Supplemental Material (not copyedited or formatted) for: Bob Week, Scott L. Nuismer. 2021. "Coevolutionary Arms Races and the Conditions for the Maintenance of Mutualism." The American Naturalist 198(2). DOI: https://doi.org/10.1086/714274.

Online Supplement:

Coevolutionary arms races and the conditions for the maintenance of mutualism,

The American Naturalist

Bob Week[1,*]

Scott L. Nuismer[2,†]

1. Program in Bioinformatics and Computational Biology, University of Idaho, Moscow, Idaho 83844;

2. Department of Biological Sciences, University of Idaho, Moscow, Idaho 83844;

∗ Corresponding author; e-mail: bobweek@gmail.com.

Additional Methods

§A: Derivation of evolutionary dynamics from individual-based models

Our approach to deriving models of evolutionary dynamics follows three main steps. First we introduce the individual fitness functions for the trait-differences and offset-matching interaction mechanisms. Second, we derive the continuous-time growth rates of trait values using diffusion limits. Averaging these growth rates over phenotypic distributions returns population growth rates. Third, following Week et al. (2020), we apply the Stochastic Asexual Gaussian allelic model with Abundance dynamics (abbreviated SAGA), a continuous time stochastic model of trait dynamics that generalizes the well-known breeders equation (Lande, 1976) by accounting for demographic dynamics and arbitrary trait distributions. Assuming normally distributed traits, we use SAGA to derive mean trait dynamics in terms of growth rate gradients. We then assume infinitely large abundances to remove stochastic effects.

Individual fitness

Trait-matching. For simplicity, we begin by formulating fitness under trait-matching. Letting x denote the trait value for the individual of species X and y for species Y, we can model the effect of trait-matching on fitness for individuals of species X by the concave down quadratic polynomial $-\frac{B_X}{2}(x-y)^2$. Since we assume both species interact via the same mechanism, the formula determining their dynamics will be of the same form. Hence, we focus on species X without losing any generality in our conclusions. We call the parameter $B_X \geq 0$ the strength of biotic selection (introduced in Week and Nuismer, 2019). Denote by $R_X > 0$ the number offspring produced by individuals in species X in the absence of ecological interactions and $E_X > 0$ the multiplicative effect on R_X due to the interspecific interaction when $B_X = 0$. We call E_X the baseline effect of the interspecific interaction. Suppose each individual of species X interacts with a single individual of species Y with trait value denoted by y. Then, under trait-matching,

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we model the number of offspring produced when $B_X > 0$ by

$$w_X(x,y) = R_X E_X e^{-\frac{B_X}{2}(x-y)^2}. \tag{S1}$$

Note if $E_X e^{-\frac{B_X}{2}(x-y)^2} < 1$, the interaction is antagonistic and if $E_X e^{-\frac{B_X}{2}(x-y)^2} > 1$, species X benefits from the interaction. Following the same approach for species Y, we have

$$w_Y(y,x) = R_Y E_Y e^{-\frac{B_Y}{2}(x-y)^2}. \tag{S2}$$

Trait-differences. Following the approach taken to formulate individual fitness for the trait-matching mechanism, we replace the concave quadratic polynomial with the linear term $B_X(x-y)$, yielding

$$w_X(x,y) = R_X E_X e^{B_X(x-y)}, \tag{S3}$$

$$w_Y(y,x) = R_Y E_Y e^{B_Y(y-x)}. \tag{S4}$$

Under this model, the interaction is antagonistic if $E_X e^{B_X(x-y)} < 1$ or $E_Y e^{B_Y(y-x)} < 1$, and is a mutualism if $E_X e^{B_X(x-y)}, E_Y e^{B_Y(y-x)} > 1$.

