Evolution of plasticity and character displacement in a fluctuating environment

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Abstract:

Species that compete for the same resource may undergo ecological character displacement (CD), where the phenotype of each species evolves to deviate from its optimum in the absence of competition. As most environments are not static, interspecific competition is likely to occur in environments that fluctuate over time, which can also cause the evolution of phenotypic plasticity for traits mediating the competition. We use a quantitative genetic model to study theoretically how a randomly fluctuating environment and evolution of plasticity influence the outcome of ecological CD between two competing species. We show that environmental fluctuations make the conditions for CD more stringent, requiring stronger competitive selection relative to stabilizing selection. This occurs because environmental fluctuations reduces the average population size, and thereby competition intensity. Evolving plasticity can restore CD by buffering the impact of environmental fluctuations through phenotypic tracking, to a degree that depends on environmental predictability. Somewhat paradoxically, competition that favors phenotypic divergence among species can cause convergent CD in plasticity, when this reduces the load caused by fluctuations in phenotypic divergence. Our results shed light on how competition influence evolution of the fundamental niche in a fluctuating environment.

Running title: Character displacement and evolving plasticity

Keywords: Competition, Character displacement, Phenotypic plasticity, Environmental predictability, Phenotypic divergence, Eco-evolutionary dynamics

Introduction

Species in their natural habitats need to adapt both to the abiotic challenges imposed by their physical environment, and to interacting species in their community. In the ecological literature, these biotic and abiotic components of the environment have been related to the classical concepts of fundamental versus realized niche (Hutchinson 1957; Holt 2009). The range of abiotic environments over which a species can sustain population growth when alone and at low density, and thus persist without inputs from a more productive source population, defines the fundamental niche (Hutchinson 1957; Pulliam 1988; Holt 2009). This range can be reduced by e.g. competition, leading to a smaller realized niche (Hutchinson 1957; Holt 2009). From an evolutionary standpoint, the biotic and abiotic environment act as different, sometimes conflicting, sources of selection, the relative importance of which may change along environmental gradients. Not only does the number of interacting species change along abiotic gradients, e.g. across latitude and latitude (von Humboldt and Bonpland 1807) or salinity (Williams 1998), but the intensity and even the type of interactions may also change (Maestre *et al.* 2009). An important consequence of such variation in the strength of ecological interactions along environmental gradients is that these interactions may influence how species adaptat to the abiotic environment, thus causing evolution of the fundamental niche.

One of the best-studied examples of evolution caused by interspecific interactions is ecological character displacement (hereafter character displacement, or CD) resulting from competition between species (Brown and Wilson 1956; Grant 1972; Schluter 2000). When sympatric species compete for the same resource, then any trait involved in their interaction can evolve away from its optimum in the absence of a competitor, thereby minimizing the detrimental demographic effect of competition. This process has been documented empirically in a number of systems, mostly in vertebrate animals (Pfennig and Murphy 2000; Grant and Grant 2006; Kirschel, Blumstein and Smith 2009; Stuart *et al.* 2014), and to a lesser extent in plants (Kooyers, James and Blackman 2017). Evidence for CD also comes from the reciprocal phenomenon of character release, whereby traits or niches evolve back to their optimum after interspecific competition has been relaxed (Grant 1972; Robinson and Wilson 1994; Dayan and Simberloff 1998; Bolnick *et al.* 2010).

Interestingly, some of the most emblematic examples of CD occur in environments that fluctuate substantially over time. For instance in Darwin's finches on the Galapagos island of Daphne Major, invasion of the competitor species *Geospiza magnirostris* caused evolution of reduced beak size in the local species *Geospiza fortis* (Grant and Grant 2006). This trait was also shown to be under strongly fluctuating selection in response to variable precipitation, leading to changes in the relative abundances of different seed types (Grant and Grant 2002). Fluctuating environments, when partly predictable, can in turn cause the evolution of phenotypic plasticity, whereby a single genotype can

express different phenotypes depending on the environment (Gavrilets and Scheiner 1993a; Tufto 2000; Lande 2009). In fact, phenotypic plasticity has been invoked as a powerful mechanism for character displacement (Pfennig and Pfennig 2009), as demonstrated for the dietary polyphenism of spadefoot toad tadpoles (Pfennig and Murphy 2000). While the most direct mechanism for plastic CD would involve phenotypic responses to competitor presence or abundance, plastic responses to resources themselves, or to an abiotic environmental variable that accurately predicts selection on the trait mediating competition, should also influence the outcome of CD in a fluctuating environment. When this occurs, and if evolution of plasticity in response to the abiotic environment can be altered by the presence of competitors, then this will have cascading consequences on environmental tolerance breadth (Chevin, Lande and Mace 2010; Lande 2014), such that competition will cause evolution of the fundamental niche (Holt 2009).

Evolutionary theory has investigated the conditions for character displacement in a constant environment, in particular regarding the relative strengths of disruptive selection caused by competition, versus stabilizing selection resulting from intrinsic adaptation to the environment (Slatkin 1980; Taper and Chase 1985; Taper and Case 1992; Doebeli 1996a). More recent theory has also included a spatially variable environment, to investigate how interspecific competition influences local adaptation and evolution of geographic ranges, for species that are spread over environmental gradients (Case and Taper 2000; Goldberg and Lande 2006). A recent extension of this model has also included phenotypic plasticity (Goldberg and Price 2022), but without allowing plasticity to evolve (see also Peacor *et al.* 2006 in a more specific context of predation risk, and without a quantiative genetic model). Furthermore, this theory of evolution of CD over environmental gradients relies almost entirely on numerical simulations, owing to the difficulty in reaching analytical solutions for eco-evolutionary dynamics with gene flow and competition in a spatially heterogeneous environment. Here, we instead focus on a temporally fluctuating environment (as done previously by Johansson 2008, but without plasticity), allowing us to reach analytical results that yield deeper insights into the role of environmental variability and phenotypic plasticity in evolution of CD. We show how, and how much, a fluctuating environment and evolving phenotypic plasticity modify the conditions for CD. We also demonstrate that competition that causes *divergent* CD for a trait can lead to *convergent* CD for its plasticity.

Model

Fitness and selection

We model two sympatric competing species that adapt to a variable environment via the same phenotypic trait. These species are denoted as 1 and 2, but most equations below are written in

generic form (with indices *i* and *j*) that applies to any of these species. We assume discrete non-overlapping generations, as this makes plastic, evolutionary, and demographic responses to the fluctuating environment simpler to analyze. Under weak selection and population growth, discrete-generation models approximates continuous-time models well.

We follow Case and Taper (2000) and Goldberg and Lande (2006) in assuming that a single quantitative trait *z* influences both the density-independent component of population growth (intrinsic rate of increase), and the density-dependent component resulting from competition, within and between species. More specifically, the change in population size of species *i* (on the log scale) is

$$\Delta \ln N_i = r + r_i^s + r_i^c \tag{1}$$

where the density-independent term

$$r_i^s = -\frac{(\theta - \bar{z}_i)^2 + \sigma_{z,i}^2}{2\sigma_s^2} \tag{2}$$

is largest when the mean phenotype $\bar{z}_i$ in species *i* matches the environmentally determined phenotypic optimum θ. This leads to stabilizing selection on $\bar{z}_i$, which is stronger when the width of the fitness peak is narrower (smaller σ_s^2). In line with previous models (Case and Taper 2000; Goldberg and Lande 2006), we assume that the phenotypic optimum θ is the same for both species, such that they would evolve to the same mean phenotype without competition. The competition component of population growth stems from logistic growth,

$$r_i^c = -\frac{r}{K_i}\sqrt{\frac{\sigma_u^2}{\sigma_u^2 + \sigma_z^2}}\left\{N_i + N_j \exp\left[-\frac{\left(\bar{z}_i - \bar{z}_j\right)^2}{4(\sigma_u^2 + \sigma_z^2)}\right]\right\}, \tag{3}$$

with K_i the carrying capacity of hypothetical population with optimal phenotype in species *i*. Equation (3) shows that the population growth rate decreases with increasing population density N_i of the focal species, but also with the density N_j of the competing species. However, the latter is modulated by an Gaussian function of the mean phenotypic divergence between species $\bar{z}_i - \bar{z}_j$, such that interspecific competition is stronger when species are more phenotypically similar. This captures Darwin's (1859) classic hypothesis that "competition will generally be most severe between those forms which are most nearly related to each other in habits, constitution, and structure", as verified experimentally with respect to phylogenetic similarity (Violle *et al.* 2011). The parameter σ_u^2 is the (squared) width of the resource utilization function, which determines the extent to which individuals overlap in their resource use, and thus how much they compete (Roughgarden 1979; Taper and Chase 1985). The term in the square root in eq. (3) arises from integration of the competition function among all interacting individuals within (and between) species (Case and Taper 2000; Goldberg and Lande 2006). It shows that the strength of density dependence is overall reduced

when the phenotype distribution (with variance σ_z^2) is broader than resource utilization, such that individuals overlap little in their resource use.

In line with standard quantitative genetics, we assume that the trait is polygenic, leading to a normal distribution of breeding values (heritable component) and phenotypes. Then using Lande's equation (Lande 1976, 1982), the response to selection by the mean phenotype in species *i* is

$$\Delta\bar{z}_i = G\beta_i = G(\beta_i^s + \beta_i^c), \tag{4}$$

where G is the additive genetic variance of *z*, and the directional selection gradient β_i is decomposed into a stabilizing selection component

$$\beta_i^s = \frac{\partial \bar{r}_i^s}{\partial \bar{z}_i} = -\frac{\bar{z}_i - \theta}{\sigma_s^2} \tag{5}$$

and a competition component

$$\beta_i^c = \frac{\partial \bar{r}_i^c}{\partial \bar{z}_i} = \left(\bar{z}_i - \bar{z}_j\right)\frac{rN_j}{2K_i}\frac{\sigma_u}{(\sigma_u^2 + \sigma_z^2)^{\frac{3}{2}}}\exp\left(-\frac{\left(\bar{z}_i - \bar{z}_j\right)^2}{4(\sigma_u^2 + \sigma_z^2)}\right). \tag{6}$$

The first component of selection β_i^s pulls the mean phenotype $\bar{z}_i$ of the focal species towards the optimum determined by the environment, at a rate that depends on the squared width σ_s^2 of the fitness peak. The second component β_i^c pushes $\bar{z}_i$ away from the mean phenotype $\bar{z}_j$ of its competitor species, at a rate that depends notably on the strength of density dependence, measured by $\frac{rN_j}{2K_i}$. Taken in isolation, β_i^s would lead to a stable equilibrium for $\bar{z}_i$ at the optimum θ (where $\beta_i^s = 0$ and $\frac{\partial \beta_i^s}{\partial \bar{z}_i} < 0$, hence the term stabilizing selection), while β_i^c would lead to an unstable equilibrium for $\bar{z}_i$ at the mean phenotype $\bar{z}_j$ of the competing species (where $\beta_i^c = 0$ and $\frac{\partial \beta_i^c}{\partial \bar{z}_i} > 0$, disruptive selection).

