar{m}_i}{\partial \bar{x}_i} = a_i (\theta_i - \bar{x}_i) - c_i \sum_j N_j U_i U_j b_{ij} (\bar{x}_j - \bar{x}_i) \sqrt{\frac{b_{ij}}{2\pi}} e^{-\frac{b_{ij}}{2} (\bar{x}_i - \bar{x}_j)^2}, \quad (86)$$

$$\frac{\partial \bar{m}_i}{\partial G_i} = -\frac{a_i}{2} + \frac{c_i}{2} \sum_{j=1}^S N_j U_i U_j b_{ij} (1 - b_{ij} (\bar{x}_i - \bar{x}_j)^2) \sqrt{\frac{b_{ij}}{2\pi}} e^{-\frac{b_{ij}}{2} (\bar{x}_i - \bar{x}_j)^2}. \quad (87)$$

197 In particular

$$\frac{\partial \bar{m}_i}{\partial G_i} - \frac{\partial \bar{m}_i}{\partial G_i} = -\frac{a_i}{2} + \frac{c_i}{2} \left(N_i U_i^2 b_{ii} \sqrt{\frac{b_{ii}}{2\pi}} + \sum_{j=1}^S N_j U_i U_j b_{ij} (1 - b_{ij} (\bar{x}_i - \bar{x}_j)^2) \sqrt{\frac{b_{ij}}{2\pi}} e^{-\frac{b_{ij}}{2} (\bar{x}_i - \bar{x}_j)^2} \right). \quad (88)$$

198 Applying equations (37a), (47a) and (47b) of the main text recovers system (52) of the main text.

199 **10 The relation between competition coefficients and selection**

200 **10.1 Derivation of analytical approximations**

201 Just as with most calculations in this work, the derivations are straightforward applications of Gaussian
202 products. That is, if

$$f_1(x) = \frac{1}{\sqrt{2\pi\sigma_1^2}} \exp\left(-\frac{(\mu_1 - x)^2}{2\sigma_1^2}\right), \quad f_2(x) = \frac{1}{\sqrt{2\pi\sigma_2^2}} \exp\left(-\frac{(\mu_2 - x)^2}{2\sigma_2^2}\right), \quad (89)$$

203 then

$$f_1(x)f_2(x) = \frac{1}{\sqrt{2\pi(\sigma_1^2 + \sigma_2^2)}} \exp\left(-\frac{(\mu_1 - \mu_2)^2}{2(\sigma_1^2 + \sigma_2^2)}\right) \frac{1}{\sqrt{2\pi\tilde{\sigma}^2}} \exp\left(-\frac{(\tilde{\mu} - x)^2}{2\tilde{\sigma}^2}\right), \quad (90)$$

204 where

$$\tilde{\mu} = \frac{\sigma_2^2 \mu_1 + \sigma_1^2 \mu_2}{\sigma_1^2 + \sigma_2^2}, \quad \tilde{\sigma}^2 = \frac{\sigma_1^2 \sigma_2^2}{\sigma_1^2 + \sigma_2^2}. \quad (91)$$

205 **10.1.1 Caclulating $\text{Cov}_{f_{\bar{X}}}(\alpha, \gamma)$**

206 Recalling

$$\alpha(\bar{x}_i, \bar{x}_j) = \frac{c}{\bar{r}} \sqrt{\frac{b}{2\pi}} \exp\left(-\frac{b}{2}(\bar{x}_i - \bar{x}_j)^2\right), \quad (92)$$

$$\gamma(\bar{x}_i, \bar{x}_j) = cNb \left(1 - b(\bar{x}_i - \bar{x}_j)^2\right) \sqrt{\frac{b}{2\pi}} \exp\left(-\frac{b}{2}(\bar{x}_i - \bar{x}_j)^2\right), \quad (93)$$

