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**Supplementary information**

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**The evolution of niche overlap and competitive differences**

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# The evolution of niche overlap and competitive differences

## Supplementary Material

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### 1 General framework

Let there be  $S$  competing species. Individuals possess a quantitative trait  $z$  affecting their ecological performance. Each species is characterized by a population density  $N_i$  and trait distribution  $p_i(z)$ ;  $N_i p_i(z) dz$  is the population density of species  $i$ 's individuals whose phenotype values fall between  $z$  and  $z + dz$ .

The phenotype distributions are normal with mean  $\mu_i$  and variance  $\sigma_i^2$ :

$$p_i(z) = \frac{1}{\sigma_i \sqrt{2\pi}} \exp\left(-\frac{(z - \mu_i)^2}{2\sigma_i^2}\right). \quad (\text{S1})$$

This distribution is normalized, so

$$\int p_i(z) dz = 1 \quad (\text{S2})$$

at any moment of time. If we assume purely additive genetic variance, random mating, and equal sex ratios, then the phenotypic variance  $\sigma_i^2$  is the sum of the (additive) genetic variance  $\sigma_{G,i}^2$  and the environmental variance  $\sigma_{E,i}^2$ :

$$\sigma_i^2 = \sigma_{G,i}^2 + \sigma_{E,i}^2. \quad (\text{S3})$$

The ratio of genetic to total phenotypic variance is the heritability  $h_i^2$ :

$$h_i^2 = \frac{\sigma_{G,i}^2}{\sigma_i^2}. \quad (\text{S4})$$

The equations governing eco-evolutionary dynamics take the per capita growth rate  $r_i(z)$  of species  $i$ 's phenotype  $z$ , and express the change in population densities and species trait means via

$$\frac{dN_i}{dt} = N_i \int r_i(z) p_i(z) dz, \quad (\text{S5})$$

$$\frac{d\mu_i}{dt} = h_i^2 \int (z - \mu_i) r_i(z) p_i(z) dz \quad (\text{S6})$$

(Barabás and D'Andrea 2016). This framework is a continuous-time version of classical quantitative genetic recursion models (Roughgarden 1979, Taper and Case 1985, 1992, Schreiber et al. 2011, Vasseur et al. 2011), derived using the infinitesimal model of quantitative genetics (Bulmer 1980, Barton et al. 2017, Turelli 2017) and the breeder's equation (Falconer 1981) in the weak selection limit (Bürger 2011). Given a set of arbitrary species- and phenotype-specific per capita growth rates  $r_i(z)$  and the parameters of species' phenotype distributions, Eqs. S5-S6 convert the ecological dynamics prescribed by these growth rates into eco-evolutionary dynamics.

## 2 Consumer-resource dynamics

Let us consider a gradient of abiotic resources, with  $R(y)$  being the availability of resources with quality  $y$  along the gradient. Consumer species feed on these resources. Each individual is characterized by a phenotype,  $z$ , which is more or less well suited for consuming resources of various quality  $y$ . This suitedness is given by  $u(z, y)$ , the degree to which an individual of phenotype  $z$  can utilize resource  $y$ . The per capita growth rate of individuals with phenotype  $z$  is proportional to their total resource consumption, and to a species- and phenotype-specific mortality rate  $m_i(z)$ :

$$r_i(z) = \int u(z, y)R(y) dy - m_i(z) \quad (\text{S7})$$

(MacArthur 1970), where  $r_i(z)$  is the per capita growth rate of individuals of species  $i$  with phenotype  $z$ . Formally, the limits of integration extend from minus to plus infinity, with the understanding that while resources cannot extend forever, the utilization function  $u(z, y)$  is confined to a finite region and so the integral's contribution from outside this region becomes negligible.

The abiotic resources are assumed to operate on a fast time scale compared to the population dynamics (MacArthur 1970), and are therefore always in a state of quasi-equilibrium:

$$R(y) = R_0(y) - \sum_{j=1}^S \int u(y, z')N_j p_j(z') dz', \quad (\text{S8})$$

where  $R_0(y)$  is the saturation concentration of resource  $y$  in the absence of consumption,  $S$  is the number of consumer species, and  $N_j p_j(z')$  is the fraction of species  $j$ 's individuals that have phenotype  $z'$ . The fact that resource depletion is weighted by the same function,  $u(z, y)$ , as population growth in Eq. S7 expresses the assumption that the benefit an individual gains from resource  $y$  is proportional to its consumption of the same resource.