Fluctuating environment and plasticity

To model the influence of a fluctuating environment on character displacement, we assume that an environmental variable ε (e.g. temperature) causes linear changes in the optimum,

$$\theta = A + B\varepsilon_S \tag{7}$$

where B is the environmental sensitivity of selection (Lande 2009; Chevin, Lande and Mace 2010), and ε_S is the environment at the time of selection. The expressed phenotype may also depend on the environment through phenotypic plasticity. We assume developmental plasticity with a linear reaction norm,

$$z = a + b\varepsilon_D + e, \tag{8}$$

such the expressed phenotype depends the environment ε_D experienced when the individual matured and the plastic response was fixed (Lande 2009). The reaction norm intercept a and slope b – the latter quantifying plasticity – are assumed to be normally distributed quantitative traits, with

additive genetic variances G_a and G_b, respectively, and covariance G_{ab}. Reaction norm intercept is defined (without loss of generality) in a reference environment where it is uncorrelated with reaction norm slope ($G_{ab} = 0$), which always exists with linear reaction norms (Gavrilets and Scheiner 1993b; Lande 2009). The normally distributed residual component of phenotypic variation e has mean 0 and variance V_e. Under these assumptions, the selection gradients on reaction norm intercept and slope are

$$\beta_a = \beta_z \qquad (9)$$
$$\beta_b = \beta_z \varepsilon_D,$$

where β_z is the selection gradient on the expressed trait (defined as β_i for species *i* above) (Gavrilets and Scheiner 1993a; Lande 2009). Because the reaction norm parameters are not genetically correlated, their selection responses can be treated as univariate,

$$\Delta\bar{a} = G_a \beta_a \qquad (10)$$
$$\Delta\bar{b} = G_b \beta_b.$$

We assume that the environmental variable affecting both plasticity and selection fluctuates randomly over time, with a stationary normal distribution with mean 0 and variance σ_ε^2, and positive autocorrelation that declines geometrically with time difference. In other words, ε_t undergoes a first-order autoregressive process (AR1), or an Ornstein-Uhlenbeck process sampled at discrete intervals (Karlin and Taylor 1981). We define ρ as the autocorrelation of ε_t between development and selection, separated by a time interval τ (lower than the generation time), with autocorrelation over any other time interval Δt being $\rho^{\frac{\Delta t}{\tau}}$. If the competing species have different developmental times, then ρ is defined for species 1 (with delay τ_1 between development and selection). Note that such stationary stochastic fluctuations different from the non-stationary, random walk modeled by Johansson (2008) under a similar form of competitive selection.

Mathematical analysis

To make the model analytically tractable, we relied on several assumptions, some of which we relaxed in simulations below. First, we mostly focused on the symmetric case where all demographic and selective parameters are identical in both species (i.e. same carrying capacity K, phenotypic variance σ_z^2, etc). This not only simplifies the system by halving its number of parameters and dynamical variables, but also corresponds to the most favorable case for character displacement to exist in both species, rather than competitive exclusion and maintenance of a single species with optimum mean phenotype. In addition, since the full eco-evolutionary system with joint demographic (eq. 1) and evolutionary (eq. 4) dynamics proved challenging to solve (or led to unwieldy results), our strategy to identify threshold conditions for character displacement (CD) was to derive the equilibrium population density assuming that the mean phenotype was at the optimum

in both species ($\bar{z}_1 = \bar{z}_2 = \theta$, i.e. no CD) in eq. (1), and then used this equilibrium population density to search for evolutionary equilibrium using eq. (4).

Simulations

The behavior of the model under scenarios of interest was explored by thorough simulations, using a program coded in Python3. These eco-evolutionary simulations consisted of joint recursions for demography (eqs. 1-3) and evolution (eqs 4-6), assuming constant genetic variance for simplicity (as in similar models by Case and Taper 2000; Goldberg and Lande 2006; Goldberg and Price 2022). This assumption amounts to considering that genetic variance has reached an equilibrium between mutation and stabilizing selection, and neglecting the additional noise caused by fluctuations of genetic variance around this equilibrium. The simulations took as input the initial values for the reaction norm parameters $\bar{a}_0$, $\bar{b}_0$ and population size N_0, for each species. The scenarios we investigated differed regarding whether or not they included fluctuating selection ($B = 0$ vs $B \neq 0$), initial plasticity ($\bar{b}_0 = 0$ vs $\bar{b}_0 \neq 0$), and evolution of plasticity ($G_b = 0$ vs $G_b \neq 0$). Other parameters that varied (summarized in Table 1) were the variance and autocorrelation of environmental fluctuations (σ_ε^2 and ρ), and the delay between maturation and selection, which could differ between species (τ_1 and τ_2).

For each scenario, we conducted extensive parameter exploration with respect to the peak width for stabilizing selection (σ_s^2) and the width of utilization function (σ_u^2). We used the package pypet (Meyer and Obermayer 2016), which allows efficient multiprocessing and facilitates parameter manipulation for multiple runs of a model. For each parameter combination in this exploration, the populations were left to evolve for >200,000 generations, and the last 10,000 generations were averaged over time to obtain the stationary values for the mean reaction norms elevation $\bar{a}$ and slope $\bar{b}$ (plasticity), expressed trait $\bar{z}$, and population size N, for each species. The complete commented code along with execution instructions is hosted along with results at *ANONYMIZED*.

Results

We wish to understand how a fluctuating environment and evolving phenotypic plasticity affect evolution of character displacement (CD) in two sympatric competing species. As a point of reference to characterize these effects, we start by analyzing a model with a constant environment and no plasticity. Our main argument focuses on symmetric conditions where both species are equivalent and interchangeable, such that most indexes for species can be dropped.

CD depends on the relative strengths of stabilizing vs competitive selection

In a constant environment, an evolutionary equilibrium occurs when stabilizing selection exactly compensates for competition-mediated disruptive selection, that is, when $\beta_i^s = -\beta_i^c$ in both species (from equations 4-6). A trivial solution is where both gradients vanish, $\beta_i^s = \beta_i^c = 0$ (for $i = 1, 2$), such that the mean phenotype is at the optimum for both species and there is no CD ($\bar{z}_1 = \bar{z}_2 = \theta$). Another non-trivial solution with CD is straightforward to find in the symmetric case where phenotypic maladaptation and equilibrium population size are identical in both species. Then denoting as $d = \bar{z}_1 - \theta$ the deviation from optimum in species 1 (and thus $\bar{z}_2 - \theta = -d$ in species 2), solving for $\Delta\bar{z}_i = 0$ in eq. (4) assuming $d \neq 0$ leads to

$$d = \pm\sqrt{(\sigma_u^2 + \sigma_z^2)\ln\left(\frac{rN}{K}\frac{\sigma_u\sigma_s^2}{(\sigma_u^2 + \sigma_z^2)^{\frac{3}{2}}}\right)}. \tag{11}$$

This solution is real when the term inside the logarithm is larger than 1, such that d is the square root is positive number. This leads to a criterion for CD in terms of the width σ_s of the fitness peak,

$$\sigma_s^2 \geq \frac{K}{rN}\sigma_u^2\left(1 + \frac{\sigma_z^2}{\sigma_u^2}\right)^{\frac{3}{2}}, \tag{12}$$

Equation (12) shows that CD can only occur when stabilizing selection is sufficiently weak relative to competitive selection (σ_s^2 is sufficiently large relative to σ_u^2). Stronger competitive selection, caused by either a larger (scaled) population density N/K or a narrower utilization curve (smaller σ_u^2, as long as $\sigma_u^2 > \sigma_z^2/2$) allows CD to exist in the face of stronger stabilizing selection. Nevertheless, the criterion in eq. (12) is a necessary but not sufficient condition for CD to exist. If both species start exactly at the optimum phenotype, then they remain "trapped" in the trivial equilibrium without CD, even for parameter values that could lead to CD. This trivial equilibrium is however unstable, and any minor deviation from it (caused by e.g. random genetic drift or a fluctuating environment, see below) eventually leads to CD when criterion (12) is met. This is illustrated in Figure 1A, where both competing species start with mean phenotypes close to the optimum θ, but slight deviations above and below this unstable equilibrium leads to phenotypic divergence and character displacement. Note also that the threshold in eq. (12) correspond to conditions at which $d = 0$, such that the equilibrium with CD disappears (bifurcation).

The criterion for CD can be expressed in a simpler form by replacing the scaled population density N/K by its equilibrium value. Taking advantage of the fact that the deviation from optimum is negligible near the threshold for CD (at which $\bar{z}_1 - \theta = \bar{z}_2 - \theta = \bar{z}_1 - \bar{z}_2 \approx 0$), we can combine

eqs (1) to (3) to get the equilibrium population size (identical in both species in the symmetric system),

$$N_{\mathrm{eq}|0} = \frac{K}{2\,r}\left(r - \frac{\sigma_z^2}{2\sigma_s^2}\right)\sqrt{1 + \frac{\sigma_z^2}{\sigma_u^2}}. \tag{13}$$

Equation (13) shows that the equilibrium population size is smaller when stabilizing selection is stronger (smaller σ_s^2), all the more as phenotypic variance σ_z^2 is large, because more individuals have phenotypes away from the optimum, thus reducing population growth through a standing load (Lande and Shannon 1996). In contrast, the equilibrium population size becomes larger under narrower utilization function (smaller σ_u^2).

Replacing the population density in eq. (12) by its equilibrium without CD from eq. (13) leads, after some algebra, to a much simpler criterion for CD,

$$\sigma_s^2 \geq \frac{4\sigma_u^2 + 5\sigma_z^2}{2r}. \tag{14}$$

Importantly, the threshold for CD in eq. (14) only depends on the width of the utilization function, the phenotypic variance, and the intrinsic rate of increase of the species. In particular, eq. (14) predicts that the boundary of the parameter space allowing for CD is linear in the σ_u^2 x σ_s^2 phase plane, with steeper slope when the intrinsic growth rate *r* is smaller. These predictions from eqs (12) and (14) are compared to intensive numerical simulations across values of σ_u^2 and σ_s^2 in Figure 2A.