Offset-matching. Offset-matching is just a slight modification of trait-matching, summarized by

$$w_X(x,y) = R_X E_X e^{-\frac{B_X}{2}(y+\delta_X-x)^2}, \tag{S5}$$

$$w_Y(y,x) = R_Y E_Y e^{-\frac{B_Y}{2}(x+\delta_Y-y)^2}. \tag{S6}$$

Here we have assumed the optimal offset δ_X of species X is distinct from the optimal offset δ_Y of species Y. This seems more likely to occur in nature rather than identical offsets between the two species. However, we can always reduce such asymmetry via the change of variables $\delta = \frac{\delta_X+\delta_Y}{2}$, $x' = x + \frac{\delta_Y}{2}$ and $y' = y + \frac{\delta_X}{2}$. Thus, from hereon we assume the common optimal offset δ for both species.

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§B: Deriving growth rates

To derive the dynamical equations of the main text starting with individual fitness we begin by taking a diffusion limit. Our approach follows a special case of the framework developed by Week et al. (2020), which we now summarize.

Outline of diffusion limits. In the special case treated here, a diffusion limit implies that we begin with a population at the initial time $t = 0$ of n discrete individuals and rescale their ”mass” by N_0/n for some continuously-valued positive number $N_0 > 0$. We then consider the limit $n \to \infty$. The total mass of the population, which is interpreted as the initial abundance $N(0)$, is computed as the sum of individual masses and hence remains equal to

$$N(0) = \sum_{i=1}^{n} \frac{N_0}{n} = N_0 \tag{S7}$$

as we send $n \to \infty$. Once the diffusion limit is taken, we arrive at a model for the dynamics of the abundance $N(t)$. When taken appropriately, this diffusion limit results in a continuous-time, continuous-state stochastic process where the magnitude of stochasticity is modulated by the variance in reproductive output and rates of birth and death. Here assume constant rates of birth and death to prevent noise-induced selection. We also assume offspring number follows a Poisson distribution with expectation $w(x)$ for parents carrying trait value x.

Starting with individual-based models of discrete individuals allows us to formulate mechanistic models of fitness and, by taking their diffusion limits, we formally derive models at the population level. In particular, these diffusion limits track the dynamics of abundance and phenotypic distribution instead of tracking the dynamics of a discrete set of individuals. Week et al. (2020) showed these dynamics can be summarized by a set of stochastic differential equation tracking the dynamics of abundance and phenotypic moments. Under the assumption of normally distributed phenotypes, the population can be completely described by abundance $N(t)$, mean trait $\bar{x}(t)$ and trait variance $\sigma^2(t)$. Since the dynamics of abundance and phenotypic

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moments are interwoven via the expected reproductive output as a function of phenotype (ie., individual fitness) $w(x)$, the crux component for deriving the dynamics of $N(t)$, $\bar{x}(t)$ and $\sigma^2(t)$ is calculating a rescaled limit of $w(x)$. There are many ways to compute this limit, as formally demonstrated by Méléard and Roelly (1992, 1993). To translate their result, the rescaling used must ensure rates of reproduction and mortality increase sufficiently fast, the mass of individuals decreases sufficiently quickly, expected lifetime reproductive output converges to unity and the variance of reproductive output converges to a finite number. For simplicity, we rescale rates of reproduction and mortality by n, individual mass by N_0/n as above and expected offspring number to $w(x)^{1/n}$. Under this rescaling, the result of Méléard and Roelly (1992, 1993) proves the growth rate can be found using the limit

$$m(x) = \lim_{n\to\infty} n\left(w(x)^{1/n} - 1\right). \tag{S8}$$

When fitness is constant with respect to trait value (ie., $w(x) \equiv w$), then this limit converges to $m(x) = \ln w$ for each x. When this limit converges in general, $m(x)$ is the Malthusian (ie., continuous time) growth rate associated with trait value x. The average of $m(x)$ across all trait values in the population, denoted $\bar{m}$, is the growth rate of the population as a whole. Week et al. (2020) showed, under the assumption of normally distributed phenotypes, the dynamics of mean trait can be derived by taking partial derivatives of $\bar{m}$ and $m(x)$ with respect to $\bar{x}$. While the partial derivative $\frac{\partial \bar{m}}{\partial \bar{x}}$ represents the effect of frequency independent selection on mean trait evolution, the partial derivative $\frac{\partial m(x)}{\partial \bar{x}}$ represents the effect of frequency dependent selection on mean trait evolution. Week et al. (2020) extended this observation by noting, again under normally distributed phenotypes, the action of selection on the evolution of phenotypic variance can be summarized by the partial derivatives $\frac{\partial \bar{m}}{\partial \sigma^2}$, $\frac{\partial m(x)}{\partial \sigma^2}$ which again represent frequency independent and frequency dependent selection respectively. The resulting stochastic differential equations describing the dynamics of $N(t)$ and the evolution of $\bar{x}(t)$ and $\sigma^2(t)$ are provided below in the section titled *Deriving evolution equations*.