207 we have

$$\begin{aligned} \bar{\alpha} &= \int_{\mathbb{R}} \int_{\mathbb{R}} \alpha(\bar{x}_i, \bar{x}_j) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j \\ &= \frac{c}{\bar{r}} \int_{\mathbb{R}} \frac{1}{\sqrt{2\pi(b^{-1} + V_{\bar{X}})}} \exp\left(-\frac{(\bar{x} - \bar{x}_j)^2}{2(b^{-1} + V_{\bar{X}})}\right) f_{\bar{X}}(\bar{x}_j) d\bar{x}_j = \frac{c/\bar{r}}{\sqrt{2\pi(b^{-1} + 2V_{\bar{X}})}}, \end{aligned} \quad (94)$$

$$\begin{aligned} \bar{\gamma} &= \int_{\mathbb{R}} \int_{\mathbb{R}} \gamma(\bar{x}_i, \bar{x}_j) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j \\ &= cNb \int_{\mathbb{R}} \left\{ 1 - \left[\left(\frac{\bar{x} + bV_{\bar{X}}\bar{x}_j}{1 + bV_{\bar{X}}} - \bar{x}_j \right)^2 + \frac{V_{\bar{X}}}{1 + bV_{\bar{X}}} \right] \right\} \frac{1}{\sqrt{2\pi(b^{-1} + V_{\bar{X}})}} \exp\left(-\frac{(\bar{x} - \bar{x}_j)^2}{2(b^{-1} + V_{\bar{X}})}\right) f_{\bar{X}}(\bar{x}_j) d\bar{x}_j \\ &= cNb \int_{\mathbb{R}} \left\{ 1 - \left[\left(\frac{\bar{x} - \bar{x}_j}{1 + bV_{\bar{X}}} \right)^2 + \frac{V_{\bar{X}}}{1 + bV_{\bar{X}}} \right] \right\} \frac{1}{\sqrt{2\pi(b^{-1} + V_{\bar{X}})}} \exp\left(-\frac{(\bar{x} - \bar{x}_j)^2}{2(b^{-1} + V_{\bar{X}})}\right) f_{\bar{X}}(\bar{x}_j) d\bar{x}_j \\ &= cNb \left(1 - \frac{(1 + bV_{\bar{X}})V_{\bar{X}}}{1 + 2bV_{\bar{X}}} \frac{1}{(1 + bV_{\bar{X}})^2} - \frac{V_{\bar{X}}}{1 + bV_{\bar{X}}} \right) \frac{1}{\sqrt{2\pi(b^{-1} + 2V_{\bar{X}})}} \\ &= cNb \left[1 - \left(\frac{1}{1 + 2bV_{\bar{X}}} + 1 \right) \frac{V_{\bar{X}}}{1 + bV_{\bar{X}}} \right] \frac{1}{\sqrt{2\pi(b^{-1} + 2V_{\bar{X}})}} \\ &= cNb \left(1 - \frac{2V_{\bar{X}}}{1 + 2bV_{\bar{X}}} \right) \sqrt{\frac{b}{2\pi(1 + 2bV_{\bar{X}})}}, \end{aligned} \quad (95)$$

$$\begin{aligned} \text{Var}_{f_{\bar{X}}}(\alpha) &= \int_{\mathbb{R}} \int_{\mathbb{R}} (\bar{\alpha} - \alpha(\bar{x}_i, \bar{x}_j))^2 f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j \\ &= \frac{c^2}{\bar{r}^2} \left(\sqrt{\frac{b}{4\pi}} \int_{\mathbb{R}} \int_{\mathbb{R}} \sqrt{\frac{b}{\pi}} \exp(-b(\bar{x}_i - \bar{x}_j)^2) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j - \frac{1}{2\pi(b^{-1} + 2V_{\bar{X}})} \right) \\ &= \frac{c^2}{\bar{r}^2} \left(\sqrt{\frac{b}{4\pi}} \int_{\mathbb{R}} \sqrt{\frac{1}{2\pi(\frac{1}{2b} + V_{\bar{X}})}} \exp(-b(\bar{x} - \bar{x}_j)^2) f_{\bar{X}}(\bar{x}_j) d\bar{x}_j - \frac{1}{2\pi(b^{-1} + 2V_{\bar{X}})} \right) \\ &= \frac{c^2}{\bar{r}^2} \left(\sqrt{\frac{b}{4\pi}} \sqrt{\frac{1}{2\pi(\frac{1}{2b} + 2V_{\bar{X}})}} - \frac{1}{2\pi(b^{-1} + 2V_{\bar{X}})} \right) = \frac{c^2 b}{2\pi \bar{r}^2} \left(\frac{1}{\sqrt{1 + 4bV_{\bar{X}}}} - \frac{1}{1 + 2bV_{\bar{X}}} \right), \end{aligned} \quad (96)$$