Lastly, inserting the predicted population size from (13) into the character displacement in (11) yields

$$d = \pm\sqrt{(\sigma_u^2 + \sigma_z^2)\ln\left(\frac{2\sigma_s^2 r - \sigma_z^2}{4(\sigma_u^2 + \sigma_z^2)}\right)}. \tag{15}$$

Because this prediction is based on an equilibrium population size N_{eq} that neglects CD, it is expected to underestimate the amount of CD, as relaxed competition under CD leads to higher equilibrium population size, and thus to higher CD (larger d in eq. 11). This can be seen in Figure 1A, where the dashed arrows representing eq. (15) underestimate the true CD, while the prediction from eq. (11) combined with the actual equilibrium population size from simulations (continuous arrow) matches the simulated CD.

Environmental fluctuations can cause the collapse of CD

When a randomly fluctuating environment causes the optimum phenotype to vary over time, the evolutionary process is no longer deterministic but stochastic, even in an infinite population. Below we focus on expectations under this process, denoted as $\langle\ \rangle$, but keeping in mind that stochasticity may lead to substantial variation around this expectation.

To understand the influence of random environmental fluctuations on the expected CD, we start by observing that fluctuations in the optimum only affect the component of fitness due to stabilizing selection r_i^s (eq. 2), not the competition term r_i^c (eq. 3). In addition, the expressions for the selection gradient components in eq. (5) and (6) remain essentially unchanged by fluctuations, if we replace population sizes and mean phenotypes by their expectations. However, the expected population size (appearing in eq. (6)) is biased downwards, because environmental fluctuations add stochastic variance to the phenotypic mismatch with optimum, causing a reduction in expected Malthusian fitness (via eq. 2), which can be described as the stochastic lag load (Chevin, Cotto and Ashander 2017). Denoting as x the stochastic component of deviations from the optimum, with mean 0 and variance σ_x^2, the expected stabilizing selection component of fitness is

$$\langle r_i^s \rangle = -\frac{\sigma_z^2 + \sigma_x^2 + (\langle\theta\rangle - \langle\bar{z}_i\rangle)^2}{2\sigma_s^2}. \tag{16}$$

Replacing this for eq. (2) yields for the expected population size with fluctuations, in the symmetric case without CD,

$$\begin{aligned}\langle N_{\mathrm{eq|Fluct}} \rangle &= \frac{K}{2\,r}\left(r - \frac{\sigma_z^2 + \sigma_x^2}{2\sigma_s^2}\right)\sqrt{1 + \frac{\sigma_z^2}{\sigma_u^2}} \\ &= \left(1 - \frac{\sigma_x^2}{2r\sigma_s^2 - \sigma_z^2}\right) N_{\mathrm{eq|0}},\end{aligned} \tag{17}$$

where $N_{\mathrm{eq|0}}$ is the equilibrium population size in a constant environment (eq. 13). The main influence of fluctuations in the optimum on character displacement is thus to reduce the average population size in by a proportion $\frac{\sigma_x^2}{2r\sigma_s^2 - \sigma_z^2}$ (assuming stabilizing selection is weak enough that $2r\sigma_s^2 > \sigma_z^2$). As lower population size leads to weaker competitive selection, stabilizing selection then also needs to be weaker to allow for CD. This prediction can be made more precise by inserting eq. (17) into eq. (11), leading to the criterion for CD with fluctuations

$$\sigma_s^2 \geq \frac{4\sigma_u^2 + 5\sigma_z^2 + \sigma_x^2}{2r}. \tag{18}$$

Hence, the threshold peak width σ_s^2 above which CD is possible increases by $\frac{\sigma_x^2}{2r}$ relative to the case without fluctuations, where σ_x^2 is the variance of deviations from the optimum (phenotypic mismatch). Interestingly, the criterion otherwise retains the same dependency to σ_u^2, that is, the threshold remains a straight line with same slope in the σ_u^2 x σ_s^2 plane, but shifted upwards by $\frac{\sigma_x^2}{2r}$. This prediction is compared to numerical simulations across values of σ_u^2 and σ_s^2 in Figure 2A (blue line and symbols). In the simulations, σ_x^2 was replaced by σ_θ^2, the variance of the optimum phenotype, thereby neglecting evolutionary tracking of the optimum by the mean phenotype. This will be a good approximation as long as additive genetic variance of the trait and autocorrelation of

the optimum are not large; when these assumptions are violated, more complete expressions exist for adaptive tracking of an autocorrelated random optimum (Charlesworth 1993; Lande and Shannon 1996; Chevin 2013; Chevin, Cotto and Ashander 2017).

Character displacement may be preserved on average under moderate environmental fluctuations, but with reduced magnitude as illustrated in Figure 1B. However, large environmental fluctuations cause a collapse of CD, where two species that experienced CD in a constant (or moderately fluctuating) environment converge to the same mean phenotype at the average optimum $\langle\theta\rangle$ following onset (or amplification) of environmental fluctuations (Figure 1C). This occurs because the criterion for CD requires weaker stabilizing selection under a fluctuating optimum (eq. 18), such that any combination of strengths of stabilizing and competitive selection in between the blue and orange lines in Figure 2B is susceptible to collapse of CD under environmental fluctuations. Our results are consistent with those of Johansson (2008), who also found (albeit with simulations only, not complemented by analytical solutions) that a randomly fluctuating environment (in his case, a random walk) can lead to reduced population size and possibly extinction, altering the outcome of evolution under competitive selection.

Evolution of plasticity can restore CD by buffering the impact of fluctuations

The influence of phenotypic plasticity can also be understood through its effect on the stochastic variance of the mismatch with optimum. With linear reaction norms and changes in the optimum with the environment (following eqs. 7-8), neglecting adaptive tracking by evolution for simplicity (but see Michel, Chevin and Knouft 2014; Tufto 2015), the variance in phenotypic deviations from the optimum is

$$\sigma_x^2 = \sigma_\theta^2(1 + b_B(b_B - 2\rho)) \tag{19}$$

where $b_B = \bar{b}/B$ is the reaction norm slope scaled to the slope of the optimum, and ρ is the autocorrelation of the environment between development and selection (Chevin, Collins and Lefèvre 2013). This shows that phenotypic plasticity with the same sign as temporal autocorrelation ρ, and magnitude lower that $|2\rho|$, reduces the magnitude of fluctuations in mismatch with optimum. If plasticity varies genetically, then in the long run it will evolve to match the level of environmental predictability, $b_B = \rho$ (Gavrilets and Scheiner 1993a; Lande 2009), such that

$$\sigma_x^2 = \sigma_\theta^2(1 - \rho^2) \tag{20}$$

Hence, evolution of adaptive plasticity buffers the influence of a moving optimum on fluctuating selection, to an extent that depends on the predictability of selection upon development, here quantified by environmental autocorrelation ρ.

Combining eqs (18) and (21), the condition for character displacement with evolving plasticity becomes

$$\sigma_s^2 \geq \frac{4\sigma_u^2 + 5\sigma_z^2 + \sigma_\theta^2(1-\rho^2)}{2r}. \tag{21}$$

This shows that evolving plasticity can partly compensate for the detrimental effect of environmental fluctuations on CD, to an extent that depends on the predictability of selection upon development. With perfectly predictable selection ($\rho^2 = 1$) the influence of environmental fluctuations entirely vanishes because all fluctuations in the optimum can be tracked perfectly by plasticity, such that eq. (21) collapses to eq. (14).

Consider a scenario where the regime of environmental fluctuations shifts over time. While an abrupt increase in environmental fluctuations can initially lead to the collapse of CD, evolution of adaptive plasticity to match the level of environmental predictability in the longer run may later restore CD, by reducing the impact of fluctuations on population dynamics and competition strength. This scenario is illustrated in Figure 1D-E, in the case where there is initially no plasticity ($\bar{b} = 0$), as expected in an initially fully unpredictable environment. As long as plasticity remains low (left in Fig. 1E), the mean phenotypes of both species assessed in the mean environment (reaction norm intercept $\bar{a}$) are similar, and close to the mean optimum (left in Fig. 1D). However, after plasticity has evolved in both species to its equilibrium determined by environmental predictability, $\bar{b} = B\rho$ (right in Fig 1E), reaction norms intercepts $\bar{a}$ start to diverge among species, leading to CD (right in Fig 1D). This scenario, where evolution of plasticity can restore CD that was previously prevented by environmental fluctuations, occurs in the parameter range in between the blue and green lines in Figure 2C, which is larger under higher environmental predictability.

Importantly, the same level of phenotypic plasticity evolves in both species if they experience the same predictability of selection (Figure 1E). A small divergence in plasticity can be observed in the parameter space leading to phenotypic CD (Figure 2D), but with a magnitude that is negligible relative to the mean plasticity (Figure 1E). Once this equilibrium plasticity is achieved, plastic responses are essentially identical in both species, such that their phenotypic divergence remains constant across environments, even though plasticity may cause phenotypic fluctuations to be larger in both species (as shown in the inset of Figure 1D). However, in the transient phase before this evolutionary equilibrium is reached, any difference in plasticity between species will cause their phenotypic divergence to fluctuate across environments. Interestingly, this fluctuation in phenotypic divergence causes an additional component of selection on plasticity, which proves particularly important in situations where different levels of plasticity are favored in different species, as we study below.

Competition can cause convergent character displacement in plasticity

When two competing species have slightly different mechanisms for perceiving environmental cues, or different time windows of sensitivity to these cues (because of e.g. differences in life-history), then they may experience different predictabilities of selection upon induction of the plastic trait. This will cause evolutionary divergence in phenotypic plasticity in the absence of competition. However, the interplay of this process with competitive selection and character displacement is more complex.

First, when species differ in plasticity and environmental cues, the eco-evolutionary system is no longer symmetric (even when the symmetry assumptions above hold), because interspecific differences in environmental predictabilities lead to differences in expected maladaptation and population size in a fluctuating environment. Second, the interspecific difference in mean phenotype is no longer the same in all environments when they differ in plasticity (and environments of development), but instead changes with the environment. We thus need to distinguish character displacement in the reference environment (i.e., CD in mean reaction norm intercept $\bar{a}$) from CD in plasticity (i.e., CD in mean reaction norm slope $\bar{b}$). When the environment fluctuates over time, differences in plasticity also cause the magnitude of competitive selection to fluctuate (because of fluctuations in phenotypic divergence, from eq. 6), which affects the expected selection gradients on the trait and its plasticity.