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Diffusion limits for trait-differences and offset-matching. Following the main text, we isolate the effect of interaction mechanism by assuming each individual of species X interacts with a single individual of species Y and each individual of species Y interacts with a single individual of species X. To formally justify this assumption we require identical abundances for each species ($n_X = n_Y = n$). Although this will clearly never hold in the wild, this assumption acts as a mere stepping stone in our derivation as eventually we take $n_X, n_Y, n \to \infty$. In particular, for any continuously positive numbers $N_X, N_Y > 0$, we rescale individual mass by N_X/n_X for individuals in species X and by N_Y/n_Y for individuals in species Y. Hence, in the diffusion limit, the initial abundances for species X and Y are given by

$$\lim_{n_X\to\infty}\sum_{i=1}^{n_X}\frac{N_X}{n_X} = N_X \tag{S9a}$$

$$\lim_{n_Y\to\infty}\sum_{i=1}^{n_Y}\frac{N_Y}{n_Y} = N_Y. \tag{S9b}$$

In particular, since this holds for any N_X, N_Y, we can choose $N_X \neq N_Y$ in spite of setting $n_X = n_Y = n$. To picture why this is so, consider a specific case such as $n = 4$. Since we have exactly n individuals in each species, we can pair each individual of species X with a unique individual of species Y, forming n distinct pairs of interacting individuals. However, individuals in species X are weighted by N_X/n and individuals in species Y are weighted by N_Y/n and, since we can freely choose N_X and N_Y, these weights can be different. Hence, the ”total mass” of species X at time $t = 0$, which is interpreted as the initial abundance of X, is N_X for any n. By the same argument, the initial abundance of species Y is N_Y for any n.

Following Week et al. (2020), we derive the growth rates for traits x and y respectively as

$$m_X(x,y) = \lim_{n\to\infty} n\left(w_X(x,y)^{1/n} - 1\right), \tag{S10a}$$

$$m_Y(y,x) = \lim_{n\to\infty} n\left(w_Y(y,x)^{1/n} - 1\right). \tag{S10b}$$

We now we apply these limits to derive the continuous time growth rates for species X and Y under trait-differences and offset-matching.

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Trait-differences. For the trait-differences mechanism, equation (S10a) becomes

$$m_X(x,y) = \lim_{n\to\infty} n\left(\Big(w_X(x,y)\Big)^{1/n} - 1\right) = \lim_{n\to\infty} n\left((R_X E_X)^{1/n} \exp\left(\frac{B_X}{n}(x-y)\right) - 1\right). \tag{S11}$$

For large n we have

$$n\left((R_X E_X)^{1/n} \exp\left(\frac{B_X}{n}(x-y)\right) - 1\right)$$

$$\approx n\left((R_X E_X)^{1/n} \left(1 + \frac{B_X}{n}(x-y)\right) - 1\right)$$

$$= n\big((R_X E_X)^{1/n} - 1\big) + (R_X E_X)^{1/n} B_X(x-y). \tag{S12}$$

Since $n\big((R_X E_X)^{1/n} - 1\big) \to \ln(R_X E_X)$ and $(R_X E_X)^{1/n} \to 1$, we find

$$m_X(x,y) = r_X + e_X + B_X(x-y), \tag{S13}$$

where $r_X = \ln R_X$ and $e_X = \ln E_X$. Applying the same limit to equation (S10b) returns