Substituting Eq. S8 into Eq. S7 yields

$$r_i(z) = \int u(z, y) \left( R_0(y) - \sum_{j=1}^S \int u(y, z')N_j p_j(z') dz' \right) dy - m_i. \quad (\text{S9})$$

Rearranging, we get

$$r_i(z) = \underbrace{\left( \int u(z, y)R_0(y) dy - m_i \right)}_{\lambda_i(z)} - \sum_{j=1}^S \int \underbrace{\left( \int u(z, y)u(y, z') dy \right)}_{a(z, z')} N_j p_j(z') dz', \quad (\text{S10})$$

which has the form of Lotka–Volterra growth with intrinsic rates  $\lambda_i(z)$  and competition kernel  $a(z, z')$ :

$$r_i(z) = \lambda_i(z) - \sum_{j=1}^S N_j \int a(z, z')p_j(z') dz'. \quad (\text{S11})$$

Assigning parameters to this model, the resource utilization curve  $u(z, y)$  is a Gaussian function of the difference between consumer phenotype  $z$  and resource quality  $y$ :

$$u(z, y) = \sqrt{\frac{2}{\omega\sqrt{\pi}}} \exp\left(-2\frac{(z-y)^2}{\omega^2}\right). \quad (\text{S12})$$

Thus,  $z = y$  is the trait providing the best match for consuming resource  $y$ . The prefactor in front of the exponent was introduced for convenience, because the competition kernel  $a(z, z')$

between phenotypes  $z$  and  $z'$  now reads

$$a(z, z') = \int u(z, y)u(y, z') dy = \frac{2}{\omega\sqrt{\pi}} \int \exp\left(-2\frac{(z-y)^2 + (y-z')^2}{\omega^2}\right) dy = \exp\left(-\frac{(z-z')^2}{\omega^2}\right). \quad (\text{S13})$$

In turn, we assume that each resource saturates at the same level without consumption:

$$R_0(y) = A\sqrt{\frac{1}{\omega\sqrt{\pi}}}, \quad (\text{S14})$$

where  $A$  is a constant proportional to the growth rate achieved by a phenotype when resource availability is maximal, and the subsequent factor was again introduced for convenience:

$$\int u(z, y)R_0(y) dy = A\sqrt{\frac{2}{\omega^2\pi}} \int \exp\left(-2\frac{(z-y)^2}{\omega^2}\right) dy = A. \quad (\text{S15})$$

The mortalities  $m_i(z)$  are parameterized as

$$m_i(z) = M_i + z^2/\theta^2, \quad (\text{S16})$$

where  $M_i$  is a constant describing a species-specific intrinsic mortality. Mortality is thus minimal for phenotype  $z = 0$ , and increases quadratically as one moves away from this optimum. Further, this increase is faster for smaller values of the environmental breadth  $\theta$ . Using Eqs. S15 and S16, we now obtain the intrinsic rate  $\lambda_i(z)$ :

$$\lambda_i(z) = \int u(z, y)R_0(y) dy - m_i = A - M_i - \frac{z^2}{\theta^2}. \quad (\text{S17})$$

Introducing  $K_i = A - M_i$ ,

$$\lambda_i(z) = K_i - \frac{z^2}{\theta^2}. \quad (\text{S18})$$

## An alternative parameterization

The above parameterization assumes a constant resource availability  $R_0$  regardless of resource quality, plus quadratically increasing mortality rates as one moves away from  $z = 0$ . These assumptions are by no means forced. Here we present a very similar, alternative parameterization where it is resource availability that decreases quadratically. This expresses the natural assumption that resources of extreme quality (e.g., extremely large or small ones) are not available to the same extent as resources with more average quality.

First, we implement a naive version of this parameterization. We choose the resource availabilities to be

$$R_0(y) = \sqrt{\frac{1}{\omega\sqrt{\pi}}}\left(A - \frac{y^2}{\theta^2}\right), \quad (\text{S19})$$

which is quadratically decreasing, and the multiplying factor at the front was chosen for future convenience. (This function is unbiological, because it allows resource availabilities to be negative. This is why our choice is naive. We fix this problem below.) In turn, let the mortalities be

$$m_i = M_i + \frac{\omega^2/4}{\theta^2}, \quad (\text{S20})$$

where  $M_i$  is species-specific. Note the lack of trait-dependence in these mortalities. Still assuming Gaussian resource utilization functions (Eq. S12), we can calculate  $\lambda_i(z)$  from Eq. S17 by explicitly evaluating the integral:

$$\lambda_i(z) = \int u(z, y)R_0(y) dy - m_i = A - M_i - \frac{z^2}{\theta^2}, \quad (\text{S21})$$

which after defining  $K_i = A - M_i$ , is identical to the form in Eq. S18 we had before. Thus, the same equations are derived from two different interpretations of the parameters: one where mortalities are trait-dependent and resource availabilities are constant, and one where resource availabilities are trait-dependent but mortalities are (species-specific) constants.