The conditions for CD in reaction norm intercept become more stringent when species differ in plasticity and environmental cues. As shown in the Appendix, the formula for the equilibrium CD then takes a similar form as eq. (11), but with two main changes. First, the population size that matters is the average among species $N_m = (N_1 + N_2)/2$ (while the symmetric model above assumed that $N_1 = N_2 = N$). If one of the species experiences lower environmental predictability, then its stochastic lag load will be higher (even after plasticity has evolved to its equilibrium, following eq. 20), and its expected population size will be lower. Unless this is compensated by a symmetric increase in equilibrium population size in the other species, N_m will be overall reduced by asymmetries introduced by differences in plasticity. If environmental fluctuations are very large, the expected population growth rate can even become negative for the species experiencing low environmental predictability, causing them to decline towards extinction (Lande and Shannon 1996; Chevin, Cotto and Ashander 2017), affecting coexistence and the scope for CD.

The second difference with eq. (11) is that $\sigma_u^2 + \sigma_z^2$ is replaced by $\sigma_T^2 = \sigma_u^2 + \sigma_z^2 + \frac{\sigma_\delta^2}{2}$, where

$$\sigma_\delta^2 = \sigma_\varepsilon^2(\bar{b}_1^2 + \bar{b}_2^2 - 2\bar{b}_1\bar{b}_2\rho_{12}) \tag{22}$$

is the temporal variance in mean phenotypic divergence among species, arising from their differential plastic responses to the environmental fluctuations, with variance σ_ε^2 and autocorrelation ρ_{12} between the timings of development in species 1 and 2. As shown in eq. (22), the magnitude of

fluctuations in phenotypic divergence is larger when the species differ more in plasticity, and/or have uncorrelated environments of development (small ρ_{12}). Based on the results in the Appendix, we can then define an approximate criterion for CD similar to eq. (21), leading to

$$\sigma_s^2 \geq \frac{4\left(\sigma_u^2 + \sigma_\delta^2/2\right) + 5\sigma_z^2 + \sigma_\theta^2(1-\rho_m^2)}{2r}. \tag{23}$$

where $\rho_m^2 = \frac{\rho_{1S}^2+\rho_{2S}^2}{2}$ is the mean squared autocorrelation between development and selection among species. This shows that, all else being equal, stabilizing selection needs be to weaker (σ_s^2 larger) for CD to exist at the phenotypic level, all the more so as environmental fluctuations are large and species differ in plasticity, such that σ_δ^2 is large. When the conditions for CD in reaction norm intercept are satisfied, its relative magnitude in each species depends on the relative abundance of the other species exerting selection on it (that is, CD in species 1 is proportional to N_2/N_m, and reciprocally; Appendix).

Beyond its effect on reaction norm intercept, competition also influences the evolution of plasticity (reaction norms slope) when environmental cues differ among species. As shown in the Appendix, the expected selection gradient on plasticity in species i is then

$$\langle\beta_{b,i}\rangle = \sigma_\varepsilon^2\left[-\frac{\langle\bar{b}_i\rangle - B\,\rho_{iS}}{\sigma_s^2} + \frac{r\langle N_j\rangle}{K}\varphi\left(\langle\bar{b}_i\rangle - \langle\bar{b}_j\rangle\rho_{12}\right)\right] \tag{24}$$

where

$$\varphi = \frac{\sigma_u}{2\sigma_T^3}e^{-\frac{d_m^2}{\sigma_T^2}}\left(1-\frac{2d_m^2}{\sigma_T^2}\right), \tag{25}$$

$d_m = \frac{|d_1-d_2|}{2}$ is the mean magnitude of CD (deviation from optimum) in the reference environment (equal to half the interspecific divergence in reaction norm intercept), and ρ_{iS} is the correlation between the environment of selection in species i and the environment of selection. Equation (24) first shows that selection on plasticity is overall stronger, and thus plasticity will evolve faster, when the variance σ_ε^2 of environmental fluctuations is larger, consistent with previous theory (Gavrilets and Scheiner 1993a; Lande 2009). The terms in the brackets of eq. (24) further show how the two components of selection influence evolution of plasticity. Stabilizing selection (first term in brackets) pulls the mean plasticity in species i towards the slope of the optimum B multiplied by the predictability of selection in that species quantified by ρ_{iS}, consistent with previous theory without competition (Gavrilets and Scheiner 1993a; Lande 2009; Tufto 2015). On the other hand, competitive selection (second term in brackets) causes plasticity in species i to evolve in response to the plasticity in the other species $\bar{b}_j$, weighted by the correlation between their environments of development ρ_{12}.

The direction of this effect of competitive selection depends on the sign of φ, which itself depends on divergence in reaction norm intercept, quantified by d_m (from eq. 25). When d_m is small

($d_m^2 < \sigma_r^2/2$), then $\varphi > 0$ and plasticity in species *i* is pushed away from plasticity in the other species *j*, causing divergent CD in plasticity. However in the opposite regime where d_m is large ($d_m^2 > \sigma_r^2/2$), then $\varphi < 0$ and plasticity in species *i* is *pulled towards* the plasticity in species *j*. In other words, for large enough phenotypic CD in reaction norm intercept, competitive selection causes *convergent* rather than *divergent* CD for plasticity. This occurs because, when species differ in plasticity and the environment fluctuates, their phenotypic divergence also fluctuates (with variance σ_δ^2, eq. 22), which decreases the expected mean fitness (thus favoring more convergent plasticity) when CD in intercept is large, but increases it (favoring more divergent plasticity) in the opposite case. Replacing d_m by its expectation, the condition for competitive selection to cause convergent CD in plasticity becomes (Appendix)

$$\frac{rN_m}{K}\frac{\sigma_s^2}{\sigma_u^2}\left(1+\frac{\sigma_z^2}{\sigma_u^2}+\frac{1}{2}\frac{\sigma_\delta^2}{\sigma_u^2}\right)^{-\frac{3}{2}} > e^{\frac{1}{2}} \approx 1.65 \tag{26}$$

This predicts that, all else being equal, convergent CD in plasticity is more likely when (i) environmental fluctuations are small (because this leads to smaller σ_δ^2, from eq. 22); (ii) stabilizing selection is weak (large σ_s^2) and competitive selection is strong (small σ_u^2); and (iii) the mean population size in both species is large (large N_m). Conditions (ii) and (iii) coincide with those for large CD at the phenotypic level (as shown in previous sections), consistent with the fact that large (divergent) phenotypic CD in the reference environment (CD in intercept) favors convergent CD for plasticity. The net CD in plasticity under the joint influences of stabilizing and competitive selection depends on the relative magnitudes of the two components of selection, which from eq. (24) is determined by the product $r\langle N_j\rangle\varphi\sigma_s^2/K$; competitive selection dominates when this term is larger than 1, while stabilizing selection dominating otherwise.

These predictions are confronted to simulations results in Figure 3. We considered two species that differ in their time windows of sensitivity to a single fluctuating environmental variable, thus effectively responding to distinct (but correlated) cues. As predicted by the analysis, the magnitude of environmental fluctuations has critical qualitative and quantitative impacts on CD in the trait and its plasticity. When environmental fluctuations are moderate (left panels in Fig. 3), phenotypic divergence in reaction norm intercept depends little on the between-species difference in the timing of development relative to selection (τ_1 vs τ_2). In Figure 3A, the absolute difference in mean reaction intercept remains close to 9 regardless of τ_1 and τ_2, matching that without environmental fluctuations under the same strengths of stabilizing and competitive selection (compare with Fig 1A). On the other hand, the divergence in plasticity among species is strongly dependent on the difference in developmental timings. The dashed line in Figure 3B represents the predicted difference in plasticity that would evolve without competition, resulting from the between-species

difference in the predictability of cues (term $\langle \bar{b}_i \rangle - B\,\rho_{iS}$ in eq. (24)). The true divergence in mean plasticity (solid lines in Figure 3B) is always below than this baseline, because competitive selection leads to convergent CD in plasticity in these conditions.

The evolutionary outcome is qualitatively changed when the variance of environmental fluctuations is much larger (right panels in Figure 3). In this context, a situation similar to that observed under moderate fluctuations (substantial divergent CD in intercept and convergent CD for plasticity) only exists when species have similar developmental timings τ_i (i.e. near $\tau_2 = 0.1$ for the blue line, $\tau_2 = 0.5$ for the green line, and $\tau_2 = 0.9$ for the red line). Indeed, similar τ_i among species leads to a similar predictability of selection, selecting for similar plasticity, and thus moderate value of σ_δ^2 (from eq. 22), which favors convergent plasticity (from eq. 26). Conversely for more different developmental timings τ_i (and thus larger σ_δ^2), CD in reaction norm intercept collapses (Fig 3B), and divergent rather than convergent CD is observed for plasticity (solid line above dashed line in Fig 3D).

The lower panels in Figure 3 (EF) shows how divergence in plasticity, scaled to its expectation without competition, depends on the strengths of stabilizing and competitive selection. As expected from eq. (26), weak stabilizing selection and strong competitive selection (large σ_s^2 and small σ_u^2, upper left corner in Figure 3E,F) lead to convergent CD in plasticity (dark blue colors in Fig. 3E-F). In contrast, smaller σ_s^2 and larger σ_u^2 are characterized by divergent CD in plasticity (warmer colours in Figure 3 E-F). These effects can be understood through the influence of CD in reaction norm intercept on CD in plasticity, predicted by eqs (24-25). The white dots in Figure 3E-F show conditions where CD in plasticity is convergent, the black dots are where CD in intercept is lower than the threshold in eqs (24-25) ($d_m^2 < \sigma_T^2/2$), and grey dots jointly meet both these criteria. Black and white dots almost perfectly partition all the parameter space with CD (except for a small overlap with gray dots at their boundary), confirming that the magnitude of phenotypic CD in the average environment is a very good predictor of whether CD in plasticity is convergent (under large phenotypic CD) or divergent (under small phenotypic CD). The parameter regions leading to divergent CD in plasticity lies near the boundary for CD to exist at the phenotypic level, shown as black line (based on eq. 23) in figure 3EF.