$$\begin{aligned}
\text{Cov}_{f_{\bar{X}}}(\alpha, \gamma) &= \int_{\mathbb{R}} \int_{\mathbb{R}} (\bar{\alpha} - \alpha(\bar{x}_i, \bar{x}_j)) (\bar{\gamma} - \gamma(\bar{x}_i, \bar{x}_j)) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j \\
&= \frac{c^2 N b}{2\bar{r}} \sqrt{\frac{b}{\pi}} \int_{\mathbb{R}} \int_{\mathbb{R}} (1 - b(\bar{x}_i - \bar{x}_j)^2) \sqrt{\frac{b}{\pi}} \exp(-b(\bar{x}_i - \bar{x}_j)^2) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j - \bar{\alpha} \bar{\gamma} \\
&= \frac{c^2 N b}{2\bar{r}} \sqrt{\frac{b}{\pi}} \frac{1 - 2bV_{\bar{X}}}{\sqrt{2\pi((2b)^{-1} + 2V_{\bar{X}})}} - \frac{c^2 N b}{\bar{r}} \frac{1 - 2bV_{\bar{X}}}{2\pi(b^{-1} + 2V_{\bar{X}})} \\
&= \frac{c^2 b^2 N}{2\pi\bar{r}} (1 - 2bV_{\bar{X}}) \left(\frac{1}{\sqrt{1 + 4bV_{\bar{X}}}} - \frac{1}{1 + 2bV_{\bar{X}}} \right). \quad (97)
\end{aligned}$$

208 **10.1.2 Caclulating $\text{Cov}_{f_{\bar{X}}}(\alpha, |\beta|)$**

209 To calculate moments of $|\beta|$ we note that, as a random variable, $|\beta|$ takes a folded normal distribution. Setting
210 $\Phi(x)$ equal to the cumulative density function of the standard normal distribution and using the properties of
211 the folded normal distribution, we find

$$|\bar{\beta}| = \sqrt{\frac{2\text{Var}_{f_{\bar{X}}}(\beta)}{\pi}} \exp\left(-\frac{\bar{\beta}^2}{2\text{Var}_{f_{\bar{X}}}(\beta)}\right) - \bar{\beta} \left[1 - 2\Phi\left(\frac{\bar{\beta}}{\sqrt{\text{Var}_{f_{\bar{X}}}(\beta)}}\right)\right] \quad (98)$$

$$\text{Var}_{f_{\bar{X}}}(|\beta|) = \bar{\beta}^2 + \text{Var}_{f_{\bar{X}}}(\beta) - |\bar{\beta}|^2. \quad (99)$$

212 Recall that

$$\beta(\bar{x}_i, \bar{x}_j) = cNb(\bar{x}_i - \bar{x}_j) \sqrt{\frac{b}{2\pi}} \exp\left(-\frac{b}{2}(\bar{x}_i - \bar{x}_j)^2\right) \quad (100)$$

213 and hence

$$\begin{aligned}
\bar{\beta} &= \int_{\mathbb{R}} \int_{\mathbb{R}} \beta(\bar{x}_i, \bar{x}_j) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j \\
&= cNb \int_{\mathbb{R}} (\bar{x} - \bar{x}_j) \frac{1}{\sqrt{2\pi(b^{-1} + V_{\bar{X}})}} \exp\left(-\frac{(\bar{x} - \bar{x}_j)^2}{2(b^{-1} + V_{\bar{X}})}\right) f_{\bar{X}}(\bar{x}_j) d\bar{x}_j = 0, \quad (101)
\end{aligned}$$