To correct for the unbiological assumption of negative resource availabilities, we can introduce a cutoff which prevents the function from dropping below zero. A modification of Eq. S19 in this way can be written

$$R_0(y) = \sqrt{\frac{1}{\omega\sqrt{\pi}}} \max\left[A - \frac{y^2}{\theta^2}, 0\right], \quad (\text{S22})$$

where  $\max(\cdot)$  is the maximum function. Calculating  $\lambda_i(z)$  from Eq. S17 again, we get a more complicated expression than before:

$$\begin{aligned} \lambda_i(z) &= \int u(z, y) R_0(y) dy - m_i \\ &= \frac{\omega^2 + 4z^2 - 4A\theta^2}{8\theta^2} \left[ \operatorname{erf}\left(\frac{\sqrt{2}(z - \sqrt{A}\theta)}{\omega}\right) - \operatorname{erf}\left(\frac{\sqrt{2}(\sqrt{A}\theta + z)}{\omega}\right) \right] \\ &\quad + \frac{\omega}{\theta^2\sqrt{2\pi}} \exp\left(-\frac{2(A\theta^2 + z^2)}{\omega^2}\right) \left[ z \sinh\left(\frac{4\sqrt{A}\theta z}{\omega^2}\right) + \sqrt{A}\theta \cosh\left(\frac{4\sqrt{A}\theta z}{\omega^2}\right) \right] - m_i. \end{aligned} \quad (\text{S23})$$

While the expression is complicated, it is conceptually the same as before, in Eq. S21; it just accounts for the sharp cutoff of  $R_0(y)$  at  $\pm\theta$ .

### 3 Eco-evolutionary consumer-resource dynamics

We now convert the ecological model of Eq. S11 into an eco-evolutionary one, using Eqs. S5-S6:

$$\frac{dN_i}{dt} = N_i \left[ \int \lambda_i(z) p_i(z) dz - \sum_{j=1}^S N_j \iint p_i(z) a(z, z') p_j(z') dz' dz \right], \quad (\text{S24})$$

$$\frac{d\mu_i}{dt} = h_i^2 \left[ \int (z - \mu_i) \lambda_i(z) p_i(z) dz - \sum_{j=1}^S N_j \iint (z - \mu_i) p_i(z) a(z, z') p_j(z') dz' dz \right]. \quad (\text{S25})$$

Introducing the simplifying notations

$$b_i = \int \lambda_i(z) p_i(z) dz, \quad (\text{S26})$$

$$\alpha_{ij} = \iint p_i(z) a(z, z') p_j(z') dz' dz, \quad (\text{S27})$$

$$g_i = \int (z - \mu_i) \lambda_i(z) p_i(z) dz, \quad (\text{S28})$$

$$\beta_{ij} = \iint (z - \mu_i) p_i(z) a(z, z') p_j(z') dz' dz, \quad (\text{S29})$$

Eqs. S24 and S25 can be written as

$$\frac{dN_i}{dt} = N_i \left( b_i - \sum_{j=1}^S \alpha_{ij} N_j \right), \quad (\text{S30})$$

$$\frac{d\mu_i}{dt} = h_i^2 \left( g_i - \sum_{j=1}^S \beta_{ij} N_j \right). \quad (\text{S31})$$

The newly introduced quantities can be explicitly evaluated. We first calculate  $b_i$  and  $g_i$  by writing Eq. S18 into Eqs. S26 and S28, and integrating:

$$b_i = \int \left( K_i - \frac{z^2}{\theta^2} \right) p_i(z) dz = K_i - \frac{\mu_i^2 + \sigma_i^2}{\theta^2}, \quad (\text{S32})$$

$$g_i = \int (z - \mu_i) \left( K_i - \frac{z^2}{\theta^2} \right) p_i(z) dz = -\frac{2\mu_i\sigma_i^2}{\theta^2}. \quad (\text{S33})$$