As the magnitude of environmental fluctuations increases, the parameter region leading to divergent CD in plasticity expands (Figure 3F vs 3E), but convergent CD also becomes more pronounced (darker blue in upper left corner in Figure 3F). Furthermore, large environmental fluctuations are characterized by high instability, where the system can change from divergent to convergent CD in plasticity (and concomitantly from large to no CD in reaction norm intercept) for a small parameter change, probably because of an influence of initial conditions (Fig. 3F). This instability can also by visualized in Fig. 3D, where the solid green line "flickers" as τ_2 reaches large values.

The lower right corner in Figure 3E-F, with small σ_s^2 and larger σ_u^2, leads to extinction of at least one of the species, thus preventing computation of their divergence. This occurs because of the stochastic load imposed by a randomly fluctuating environment. Note that the parameter region leading to extinction moves up under larger environmental fluctuations (Figure 3F). This means that larger environmental fluctuations cause extinction even when the fitness peak is broader, as expected since the stochastic load depends on the ratio of the magnitude of environmental fluctuations σ_ε^2 to the strength of stabilizing selection σ_s^2 (Lande and Shannon 1996; Chevin, Cotto and Ashander 2017).

Discussion

Both the biotic and abiotic environment contribute to the niche of a species, but how much each of them drives adaptation, and how important their interaction is for evolution, remain little understood. When the physical environment changes (e.g. rising temperature), is directional selection mostly caused by this change *per se*, or by interacting species that respond to it? And how often does adaptation to interacting species cause evolution of the fundamental niche? As the intensity of ecological interactions varies along gradients of e.g. temperature or salinity (von Humboldt and Bonpland 1807; Williams 1998; Maestre *et al.* 2009), so will vary the selective pressures, from being driven mostly by the physical environment, to resulting mostly from interacting species. If these components of selection act on the same or on correlated traits (as implied by the notion of ecological trade-offs), then selection caused by ecological interactions will influence adaptation to the abiotic environment, even when latter is assessed in the absence of interactors. Therefore, studies investigating environmental tolerance curves in the laboratory, without interacting species, are likely to reveal variation in fitness that partly reflects adaptation to interacting species along the same environmental gradient in nature.

Ecological character displacement (CD) mediated by competition illustrates this phenomenon well. In environments where CD is most pronounced, mean phenotypes deviate from their optimum set by the intrinsic requirements of the environment, and thus appear as maladapted in the absence of competitors. As a result, the environment where the tolerance curve reaches its maximum is displaced, and the fundamental niche is shifted towards environments where competition has been less intense over recent evolutionary history (Slatkin 1980; Case and Taper 2000). Nevertheless, we show here that this process can be altered when the environment fluctuates over time. A randomly fluctuating optimum causes variance in phenotypic mismatch that reduces the expected mean fitness, such that the equilibrium population size is lower on average than without fluctuations (Lynch and Lande 1993; Lande and Shannon 1996; Chevin, Cotto and Ashander 2017). This leads to decreased competition intensity, tilting the balance from competitive towards stabilizing selection,

487 and reducing the likelihood and magnitude of CD (as also shown by Johansson 2008 under a random
488 walk, rather than the stationary fluctuations as assumed here). This influence of a fluctuating
489 environment on CD, mediated by the effect of environmental fluctuations on the expected
490 population size, and thus on the intensity of competition, is similar to the way environmental
491 fluctuations can cause shifts from *K*- towards *r*-selected phenotypes under density-dependent
492 selection (Lande, Engen and Sæther 2009; Engen, Lande and Sæther 2013).

493 Adaptive phenotypic plasticity can partly reverse this influence of environmental fluctuations
494 on CD, to an extent that depends on the predictability of fluctuations. That phenotypic plasticity can
495 buffer the influence of environmental fluctuations on maladaptation and demography when it
496 matches the level of environmental predictability has long been known theoretically (Reed *et al.*
497 2010; Chevin, Collins and Lefèvre 2013). Empirically, a meta-analysis of breeding time in birds and
498 mammals has indeed shown that plastic responses covary with movements of the optimum
499 phenotype, thus partly buffering the impact of environmental fluctuations on phenotypic mismatch
500 (de Villemereuil *et al.* 2020). On the other hand, detailed analysis of one population of great tits in
501 this database showed that greater phenotypic mismatch does not necessarily lead to reduced
502 population growth, because fewer surviving offspring at this stage of the life cycle is compensated to
503 reduced competition at a later stage, with no net demographic cost (Reed *et al.* 2013). Beyond this
504 study case, the extent to which phenotypic mismatch (including the influence of phenotypic
505 plasticity) drives population dynamics, the strength of competition, and evolution of CD, will depend
506 on the degree of excess fertility in a population, that is, on how much the total number offspring
507 exceeds the requirement for replacement (as discussed in Chevin and Bridle 2025).

508 An unexpected outcome of our analysis was that competition that favors more different
509 phenotypes, as commonly assumed in models of character displacement (Slatkin 1980; Taper and
510 Case 1992; Doebeli 1996b; Goldberg and Lande 2006), can lead to *convergent* rather than *divergent*
511 phenotypic plasticity among species (Figure 3). That character displacement can lead to phenotypic
512 convergence has been highlighted previously (Grant 1972; Abrams 1987; Fox and Vasseur 2008), but
513 not with respect to phenotypic plasticity under a simple scenario of competition for nutritionally
514 substitutable resources. While this result seems paradoxical, it is in fact meaningful in hindsight.
515 When species differ in their degree of phenotypic plasticity, their phenotypic divergence changes
516 plastically across environments. Such plastic variation in CD was not specifically favored in the simple
517 ecological scenarios we explored (neither was it in previous work on ecological CD). In the presence
518 of environmental fluctuations, differences in plasticity cause an additional term in expected mean
519 fitness and selection gradients, which favors more similar plasticity among species when their CD in
520 the average environment is large (eqs. 24-25). This effect may however be reversed in more complex
521 scenarios favoring variation in phenotypic divergence among environments. This could occur when

the balance between competitive and stabilizing selection varies across environments, for instance because of a change in carrying capacity (see eqs 4-6 and 11). We have briefly explored this type of scenario (not shown), but have not been able to find conditions cancelling convergent CD in plasticity, so we leave a more thorough investigation of this question to future studies.

More generally, extensions to other scenarios would be worth investigating. In particular, we assumed that a single trait mediates both competition and adaptation to the abiotic environment, in line with earlier models of CD (Slatkin 1980; Case and Taper 2000; Goldberg and Lande 2006; Goldberg and Price 2022), and that a single environmental variable influences both the position of the optimum and plasticity, also in line with most models of plasticity (de Jong 1990; Gavrilets and Scheiner 1993a; Lande 2009; Goldberg and Price 2022). Regarding the latter, temperature for instance is known to induce plasticity in a number of traits, and to also affect phenotypic selection, sometimes on the same traits. For instance breeding time in hole-nesting birds responds plastically to temperature, and has an optimum that also depends on temperature (Charmantier *et al.* 2008; Reed *et al.* 2013; Chevin, Visser and Tufto 2015). The timing of breeding should also impact the intensity of resource competition, since an enormous amount of caterpillars are required to feed each chick until fledgling (Visser, Holleman and Gienapp 2006), such that synchronicity with other individuals or species should increase competition strength. Beyond this example, it is unclear to what extent the same traits are likely to mediate competition and adaptation to the changing environment in general. Extending the model to include two genetically correlated traits, one of which mediates competition while the other is under stabilizing selection, would be straightforward in principle, but this would make it challenging to define character displacement at the phenotypic level, instead requiring other criteria based on e.g. invasion analysis (Germain *et al.* 2018).

Another interesting extension would be to allow for plasticity in response to the type of consumed resources, or to the presence/abundance of competitors, as shown experimentally by Pfennig and Murphy (2000). If plasticity in response to the abiotic environment and to competitor presence both vary genetically, then multivariate cues for plasticity can evolve (Chevin and Lande 2015). For instance, the abiotic environment could become an indirect cue for the presence of competitors, or conversely plasticity could evolve to be mostly in response to competitor presence, without an influence of the abiotic environment. Exploring how these scenarios influence the onset and magnitude of character displacement would further improve our understanding of the role of competition on evolution of the fundamental niche.

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Figures and tables

Table 1: Summary of variables and parameters of the model. All parameters are assumed to have the same values for both species (symmetric system), unless specified otherwise (notably for ε_D and τ in Figure 3).

Symbol	Description	Value
N	Population size	-
r	Maximum intrinsic growth rate	0.1
K	Carrying capacity	60000
$\bar{a}$	Reaction norm intercept	-
$\bar{b}$	Reaction norm slope, quantifying plasticity	-
$\bar{z}$	Expressed trait, accounting for plasticity	-
σ_z^2	Phenotypic variance of expressed trait	-
σ_e^2	Residual phenotypic variance for a given genotype in a given environment	0.5
G_a, G_b	Additive genetic variances of reaction norm intercept and slope, respectively	$0.5, 0.045$
G_{ab}	Additive genetic covariance between reaction norm intercept and slope	0
ε_D / ε_S	Environment at development / selection	-
σ_ε^2	Temporal variance of environment ε	-
ρ	Environmental autocorrelation between development (ε_D) and selection (ε_S) for focal species (species 1)	0.5
τ	Fraction of generation time between development and selection	0.5
σ_s^2	Width ("variance") of stabilizing selection curve	550
σ_u^2	Width ("variance") of resource utilization curve	10
A, B	Intercept and slope of changes in the optimum phenotype with the environment	$10, 3$