$$\begin{aligned}
\text{Var}_{f_{\bar{X}}}(\beta) &= \int_{\mathbb{R}} \int_{\mathbb{R}} (\bar{\beta} - \beta(\bar{x}_i, \bar{x}_j))^2 f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j \\
&= \int_{\mathbb{R}} \int_{\mathbb{R}} c^2 N^2 b^2 (\bar{x}_i - \bar{x}_j)^2 \frac{b}{2\pi} \exp(-b(\bar{x}_i - \bar{x}_j)^2) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j \\
&= \sqrt{\frac{b}{4\pi}} c^2 N^2 b^2 \int_{\mathbb{R}} \left[\left(\frac{\bar{x} + 2bV_{\bar{X}}\bar{x}_j}{1 + 2bV_{\bar{X}}} - \bar{x}_j \right)^2 + \frac{V_{\bar{X}}}{1 + 2bV_{\bar{X}}} \right] \frac{\exp\left(-\frac{(\bar{x} - \bar{x}_j)^2}{2(\frac{1}{2b} + V_{\bar{X}})}\right)}{\sqrt{2\pi(\frac{1}{2b} + V_{\bar{X}})}} f_{\bar{X}}(\bar{x}_j) d\bar{x}_j \\
&= \sqrt{\frac{b}{4\pi}} c^2 N^2 b^2 \int_{\mathbb{R}} \left[\frac{(\bar{x} - \bar{x}_j)^2}{(1 + 2bV_{\bar{X}})^2} + \frac{V_{\bar{X}}}{1 + 2bV_{\bar{X}}} \right] \frac{\exp\left(-\frac{(\bar{x} - \bar{x}_j)^2}{2(\frac{1}{2b} + V_{\bar{X}})}\right)}{\sqrt{2\pi(\frac{1}{2b} + V_{\bar{X}})}} f_{\bar{X}}(\bar{x}_j) d\bar{x}_j \\
&= \sqrt{\frac{b}{4\pi}} c^2 N^2 b^2 \left[\frac{(1 + 2bV_{\bar{X}})V_{\bar{X}}}{1 + 4bV_{\bar{X}}} \frac{1}{(1 + 2bV_{\bar{X}})^2} + \frac{V_{\bar{X}}}{1 + 2bV_{\bar{X}}} \right] \frac{1}{\sqrt{2\pi(\frac{1}{2b} + 2V_{\bar{X}})}} \\
&= \frac{b}{\pi} \frac{c^2 N^2 b^2}{\sqrt{1 + 4bV_{\bar{X}}}} \frac{V_{\bar{X}}}{1 + 2bV_{\bar{X}}} \left(\frac{1}{1 + 4bV_{\bar{X}}} + 1 \right) = \frac{2c^2 N^2 b^3 V_{\bar{X}}}{\pi(1 + 4bV_{\bar{X}})^{3/2}}. \quad (102)
\end{aligned}$$

214 Thus, using properties of the folded normal distribution, we find

$$|\bar{\beta}| = \sqrt{\frac{2}{\pi}} \frac{cNb^{3/2}}{(1 + 4bV_{\bar{X}})^{3/4}} \sqrt{\frac{2V_{\bar{X}}}{\pi}} = \frac{2}{\pi} \frac{cNb^{3/2}}{(1 + 4bV_{\bar{X}})^{3/4}} \sqrt{V_{\bar{X}}}, \quad (103)$$

$$\text{Var}_{f_{\bar{X}}}(|\beta|) = \frac{c^2 N^2 b^3}{(1 + 4bV_{\bar{X}})^{3/2}} \frac{2V_{\bar{X}}}{\pi} \left(1 - \frac{2}{\pi} \right). \quad (104)$$

215 We also calculate

$$\begin{aligned}
\text{Cov}_{f_{\bar{X}}}(\alpha, \beta) &= \int_{\mathbb{R}} \int_{\mathbb{R}} (\bar{\alpha} - \alpha(\bar{x}_i, \bar{x}_j))(\bar{\beta} - \beta(\bar{x}_i, \bar{x}_j)) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j \\
&= \frac{c^2 Nb}{2\bar{r}} \sqrt{\frac{b}{\pi}} \int_{\mathbb{R}} \int_{\mathbb{R}} (\bar{x}_i - \bar{x}_j) \sqrt{\frac{b}{\pi}} \exp(-b(\bar{x}_i - \bar{x}_j)^2) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j = 0. \quad (105)
\end{aligned}$$

216 In attempt to calculate $\text{Cov}_{f_{\bar{X}}}(\alpha, |\beta|)$ we find

$$\begin{aligned}
\text{Cov}_{f_{\bar{X}}}(\alpha, |\beta|) &= \int_{\mathbb{R}} \int_{\mathbb{R}} \alpha(\bar{x}_i, \bar{x}_j) |\beta(\bar{x}_i, \bar{x}_j)| f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j - \bar{\alpha} |\bar{\beta}| \\
&= \int_{\mathbb{R}} \int_{\mathbb{R}} \frac{c}{\bar{r}} \sqrt{\frac{b}{2\pi}} \exp\left(-\frac{b}{2}(\bar{x}_i - \bar{x}_j)^2\right) cNb |\bar{x}_i - \bar{x}_j| \sqrt{\frac{b}{2\pi}} \exp\left(-\frac{b}{2}(\bar{x}_i - \bar{x}_j)^2\right) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j - \bar{\alpha} |\bar{\beta}| \\
&= \frac{c^2 Nb}{\bar{r}} \sqrt{\frac{b}{4\pi}} \int_{\mathbb{R}} \int_{\mathbb{R}} |\bar{x}_i - \bar{x}_j| \sqrt{\frac{b}{\pi}} \exp(-b(\bar{x}_i - \bar{x}_j)^2) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j - \bar{\alpha} |\bar{\beta}|. \quad (106)
\end{aligned}$$