$$m_Y(y,x) = r_Y + e_Y + B_Y(y-x). \tag{S14}$$

Recall that we assumed individuals interact at random with each other. This implies the growth rates $m_X(x,\cdot)$ and $m_Y(y,\cdot)$ are random variables with means

$$\mathbb{E}_x(m_X) = r_X + e_X + B_X(x-\bar{y}), \tag{S15a}$$

$$\mathbb{E}_y(m_Y) = r_Y + e_Y + B_Y(y-\bar{x}), \tag{S15b}$$

and variances

$$\mathbb{V}_x(m_X) = B_X^2 \sigma_Y^2, \tag{S16a}$$

$$\mathbb{V}_y(m_Y) = B_Y^2 \sigma_X^2. \tag{S16b}$$

However, by formally following our assumption that individuals interact with a single individual of the other species, averaging $m_X(x,y)$ across species X requires us to simultaneously average $m_X(x,y)$ across species Y as well and vice versa for average $m_Y(y,x)$ across species Y. Hence, we find the population growth rates

$$\bar{m}_X = r_X + e_X + B_X(\bar{x} - \bar{y}), \tag{S17}$$

$$\bar{m}_Y = r_Y + e_Y + B_Y(\bar{y} - \bar{x}), \tag{S18}$$

where $\bar{x}, \bar{y}$ are the mean traits for species X and Y respectively.

Offset-matching. For the offset-matching mechanism, equation (S10a) becomes

$$\begin{aligned} m_X(x,y) &= \lim_{n\to\infty} n\left(\left(w_X(x,y)\right)^{1/n} - 1\right) \\ &= \lim_{n\to\infty} n\left((R_X E_X)^{1/n} \exp\left(-\frac{B_X}{2n}(y+\delta-x)^2\right) - 1\right). \end{aligned} \tag{S19}$$

For large n we have

$$\begin{aligned} & n\left((R_X E_X)^{1/n} \exp\left(-\frac{B_X}{2n}(y+\delta-x)^2\right) - 1\right) \\ &\approx n\left((R_X E_X)^{1/n} \left(1 - \frac{B_X}{2n}(y+\delta-x)^2\right) - 1\right) \\ &= n\big((R_X E_X)^{1/n} - 1\big) - (R_X E_X)^{1/n}\frac{B_X}{2}(y+\delta-x)^2. \end{aligned} \tag{S20}$$

Hence,

$$m_X(x,y) = r_X + e_X - \frac{B_X}{2}(\delta + y - x)^2. \tag{S21}$$

Applying the same limit to equation (S10b) returns

$$m_Y(y,x) = r_Y + e_Y - \frac{B_Y}{2}(x+\delta-y)^2. \tag{S22}$$

Then, following the same argument made in deriving growth rates under trait-differences, we find the population growth rates

$$\bar{m}_X = r_X + e_X - \frac{B_X}{2}(\bar{y}+\delta-\bar{x})^2 - \frac{B_X}{2}(\sigma_X^2+\sigma_Y^2), \tag{S23}$$

$$\bar{m}_Y = r_Y + e_Y - \frac{B_Y}{2}(\bar{x}+\delta-\bar{y})^2 - \frac{B_Y}{2}(\sigma_X^2+\sigma_Y^2), \tag{S24}$$

where σ_X^2, σ_Y^2 are the trait variances for species X and Y respectively.

§C: *Deriving evolution equations*

With the growth rates for each mechanism derived, we apply a general formula for the dynamics of abundances N_X, N_Y, mean traits $\bar{x}, \bar{y}$ and additive genetic variances G_X, G_Y following the Stochastic Asexual Gaussian allelic model with Abundance dynamics introduced in Week et al. (2020). We also assume a simple model of inheritance where expressed traits are normally distributed around genotypic values (ie., breeding values). This implies $\sigma_X^2 = \eta_X + G_X$ and $\sigma_X^2 = \eta_X + G_X$ where η_X, η_Y capture developmental noise (Walsh and Lynch, 2018). In particular, assuming normally distributed trait values, normally distributed offspring breeding values, and normally distributed mutational effects, the dynamics of abundances, mean traits and additive genetic variances are given by the stochastic differential equations;