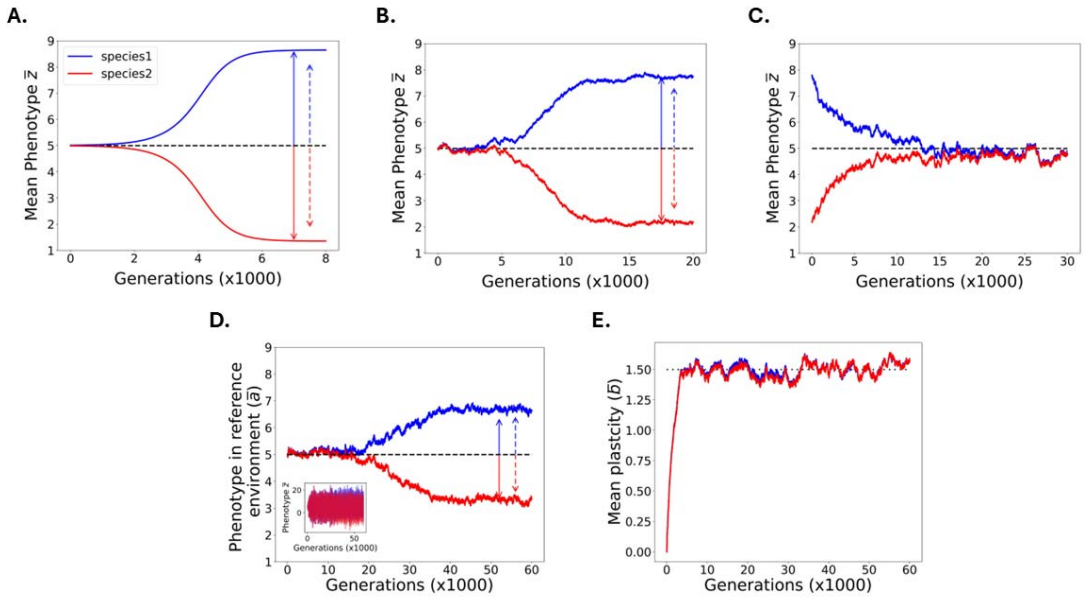

Figure 1: Influence of environmental fluctuations and evolution of plasticity on character displacement. The evolutionary dynamics of the mean phenotype $\bar{z}$ (A-C) and the mean reaction norm intercept $\bar{a}$ (D, with $\bar{z}$ as inset) and slope $\bar{b}$ quantifying plasticity (E) are shown for individual simulations of two symmetrically competing species (represented in blue and red). The environment is constant in A but fluctuates moderately ($\sigma_\varepsilon^2 = 4$) in B and strongly ($\sigma_\varepsilon^2 = 8$) in C-E. Phenotypic plasticity is either absent and non-evolvable (A-C: $G_b = 0$), or evolvable (D-E: $G_b = 0.045$). The dashed black lines in A-D represent the optimum phenotype, or its expectation in a fluctuating environment, and the dotted line in E represents the expected equilibrium plasticity, $\bar{b} = B\rho$. In panels A, B, and D, the vertical arrows show the expected character displacement, based either on eq. (11) combined with the mean population size computed over the last 1000 generations in the simulation (continuous arrows), or the approximation in eq. (15) that assumes the population size is at the equilibrium from eq. (13) (or eq. (17) in a fluctuating environment) (dashed arrows). All other parameter values are given in Table 1.

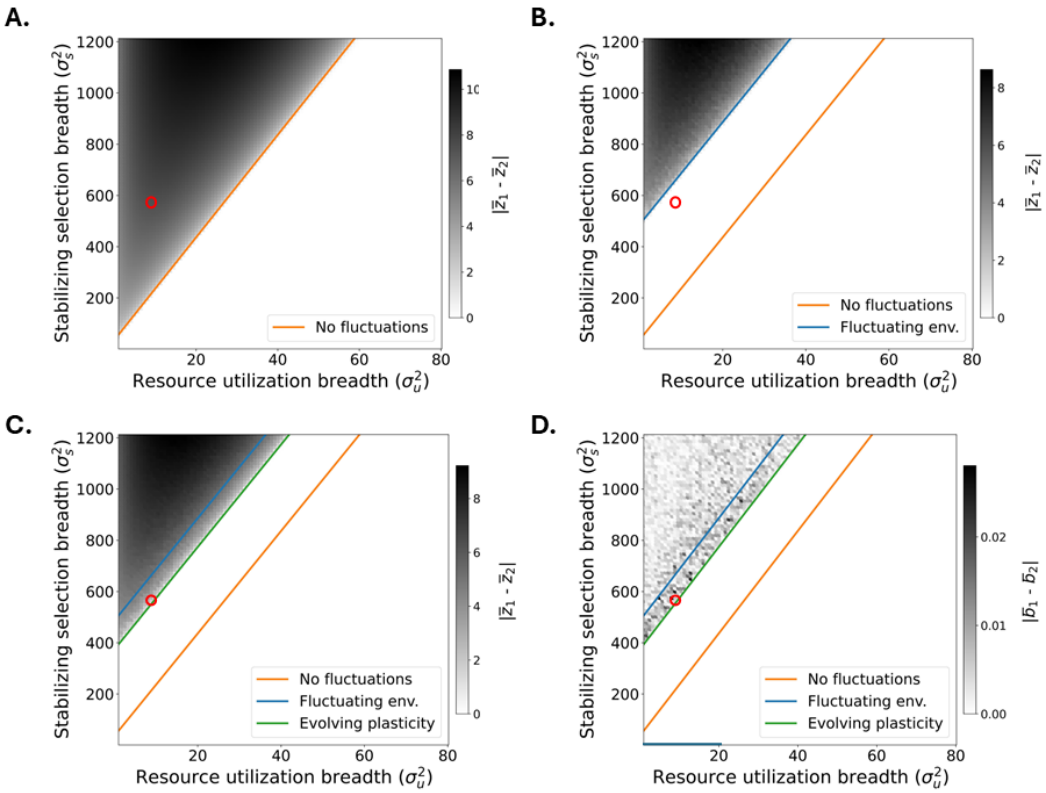

Figure 2: Influence of environmental fluctuations and evolution of plasticity on the conditions for character displacement. A-C. The absolute divergence in mean phenotype $\bar{z}$ among the two competing species, averaged over 10000 generations, is shown as shading levels, for varying values of resource utilization breadth σ_u^2 (x-axis) and stabilizing selection breadth σ_s^2 (y-axis). Simulations were performed in a constant environment with no plasticity (A: $\sigma_\varepsilon^2 = 0$, $G_{bb} = 0$), in a fluctuating environment with no plasticity (B: $\sigma_\varepsilon^2 = 10$, $G_b = 0$), or in a fluctuating environment with evolving plasticity (C: $\sigma_\varepsilon^2 = 10$, $G_b = 0.045$). Colored lines show the analytical conditions for character displacement in these 3 contexts (eqs 14, 18, and 21 for orange, blue, and green, respectively). D: The absolute divergence in mean plasticity $\bar{b}$ among species is shown as shading levels (note the much smaller range than in A-C) in the scenario with fluctuating environment and evolving plasticity ($\sigma_{eps}^2 = 10$, $G_{bb} = 0.045$), with colored lines from C reproduced for comparison. Parameter values are $A = 5$, $\tau = 0.5$, and the rest is as specified in Table 1. The open red circles show the combination of σ_u^2 and σ_s^2 (10 and 550 respectively) used for the simulations shown in Figure 1.

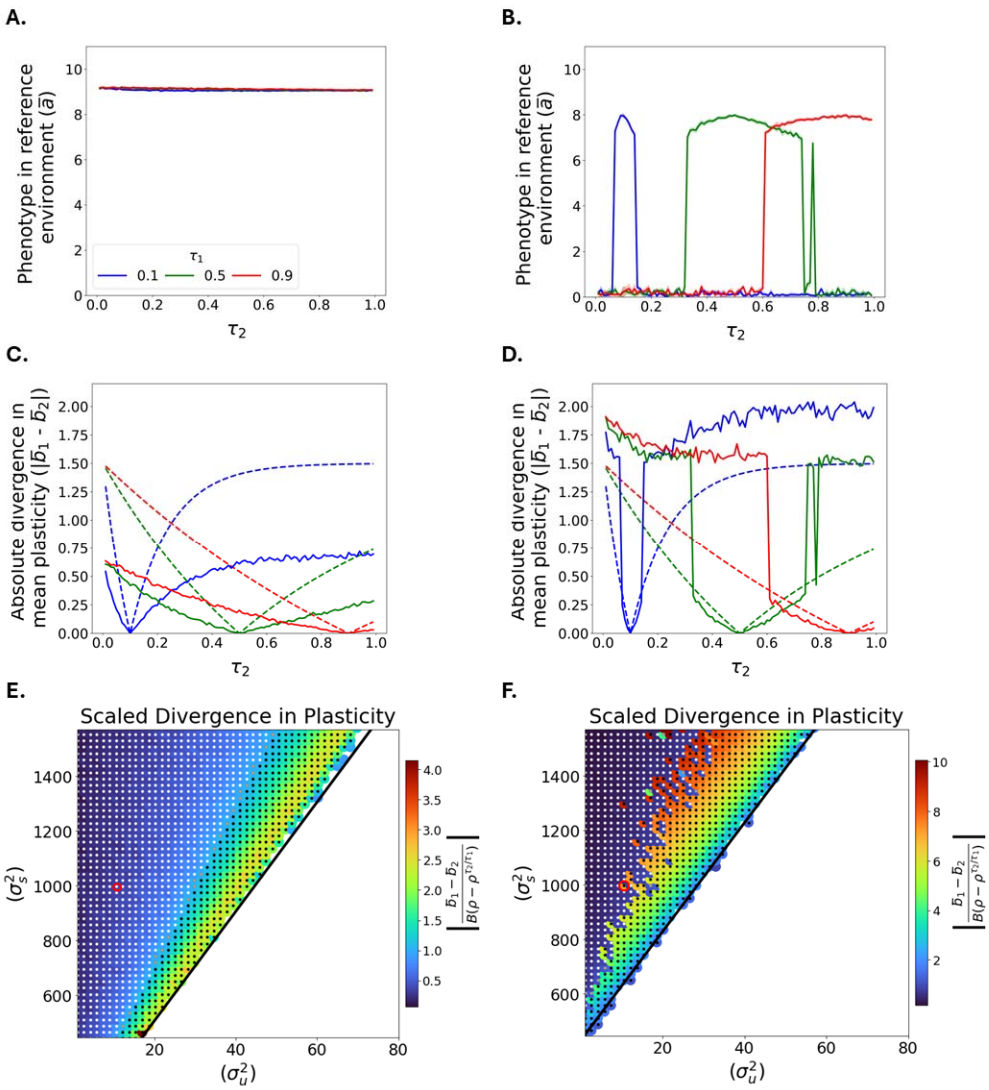

Figure 3: Character displacement in trait and plasticity when environmental predictability differs among species. The magnitude of between-species differences in mean reaction norm intercept $\bar{a}$ (A-B), and slope $\bar{b}$ quantifying plasticity (C-D), are shown against the lag τ_2 between development and selection in species 2, for several values of the corresponding lag τ_1 in species 1 (colors). The dashed lines in C-D show the predicted difference in plasticity in the absence of competitive selection, which is proportional to the absolute difference in environmental predictabilities, $|\bar{b}_1 - \bar{b}_2| = \left|B\left(\rho - \rho^{\frac{\tau_2}{\tau_1}}\right)\right|$ (where $\rho = 0.5$ is the autocorrelation over time τ_1 by definition). In the lower row (E-F), the divergence in plasticity, scaled to its expectation under no competitive selection, is shown as color levels, for varying values of resource utilization breadth σ_u^2 (x-axis) and stabilizing selection breadth σ_s^2 (y-axis). The developmental lag is $\tau_1 = 0.5$ in species 1 and $\tau_2 = 0.4$ in species 2. The predicted criterion for CD to exist at the phenotypic level is also shown as continuous black line, based on eq. (23) where σ_δ^2 was obtained by replacing, in eq. (22), the plasticity in each species by its expectation without competition, $\bar{b}_1 = B\rho$ and $\bar{b}_2 = B\rho^{\frac{\tau_2}{\tau_1}}$, and the correlation between the