217 Just as we used the folded normal to find $|\bar{\beta}|$ and $\text{Var}_{f_{\bar{X}}}(|\beta|)$, we can calculate $\text{Cov}_{f_{\bar{X}}}(\alpha, |\beta|)$ by considering

$$\int_{\mathbb{R}} \int_{\mathbb{R}} (\bar{x}_i - \bar{x}_j) \sqrt{\frac{b}{\pi}} \exp(-b(\bar{x}_i - \bar{x}_j)^2) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j = 0 \quad (107)$$

218 and

$$\begin{aligned}
& \int_{\mathbb{R}} \int_{\mathbb{R}} (\bar{x}_i - \bar{x}_j)^2 \frac{b}{\pi} \exp(-2b(\bar{x}_i - \bar{x}_j)^2) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j \\
&= \sqrt{\frac{2b}{\pi}} \int_{\mathbb{R}} \int_{\mathbb{R}} (\bar{x}_i - \bar{x}_j)^2 \frac{1}{\sqrt{2\pi \frac{1}{4b}}} \exp\left(-\frac{(\bar{x}_i - \bar{x}_j)^2}{2 \frac{1}{4b}}\right) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j \\
&= \sqrt{\frac{2b}{\pi}} \int_{\mathbb{R}} \left[\left(\frac{\bar{x} + 4bV_{\bar{X}}\bar{x}_j}{1 + 4bV_{\bar{X}}} - \bar{x}_j \right)^2 + \frac{V_{\bar{X}}}{1 + 4bV_{\bar{X}}} \right] \frac{1}{\sqrt{2\pi(\frac{1}{4b} + V_{\bar{X}})}} \exp\left(-\frac{(\bar{x} - \bar{x}_j)^2}{2(\frac{1}{4b} + V_{\bar{X}})}\right) f_{\bar{X}}(\bar{x}_j) d\bar{x}_j \\
&= \sqrt{\frac{2b}{\pi}} \int_{\mathbb{R}} \left[\left(\frac{\bar{x} - \bar{x}_j}{1 + 4bV_{\bar{X}}} \right)^2 + \frac{V_{\bar{X}}}{1 + 4bV_{\bar{X}}} \right] \frac{1}{\sqrt{2\pi(\frac{1}{4b} + V_{\bar{X}})}} \exp\left(-\frac{(\bar{x} - \bar{x}_j)^2}{2(\frac{1}{4b} + V_{\bar{X}})}\right) f_{\bar{X}}(\bar{x}_j) d\bar{x}_j \\
&= \sqrt{\frac{2b}{\pi}} \left[\frac{(1 + 4bV_{\bar{X}})V_{\bar{X}}}{1 + 8bV_{\bar{X}}} \frac{1}{(1 + 4bV_{\bar{X}})^2} + \frac{V_{\bar{X}}}{1 + 4bV_{\bar{X}}} \right] \frac{1}{\sqrt{2\pi(\frac{1}{4b} + 2V_{\bar{X}})}} \\
&= \sqrt{\frac{2b}{\pi}} \frac{2V_{\bar{X}}}{1 + 8bV_{\bar{X}}} \sqrt{\frac{4b}{2\pi(1 + 8bV_{\bar{X}})}} = \frac{b}{\pi} \frac{4V_{\bar{X}}}{(1 + 8bV_{\bar{X}})^{3/2}}. \quad (108)
\end{aligned}$$

219 Hence

$$\int_{\mathbb{R}} \int_{\mathbb{R}} |\bar{x}_i - \bar{x}_j| \sqrt{\frac{b}{\pi}} \exp(-b(\bar{x}_i - \bar{x}_j)^2) f_{\bar{X}}(\bar{x}_i) f_{\bar{X}}(\bar{x}_j) d\bar{x}_i d\bar{x}_j = \sqrt{\frac{2}{\pi}} \sqrt{\frac{b}{\pi} \frac{4V_{\bar{X}}}{(1 + 8bV_{\bar{X}})^{3/2}}} = \frac{2}{\pi} \frac{\sqrt{2bV_{\bar{X}}}}{(1 + 8bV_{\bar{X}})^{3/4}} \quad (109)$$