$$\frac{dN_X}{dt} = \bar{m}_X N_X + \sqrt{N_X}\frac{dW_{N_X}}{dt}, \tag{S25a}$$

$$\frac{dN_Y}{dt} = \bar{m}_Y N_Y + \sqrt{N_Y}\frac{dW_{N_Y}}{dt}, \tag{S25b}$$

$$\frac{d\bar{x}}{dt} = G_X\left(\frac{\partial \bar{m}_X}{\partial \bar{x}} - \overline{\frac{\partial m_X}{\partial \bar{x}}}\right) + \sqrt{\frac{G_X}{N_X}}\frac{dW_{\bar{x}}}{dt}, \tag{S25c}$$

$$\frac{d\bar{y}}{dt} = G_Y\left(\frac{\partial \bar{m}_Y}{\partial \bar{y}} - \frac{\overline{\partial m_Y}}{\partial \bar{y}}\right) + \sqrt{\frac{G_Y}{N_Y}}\frac{dW_{\bar{y}}}{dt}, \tag{S25d}$$

$$\frac{dG_X}{dt} = \left[2G_X^2\left(\frac{\partial \bar{m}_X}{\partial G_X} - \frac{\overline{\partial m_X}}{\partial G_X}\right) + \mu_X - \frac{G_X}{N_X}\right] + G_X\sqrt{\frac{2}{N_X}}\frac{dW_{G_X}}{dt}, \tag{S25e}$$

$$\frac{dG_Y}{dt} = \left[2G_Y^2\left(\frac{\partial \bar{m}_Y}{\partial G_Y} - \frac{\overline{\partial m_Y}}{\partial G_Y}\right) + \mu_Y - \frac{G_Y}{N_Y}\right] + G_Y\sqrt{\frac{2}{N_Y}}\frac{dW_{G_Y}}{dt}. \tag{S25f}$$

Here $\mu_X, \mu_Y \geq 0$ are rates of mutation, terms of the form $\frac{dW_Q}{dt}$ represent independent white noise processes driving the stochastic component of variable Q and the terms $\overline{\frac{\partial m_X}{\partial Q}}$ and $\overline{\frac{\partial m_Y}{\partial Q}}$ are averages of the partial derivatives $\frac{\partial m_X}{\partial Q}$ and $\frac{\partial m_Y}{\partial Q}$ with respect trait distributions of species X and Y respectively. As noted above, these partial derivatives capture frequency dependent selection. With respect to both trait-differences and offset-matching mechanisms, we find

$$\frac{\partial m_X}{\partial \bar{x}} = \frac{\partial m_Y}{\partial \bar{y}} = \frac{\partial m_X}{\partial G_X} = \frac{\partial m_Y}{\partial G_Y} = 0. \tag{S26}$$

Hence, frequency dependent selection is absent in our models of trait evolution. In contrast, frequency independent selection is summarized by;

$$\mathcal{D}\begin{cases} \frac{\partial \bar{m}_X}{\partial \bar{x}} = B_X, \\ \frac{\partial \bar{m}_Y}{\partial \bar{y}} = B_Y, \\ \frac{\partial \bar{m}_X}{\partial G_X} = 0, \\ \frac{\partial \bar{m}_Y}{\partial G_Y} = 0. \end{cases} \tag{S27}$$

$$\mathcal{O}\begin{cases} \frac{\partial \bar{m}_X}{\partial \bar{x}} = B_X(\bar{y} + \delta - \bar{x}), \\ \frac{\partial \bar{m}_Y}{\partial \bar{y}} = B_Y(\bar{x} + \delta - \bar{y}), \\ \frac{\partial \bar{m}_X}{\partial G_X} = B_X/2, \\ \frac{\partial \bar{m}_Y}{\partial G_Y} = B_Y/2. \end{cases} \tag{S28}$$