environments of development in species 1 and 2 is $\rho_{12} = \rho^{\frac{|\tau_2 - \tau_1|}{\tau_1}}$. Parameter values where CD in plasticity is convergent (lower divergence than expected without competition) are marked by a white dot, those where CD in reaction norm intercept is lower than the threshold in eq. (25) (i.e., $d_m^2 < \sigma_T^2/2$) with a black dot, and those satisfying both criteria with a grey dot. The variance of environmental fluctuations is $\sigma_\varepsilon^2 = 2$ on the left (panels A, C , E) and $\sigma_\varepsilon^2 = 10$ on the right (panels B, D, F). The open red circles in panels E-F show the combination of σ_u^2 and σ_s^2 used for the simulations shown in panels A-D.

Appendix: Details of derivations

Equilibrium character displacement in a constant environment

From the evolutionary recursion in eq. (4), in the symmetric case (where indexes for species can be dropped for simplicity), denoting as d the deviation from optimum in species 1 (and thus $-d$ in species 2), the evolutionary equilibrium satisfies

$$2d\,\frac{rN}{2K}\frac{\sigma_u}{(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}}\exp\left(-\frac{(2d)^2}{4(\sigma_u^2+\sigma_z^2)}\right)-\frac{d}{\sigma_s^2}=0 \tag{A1}$$

$$d\left(\frac{rN}{K}\frac{\sigma_u}{(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}}\exp\left(-\frac{d^2}{(\sigma_u^2+\sigma_z^2)}\right)-\frac{1}{\sigma_s^2}\right)=0$$

An equilibrium with $d\neq 0$ exists when

$$\frac{rN}{K}\frac{\sigma_u}{(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}}\exp\left(-\frac{d^2}{(\sigma_u^2+\sigma_z^2)}\right)-\frac{1}{\sigma_s^2}=0 \tag{A2}$$

$$\frac{rN\sigma_u\sigma_s^2\exp\left(-\frac{d^2}{(\sigma_u^2+\sigma_z^2)}\right)-K(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}}{K(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}\sigma_s^2}=0$$

$$rN\sigma_u\sigma_s^2\exp\left(-\frac{d^2}{(\sigma_u^2+\sigma_z^2)}\right)=K(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}$$

$$\frac{rN\sigma_u\sigma_s^2}{K(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}}=\exp\left(\frac{d^2}{(\sigma_u^2+\sigma_z^2)}\right)$$

$$(\sigma_u^2+\sigma_z^2)\ln\left(\frac{rN\sigma_u\sigma_s^2}{K(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}}\right)=d^2$$

The criterion for the logarithm to be positive is

$$\sigma_s^2\geq\frac{K}{rN}\frac{(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}}{\sigma_u} \tag{A3}$$

Near the threshold for CD, in the symmetric system the equilibrium population size satisfies

$$r-\frac{2\,N_{\mathrm{eq}|0}r}{K}\sqrt{\frac{\sigma_u^2}{\sigma_u^2+\sigma_z^2}}-\frac{\sigma_z^2}{2\sigma_s^2}=0 \tag{A4}$$

Solving yields the equilibrium population size in eq. (13) in the main text, which can then be replaced in the criterion for CD (eq. 12) to yield

$$\sigma_s^2\,\frac{K}{2\,r}\left(r-\frac{\sigma_z^2}{2\sigma_s^2}\right)\sqrt{1+\frac{\sigma_z^2}{\sigma_u^2}}\geq\frac{K}{r}\sigma_u^2\left(1+\frac{\sigma_z^2}{\sigma_u^2}\right)^{\frac{3}{2}} \tag{A5}$$

$$\frac{K}{2\,r}\frac{2r\sigma_s^2-\sigma_z^2}{2}\left(1+\frac{\sigma_z^2}{\sigma_u^2}\right)^{1/2}\geq\frac{K}{r}\sigma_u^2\left(1+\frac{\sigma_z^2}{\sigma_u^2}\right)^{\frac{3}{2}}$$

$$\frac{2r\sigma_s^2-\sigma_z^2}{4}\geq\sigma_u^2\left(1+\frac{\sigma_z^2}{\sigma_u^2}\right)$$

$$2r\sigma_s^2 - \sigma_z^2 \geq 4(\sigma_u^2 + \sigma_z^2)$$
$$2r\sigma_s^2 \geq 4\sigma_u^2 + 5\sigma_z^2$$

Equilibrium character displacement in a fluctuating environment

In the presence of fluctuations, near the threshold for CD in the symmetric system the expected equilibrium population size satisfies

$$r - \frac{2\,r\langle N_{\mathrm{eq|Fluct}}\rangle}{K}\sqrt{\frac{\sigma_u^2}{\sigma_u^2+\sigma_z^2}} - \frac{\sigma_z^2+\sigma_x^2}{2\sigma_s^2} = 0, \tag{A6}$$

where $\langle\ \ \rangle$ denotes an expectation over the stochastic process of the fluctuating environment. Rearranging yields

$$r - \frac{\sigma_z^2+\sigma_x^2}{2\sigma_s^2} = \frac{2\,r\langle N_{\mathrm{eq|Fluct}}\rangle}{K}\sqrt{\frac{\sigma_u^2}{\sigma_u^2+\sigma_z^2}} \tag{A7}$$

$$\langle N_{\mathrm{eq|Fluct}}\rangle = \frac{K}{2\,r}\left(r - \frac{\sigma_z^2+\sigma_x^2}{2\sigma_s^2}\right)\sqrt{1+\frac{\sigma_z^2}{\sigma_u^2}}.$$

The ratio of the equilibrium population size with to without fluctuations is

$$\frac{\langle N_{\mathrm{eq|Fluct}}\rangle}{\langle N_{\mathrm{eq|o}}\rangle} = \frac{\frac{K}{2\,r}\left(r-\frac{\sigma_z^2+\sigma_x^2}{2\sigma_s^2}\right)\sqrt{1+\frac{\sigma_z^2}{\sigma_u^2}}}{\frac{K}{2\,r}\left(r-\frac{\sigma_z^2}{2\sigma_s^2}\right)\sqrt{1+\frac{\sigma_z^2}{\sigma_u^2}}} = \frac{r-\frac{\sigma_z^2+\sigma_x^2}{2\sigma_s^2}}{r-\frac{\sigma_z^2}{2\sigma_s^2}} = \frac{2r\sigma_s^2-\sigma_z^2-\sigma_x^2}{2r\sigma_s^2-\sigma_z^2} = 1 - \frac{\sigma_x^2}{2r\sigma_s^2-\sigma_z^2}. \tag{A8}$$

Note that the terms containing σ_u^2 cancel out, so the expected proportional reduction in equilibrium population size caused by fluctuations is the same, whether or not density regulation is mediated by phenotype (ie, with or without competitive selection).

When CD exists under a fluctuating optimum, its expected value is

$$\langle d\rangle = \pm\sqrt{(\sigma_u^2+\sigma_z^2)\ln\left(\frac{r\langle N_{\mathrm{eq|Fluct}}\rangle}{K}\frac{\sigma_u\sigma_s^2}{(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}}\right)}. \tag{A9}$$

Replacing the equilibrium population size by its expectation under no CD, the term in the logarithm can be simplified as

$$\frac{r\langle N_{\mathrm{eq|Fluct}}\rangle}{K}\frac{\sigma_u\sigma_s^2}{(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}} = \frac{r\frac{K}{2\,r}\left(r-\frac{\sigma_z^2+\sigma_x^2}{2\sigma_s^2}\right)\sqrt{1+\frac{\sigma_z^2}{\sigma_u^2}}}{K}\frac{\sigma_u\sigma_s^2}{(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}} \tag{A10}$$

$$= \frac{1}{2}\left(r - \frac{\sigma_z^2+\sigma_x^2}{2\sigma_s^2}\right)\sigma_s^2\sqrt{\frac{\sigma_u^2+\sigma_z^2}{\sigma_u^2}}\frac{\sigma_u}{(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}}$$

$$= \frac{1}{2}\left(\frac{2\sigma_s^2 r - \sigma_z^2 - \sigma_x^2}{2\sigma_s^2}\right)\sigma_s^2\frac{(\sigma_u^2+\sigma_z^2)^{\frac{1}{2}}}{(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}}$$

$$= \frac{2\sigma_s^2 r - \sigma_z^2 - \sigma_x^2}{4(\sigma_u^2+\sigma_z^2)}$$

This leads to the approximate formula for the expected equilibrium CD with environmental fluctuations,

$$\langle d \rangle = \pm\sqrt{(\sigma_u^2 + \sigma_z^2)\ln\left(\frac{2\sigma_s^2 r - \sigma_z^2 - \sigma_x^2}{4(\sigma_u^2+\sigma_z^2)}\right)}. \tag{A11}$$

This formula is only an approximation because it is based on an expression for the equilibrium population size that assumes no CD. However, it can be used to derive the criterion for non-zero (expected) CD with fluctuations, which needs to satisfy

$$\frac{2\sigma_s^2 r - \sigma_z^2 - \sigma_x^2}{4(\sigma_u^2+\sigma_z^2)} \geq 1 \tag{A12}$$

$$2\sigma_s^2 r - \sigma_z^2 - \sigma_x^2 \geq 4(\sigma_u^2 + \sigma_z^2)$$

$$2\sigma_s^2 r \geq 4\sigma_u^2 + 5\sigma_z^2 + \sigma_x^2$$

$$\sigma_s^2 \geq \frac{4\sigma_u^2 + 5\sigma_z^2 + \sigma_x^2}{2r}$$

With plasticity, and neglecting adaptive tracking of the optimum by evolution of the mean phenotype, the variance in phenotypic mismatch is

$$\sigma_x^2 = \langle\left(\bar{b}\varepsilon_{t-\tau} - B\varepsilon_t\right)^2\rangle = \bar{b}^2\langle\varepsilon_{t-\tau}^2\rangle + B^2\langle\varepsilon_t^2\rangle - 2B\bar{b}\langle\varepsilon_{t-\tau}\varepsilon_t\rangle \tag{A13}$$

$$= B^2\sigma_\varepsilon^2(b_B^2 + 1 - 2b_B\rho)$$

$$= \sigma_\theta^2(1 + b_B(b_B - 2\rho))$$

where $b_B = \bar{b}/B$ is the reaction norm slope (plasticity) scaled to the slope of the optimum. Without plasticity, this collapses to $\sigma_x^2 = \sigma_\theta^2$.