220 and

$$\begin{aligned}
\text{Cov}_{f_{\bar{X}}}(\alpha, |\beta|) &= \frac{c^2 N b}{\bar{r}} \sqrt{\frac{b}{4\pi}} \frac{2}{\pi} \frac{\sqrt{2bV_{\bar{X}}}}{(1 + 8bV_{\bar{X}})^{3/4}} - \bar{\alpha} |\beta| \\
&= \frac{2c^2 N b^2}{\pi \bar{r} (1 + 8bV_{\bar{X}})^{3/4}} \sqrt{\frac{V_{\bar{X}}}{2\pi}} - \frac{c}{\bar{r}} \sqrt{\frac{b}{2\pi(1 + 2bV_{\bar{X}})}} \frac{2}{\pi} \frac{c N b^{3/2}}{(1 + 4bV_{\bar{X}})^{3/4}} \sqrt{V_{\bar{X}}} \\
&= \frac{2c^2 N b^2}{\pi \bar{r} (1 + 8bV_{\bar{X}})^{3/4}} \sqrt{\frac{V_{\bar{X}}}{2\pi}} - \frac{2c^2 N b^2}{\pi \bar{r} (1 + 4bV_{\bar{X}})^{3/4}} \sqrt{\frac{V_{\bar{X}}}{2\pi(1 + 2bV_{\bar{X}})}} \\
&= \frac{2c^2 N b^2}{\pi \bar{r}} \sqrt{\frac{V_{\bar{X}}}{2\pi}} \left(\frac{1}{(1 + 8bV_{\bar{X}})^{3/4}} - \frac{1}{(1 + 4bV_{\bar{X}})^{3/4} (1 + 2bV_{\bar{X}})^{1/2}} \right). \quad (110)
\end{aligned}$$

221 10.1.3 Starting the calculation of $\text{Cov}_{f_{\bar{X}}}(\alpha, \mathfrak{C})$

222 We have

$$\mathfrak{C}(\bar{x}_i, \bar{x}_j) = c^2 N^2 b^2 \left(|\bar{x}_i - \bar{x}_j| + |1 - b(\bar{x}_i - \bar{x}_j)^2| \right)^2 \exp\left(-\frac{b}{2}(\bar{x}_i - \bar{x}_j)^2\right). \quad (111)$$

223 Note that the random variable $\delta = \bar{x}_i - \bar{x}_j$ is a mean zero Gaussian random variable with variance $2V_{\bar{X}}$. We
224 write the probability density function of δ as $f_{\Delta}(\delta)$. Substituting in δ , we can write

$$\begin{aligned}\mathfrak{C}(\delta, 0) &= c^2 N^2 b^2 \left(|\delta| + |1 - b\delta^2| \right)^2 \exp\left(-\frac{b}{2}\delta^2\right) \\ &= c^2 N^2 b^2 \left(\delta^2 + 2|\delta| - b|\delta|^3 + (1 - b\delta^2)^2 \right) \exp\left(-\frac{b}{2}\delta^2\right). \quad (112)\end{aligned}$$

From this expression, we see properties of the folded normal distribution can be used to calculate several components of the integral $\text{Cov}_{f_{\bar{X}}}(\alpha, \mathfrak{C})$, but a major technical challenge lies in calculating

$$\int_{\mathbb{R}} ||\delta| - b|\delta|^3| \exp\left(-\frac{b}{2}\delta^2\right) f_{\Delta}(\delta) d\delta. \quad (113)$$

Instead of overcoming this challenge to find an analytical form of $\text{Cov}_{f_{\bar{X}}}(\alpha, \mathfrak{C})$ we turn to a numerical approach outlined in the following section.