Taking the limits $N_X, N_Y \to \infty$ and incorporating the growth rate gradients above, equations (S25) return the ordinary differential equations;

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$$\mathcal{D}\begin{cases}\frac{d\bar{x}}{dt} = G_X B_X,\\ \frac{d\bar{y}}{dt} = G_Y B_Y,\\ \frac{dG_X}{dt} = \mu_X,\\ \frac{dG_Y}{dt} = \mu_Y,\end{cases} \tag{S29}$$

$$\mathcal{O}\begin{cases}\frac{d\bar{x}}{dt} = G_X B_X(\bar{y}+\delta-\bar{x}),\\ \frac{d\bar{y}}{dt} = G_Y B_Y(\bar{x}+\delta-\bar{y}),\\ \frac{dG_X}{dt} = \mu_X - G_X^2 B_X,\\ \frac{dG_Y}{dt} = \mu_Y - G_Y^2 B_Y.\end{cases} \tag{S30}$$

Then, to further simplify our models, for trait-differences we set $\mu_X = \mu_Y = 0$ and for offset-matching we set $G_X = \sqrt{\mu_X/B_X}$ and $G_Y = \sqrt{\mu_Y/B_Y}$ so that additive genetic variances remain fixed. This reduces each of our models to a pair of ordinary differential equations describing mean trait dynamics.

§D: Weak selection approximations

Here we show how various interaction mechanisms can be related through weak selection and/or large offset approximations.

Exponential trait-differences approximates logistic trait-differences under weak selection

Under the logistic trait-differences mechanism traditionally employed (Nuismer et. al., 2006; Nuismer 2017), fitness for an individual of species X that engages in a single interaction is captured by

$$w_X(x,y) = \frac{R_X E_X}{1+e^{2B_X(y-x)}}, \tag{S31}$$

where, as above, R_X and E_X denote the intrinsic fitness and the baseline effect on fitness due to an interaction and the variable B_X is the strength of biotic selection. We take a weak selection approximation by Taylor expanding around $B_X \approx 0$. To leading order this returns

$$w_X(x,y) \approx \frac{R_X E_X}{2}\left(1 + B_X(x-y)\right). \tag{S32}$$

Following the approach taken above, we calculate the continuous-time growth rate of individuals of species X with trait value x via $m_X(x,y) = \lim_{n\to\infty} n((w_X(x,y))^{1/n} - 1)$. This provides

$$m_X(x,y) = r_X + e_X + \ln\left(1 + B_X(x-y)\right), \tag{S33}$$

where $r_X = \ln R_X$ and $e_X = \ln E_X - \ln 2$. Following through again with our weak selection approximation, we have

$$m_X(x,y) \approx r_X + e_X + B_X(x-y). \tag{S34}$$

This approximation coincides with the growth rate we found using the exponential version of the trait-differences mechanism above. Hence, an exponential fitness curve provides an approximation for the logistic fitness curve when selection is weak.

Offset-matching approximates trait-differences under weak selection and a large offset

As mentioned in the main text, the offset-matching model is formally connected to the trait-differences model via a combined weak selection, large offset approximation. Recall individual fitness for species X under offset-matching is given by

$$w_X(x,y) = R_X E_X \exp\left(-\frac{B_X}{2}(y + \delta - x)^2\right), \tag{S35}$$

Under the substitution $B_X = \varepsilon^3$ and $\delta = 1/\varepsilon$, equation (S35) simplifies to

$$w_X(x,y) = R_X E_X \exp\left(-\varepsilon^3\frac{(y-x)^2}{2} - \varepsilon^2(y-x) + \frac{\varepsilon}{2}\right), \tag{S36}$$

Hence, a second order Taylor expansion around $\varepsilon \approx 0$ leads to

$$w_X(x,y) \approx R_X E_X\left(1 + \varepsilon^2(x-y) + \frac{\varepsilon}{2}\right). \tag{S37}$$

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This approximation of fitness has the same form as the approximation of the logistic trait-differences mechanism derived above. Thus, the offset-matching mechanism produces an approximation of trait-differences for weak selection and large offset.

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