Divergence in plasticity

When the competing species are allowed to respond to the environment at different times (because of e.g. differences in life history), and may thus evolve different reaction norms slopes, the conditions for character displacement at the phenotypic level are modified. We first note that the symmetry assumption used above breaks down in this context, because species experiencing different environmental predictabilities and with different plasticities will also have different equilibrium population sizes and phenotypic deviations from the optimum.

The total selection gradient on expressed trait *z* in species *i* in a given generation becomes (from eqs 4-6)

$$\beta_{z,i} = -\frac{d_i + \bar{b}_i\varepsilon_{D_i} - B\,\varepsilon_S}{\sigma_s^2} + \frac{rN_j}{2K}\frac{\sigma_u}{(\sigma_u^2+\sigma_z^2)^{\frac{3}{2}}}\exp\left(-\frac{\left(d_i - d_j + \bar{b}_i\varepsilon_{D_i} - \bar{b}_j\varepsilon_{D_j}\right)^2}{4(\sigma_u^2+\sigma_z^2)}\right)\left(d_i - d_j + \bar{b}_i\varepsilon_{D_i} - \bar{b}_j\varepsilon_{D_j}\right), \tag{A14}$$

where ε_{D_i} is the environment influencing plasticity for species i (and similarly for ε_{D_j} and species j), and d_i is the character displacement of reaction norm intercept in species *i*, that is, its phenotypic deviation from the optimum in the reference environment (where $\varepsilon = 0$ by convention). The character displacements of reaction norm intercepts d_i and d_j may have different magnitudes due to

the asymmetry induced by the different environmental predictabilities, but they have opposite signs, so we assume (without loss of generality) that d_1 is positive and d_2 negative, such that the magnitude of divergence between species in the reference environment is $d_1 - d_2$. We define the half divergence in reaction norm intercept (or mean CD in reference environment) as $d_m = \frac{d_1 - d_2}{2}$. Assuming that the environments of selection ε_S and development (ε_{D_i}, ε_{D_j}) are multivariate normally distributed, and integrating the gradient over this distribution leads to the expected gradient on the trait

$$\langle \beta_{z,i} \rangle = -\frac{d_i}{\sigma_s^2} + \frac{r\langle N_j \rangle d_m}{K} \frac{\sigma_u}{\sigma_T^3} \exp\left(-\frac{{d_m}^2}{\sigma_T^2}\right) \tag{A15}$$

where $\langle \quad \rangle$ denotes an expectation over the stochastic process of environmental fluctuations as before, and

$$\sigma_T = \sqrt{\sigma_u^2 + \sigma_z^2 + \frac{\sigma_\delta^2}{2}} \tag{A16}$$

where

$$\sigma_\delta^2 = \sigma_\varepsilon^2 (\bar{b}_1^2 + \bar{b}_2^2 - 2\bar{b}_1 \bar{b}_2 \rho_{12}) \tag{A17}$$

is the variance of fluctuations in phenotypic divergence among species, and ρ_{12} is the correlation in environments of development between species. The case where both species have the same plasticity ($\bar{b}_1 = \bar{b}_2$) and respond to the same environment ($\rho_{12} = 1$) is recovered for $\sigma_\delta^2 = 0$, as expected. Equations (A15-A17) shows that the main effect of divergence in plasticity and differences in environments of development between species on phenotypic selection is to add half the temporal variance of phenotypic divergence $\sigma_\delta^2/2$ to the sum $\sigma_u^2 + \sigma_z^2$.

The expected character displacements for the expressed phenotypes in both species is obtained by jointly solving $\langle \beta_{z,1} \rangle = 0$ and $\langle \beta_{z,2} \rangle = 0$ for d_1 and d_2, yielding

$$\langle d_1 \rangle = \frac{\langle N_2 \rangle}{\langle N_m \rangle} \sigma_T \sqrt{\ln\left(\frac{r\langle N_m \rangle \sigma_u \sigma_s^2}{K \sigma_T^3}\right)} \tag{A18}$$

$$\langle d_2 \rangle = -\frac{\langle N_1 \rangle}{\langle N_m \rangle} \sigma_T \sqrt{\ln\left(\frac{r\langle N_m \rangle \sigma_u \sigma_s^2}{K \sigma_T^3}\right)}$$

where $N_m = \frac{N_1 + N_2}{2}$ is the mean population size across species, and $\langle \quad \rangle$ denotes a stochastic expectation as before. This shows that in such asymmetric conditions, what determines the relative magnitudes of CD in each species (when they exist) is simply their ratio of equilibrium population sizes, $\left|\frac{\langle d_1 \rangle}{\langle d_2 \rangle}\right| = \frac{\langle N_2 \rangle}{\langle N_1 \rangle}$. In other words, the species with the largest population size at equilibrium causes the largest CD in the other species. In addition, the magnitude of CD increases with the average equilibrium population size across species $\langle N_m \rangle$, as well as with the compound competition

parameter σ_T. Provided that both species can persist (coexistence), the condition for character displacement in both species is that the term in the square root is positive, leading to

$$\sigma_s^2 \geq \frac{K}{r\langle N_m\rangle}\frac{\sigma_T^3}{\sigma_u}. \tag{A19}$$

This shows that a difference in plasticity between species makes the conditions for CD at the phenotypic level more stringent, for two reasons. First, differences in plasticity ($\bar{b}_1 \neq \bar{b}_2$) and/or in environments of development ($\rho_{12} < 1$) between species lead to $\sigma_\delta^2 > 0$, increasing σ_T, all the more so as the variance of environmental fluctuations σ_ε^2 is large (from eqs. A16-A17). And second, asymmetric maladaptation can lead one population size to be well below carrying capacity, thus decreasing the mean population size across species N_m, if not compensated by an increase of same magnitude in the other species (which is unlikely because of density dependence). Therefore, weaker stabilizing selection (larger σ_s^2) is required for CD to exist.

Divergence in plasticity is also influenced by competition in this context. To understand how, we start from the selection gradient on plasticity for species i (using eq. 9)

$$\beta_{b,i} = \beta_{z,i}\varepsilon_{D_i} \tag{A20}$$

Combining with the expression for $\beta_{z,i}$ above and integrating over the distribution of environments of selection and development of both species leads to the expected selection gradient on plasticity for species i,

$$\langle\beta_{b,i}\rangle = \sigma_\varepsilon^2\left[-\frac{\langle\bar{b}_i\rangle - B\,\rho_{iS}}{\sigma_s^2} + \frac{r\langle N_j\rangle}{K}\varphi\left(\langle\bar{b}_i\rangle - \langle\bar{b}_j\rangle\rho_{12}\right)\right] \tag{A21}$$

$$\varphi = \frac{\sigma_u}{2\sigma_T^3}e^{-\frac{d_m^2}{\sigma_T^2}}\left(1 - \frac{2d_m^2}{\sigma_T^2}\right).$$

where ρ_{iS} is the correlation between the development of selection in species i and the environment of selection. We can make more analytical progress by replacing CD in reaction norm intercept by its predicted expression (eq. A18), to get

$$\frac{d_m^2}{\sigma_T^2} = \ln\left(\frac{rN_m\sigma_u\sigma_s^2}{K\sigma_T^3}\right) \tag{A21}$$

such that

$$e^{-\frac{d_m^2}{\sigma_T^2}} = e^{-\ln\left(\frac{rN_m\sigma_u\sigma_s^2}{K\sigma_T^3}\right)} = \frac{K\sigma_T^3}{rN_m\sigma_u\sigma_s^2}$$

leading to

$$\varphi = \frac{K}{2rN_m\sigma_s^2}\left(1 - 2\ln\left(\frac{rN_m\sigma_u\sigma_s^2}{K\sigma_T^3}\right)\right)$$

and finally

$$\langle\beta_{b,i}\rangle = \frac{\sigma_\varepsilon^2}{\sigma_s^2}\left[-(\langle\bar{b}_i\rangle - B\,\rho_{iS}) + \frac{N_j}{2N_m}\left(1 - 2\ln\left(\frac{rN_m\sigma_u\sigma_s^2}{K\sigma_T^3}\right)\right)\left(\langle\bar{b}_i\rangle - \langle\bar{b}_j\rangle\rho_{12}\right)\right]. \tag{A22}$$

With this criterion, competition causes convergent CD in plasticity when

$$1 - 2\ln\left(\frac{rN_m\sigma_u\sigma_s^2}{K\sigma_T^3}\right) < 0 \tag{A23}$$

$$\Leftrightarrow \ln\left(\frac{rN_m\sigma_u\sigma_s^2}{K\sigma_T^3}\right) > \frac{1}{2}$$

$$\Leftrightarrow \frac{rN_m\sigma_u\sigma_s^2}{K\sigma_T^3} > \exp\left(\frac{1}{2}\right)$$

and divergent CD in plasticity otherwise. Replacing σ_T by its expression in eq. (A16) leads to

$$\frac{rN_m}{K}\frac{\sigma_s^2}{\sigma_u^2}\left(1 + \frac{\sigma_z^2}{\sigma_u^2} + \frac{1}{2}\frac{\sigma_\delta^2}{\sigma_u^2}\right)^{-\frac{3}{2}} > \exp\left(\frac{1}{2}\right) = \sqrt{e} \approx 1.65$$

as condition for convergent CD in plasticity.