10.2 Numerical estimates for heterogeneous N and G

To verify our analytical estimates for the covariance of selection gradients and competition coefficients, equations (60) of the main text, and for approximating the correlation of competition coefficients and a metric of pairwise coevolution, Figure 5 of the main text, we developed a numerical approach by repeatedly simulating our system (52) of the main text across a set of randomly drawn model parameters. In particular, we ran each numerical integration with $S = 100$ species for $T_1 = 1000.0$ units of time. We then continued to integrate for $T_2 = 1000.0$ units of time and calculated the covariances between competition coefficients and the quantities $|\beta|$, γ and \mathfrak{C} for each of the last T_2 time steps. We assume the temporal average of these covariances across the last T_2 units of time approximates the expectation at equilibrium. We repeated this approach for randomly drawn a and c until our sample size reached 1000. We drew values for a and c from condition log-normal distributions. For a , we set the log-normal parameters equal to $\mu = -10$ and $\sigma = 6$ and conditioned on $a < 0.01$ to prevent extinction. For c we set the log-normal parameters equal to $\mu = -4$ and $\sigma = 4$ and conditioned on $c < 1 \times 10^{-4}$ to prevent very large interspecific phenotypic variation and extinction. When extinction occurs, we aborted the simulation and restarted with newly drawn parameters. Results for $\text{Corr}_{f_{\bar{X}}}(\alpha, |\beta|)$ and $\text{Corr}_{f_{\bar{X}}}(\alpha, \gamma)$ are displayed in SM Figure 1.

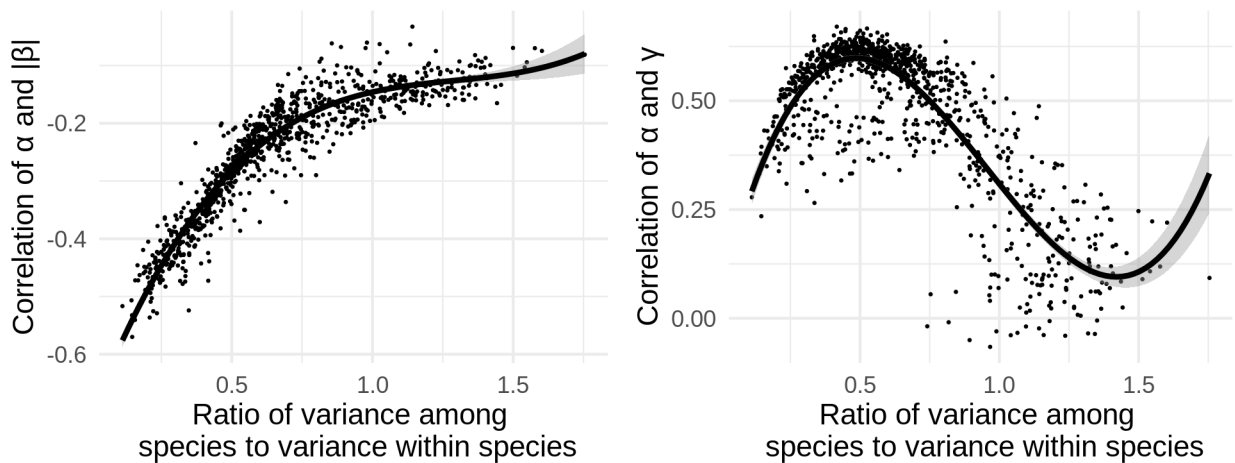


Figure 1: Numerical estimate for the correlations of selection gradients and competition coefficients.

References

- Champagnat, Nicolas, Régis Ferrière, and Sylvie Méléard. 2006. “Unifying Evolutionary Dynamics: From Individual Stochastic Processes to Macroscopic Models.” *Theoretical Population Biology* 69 (3). Elsevier BV: 297–321.
- Da Prato, Giuseppe, and Jerzy Zabczyk. 2014. *Stochastic Equations in Infinite Dimensions*. Cambridge University Press.
- Evans, Lawrence C. 2010. *Partial Differential Equations: Second Edition*. American Mathematical Society.
- Farlow, Stanley J. 1993. *Partial Differential Equations for Scientists and Engineers*. Dover.
- Méléard, M, and S Roelly. 1992. “Interacting Branching Measure Processes.” *Stochastic Partial Differential Equations and Applications (G. Da Prato and L. Tubaro, Eds.)*, 246–56.
- . 1993. “Interacting Measure Branching Processes. Some Bounds for the Support.” *Stochastics and Stochastic Reports* 44 (1-2). Informa UK Limited: 103–21.
- Zheng, Songmu. 2004. *Nonlinear Evolution Equations*. Boca Raton, Fla: Chapman & Hall/CRC Press.