To obtain  $\alpha_{ij}$  and  $\beta_{ij}$ , we substitute Eq. S13 into Eqs. S27-S29 and integrate:

$$\alpha_{ij} = \iint p_i(z) a(z, z') p_j(z') dz' dz = \sqrt{\frac{\omega^2}{\omega^2 + 2\sigma_i^2 + 2\sigma_j^2}} \exp\left(-\frac{(\mu_i - \mu_j)^2}{\omega^2 + 2\sigma_i^2 + 2\sigma_j^2}\right), \quad (\text{S34})$$

$$\beta_{ij} = \iint (z - \mu_i) p_i(z) a(z, z') p_j(z') dz' dz = \frac{-2\omega\sigma_i^2(\mu_i - \mu_j)}{(\omega^2 + 2\sigma_i^2 + 2\sigma_j^2)^{3/2}} \exp\left(-\frac{(\mu_i - \mu_j)^2}{\omega^2 + 2\sigma_i^2 + 2\sigma_j^2}\right). \quad (\text{S35})$$

## 4 Niche overlap and fitness ratio

The Lotka–Volterra model reads

$$\frac{dN_i}{dt} = N_i \left( b_i - \sum_{j=1}^S \alpha_{ij} N_j \right), \quad (\text{S36})$$

where  $N_i$  is species  $i$ 's population density,  $t$  is time,  $S$  the number of species,  $b_i$  is  $i$ 's intrinsic growth rate, and  $\alpha_{ij}$  is the competitive effect of species  $j$  on  $i$ . For  $S = 2$  competing species, the niche overlap  $\rho$  and fitness ratio  $\kappa_1/\kappa_2$  are given by

$$\rho = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}}, \quad (\text{S37})$$

$$\frac{\kappa_1}{\kappa_2} = \frac{b_1}{b_2} \sqrt{\frac{\alpha_{21}\alpha_{22}}{\alpha_{12}\alpha_{11}}}. \quad (\text{S38})$$

(Chesson 2018). Eq. S36 is equivalent to Eq. S30, the equation governing population densities in the eco-evolutionary consumer-resource model. This means we can use the above definitions of  $\rho$  and  $\kappa_1/\kappa_2$  to calculate niche overlap and the fitness ratio in our model, at any moment of time. Substituting Eqs. S32 and S34 into Eqs. S37-S38, we get

$$\rho = \exp\left(-\frac{(\mu_1 - \mu_2)^2}{\omega^2 + 2\sigma_1^2 + 2\sigma_2^2}\right) \left( \frac{(\omega^2 + 4\sigma_1^2)(\omega^2 + 4\sigma_2^2)}{(\omega^2 + 2\sigma_1^2 + 2\sigma_2^2)^2} \right)^{1/4}, \quad (\text{S39})$$

$$\frac{\kappa_1}{\kappa_2} = \frac{K_1\theta^2 - \mu_1^2 - \sigma_1^2}{K_2\theta^2 - \mu_2^2 - \sigma_2^2} \left( \frac{\omega^2 + 4\sigma_1^2}{\omega^2 + 4\sigma_2^2} \right)^{1/4}. \quad (\text{S40})$$

In the special case when  $\alpha_{ij} = \alpha_{ji}$  (symmetric competition coefficients), the fitness ratio simplifies to

$$\frac{\kappa_1}{\kappa_2} = \frac{b_1}{b_2} \sqrt{\frac{\alpha_{22}}{\alpha_{11}}}, \quad (\text{S41})$$

from which the individual  $\kappa_i$  value of species  $i$  can be consistently defined:

$$\kappa_i = \frac{b_i}{\sqrt{\alpha_{ii}}}. \quad (\text{S42})$$

In our model, which has symmetric competition coefficients (Eq. S34), we have

$$\kappa_i = \left( \frac{\omega^2 + 4\sigma_i^2}{\omega^2} \right)^{1/4} \left( K_i - \frac{\mu_i^2 + \sigma_i^2}{\theta^2} \right). \quad (\text{S43})$$

If the two intraspecific trait variances are equal ( $\sigma_1^2 = \sigma_2^2 = \sigma^2$ ), then further simplification is available, with Eqs. S39-S40 simplifying to

$$\rho = \exp\left(-\frac{(\mu_1 - \mu_2)^2}{\omega^2 + 4\sigma^2}\right), \quad (\text{S44})$$

$$\frac{\kappa_1}{\kappa_2} = \frac{K_1\theta^2 - \mu_1^2 - \sigma^2}{K_2\theta^2 - \mu_2^2 - \sigma^2}. \quad (\text{S45})$$

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