

Supporting Information. Stump, S.M., C. Song, S. Saavedra, J.M. Levine, and D.A. Vasseur. 2021. Synthesizing the effects of individual-level variation on coexistence. *Ecological Monographs*.

Appendix S1

This appendix provides additional information about each of our models. In each case, we discuss how ITV could be put into the model. We do an invasion analysis analytically. We additionally lay out how each model was studied using simulations, and provide the supplementary figures referenced in the main text.

To do an invasion analysis using the modern coexistence theory framework, we need to define the sensitivity to competition, β_j (Chesson, 2003; Barabás et al., 2018). Defining β_j requires defining a competition term in the model, $C_j(t)$. When this is done, sensitivity to competition is defined as

$$\beta_j = \frac{\partial r_j(t)}{\partial C_j(t)} \quad (\text{S1})$$

when species j is at equilibrium (or $\beta_j = \frac{\partial \lambda_j(t)}{\partial C_j(t)}$ in models of spatial variation) (Chesson, 1994). We outline how this is done in each model.

All of the invasion simulations used to generate each figure followed a similar procedure. We selected a range which we wanted ITV to vary over. We then broke that range into 350 separate values. For each possible value of σ_{T1}^2 and σ_{T2}^2 ($350^2 = 122,500$ paired values total), we calculated the invader growth rate of each species when the other was the invader. Each simulation was performed differently, and we explain our procedure for each model below. For the relative nonlinearity model, we also calculated β_i for each parameter value (in the other three models, it was constant). This allowed us to calculate the stabilizing mechanism and fitness difference for each $(\sigma_{T1}^2, \sigma_{T2}^2)$ pair. To draw the contour plots, we would select a particular value for σ_{T1}^2 , and determine all values of σ_{T2}^2 for which the stabilizing mechanism or fitness difference was below the contour for a given σ_{T2}^2 , but above it for the next value of σ_{T2}^2 . A small black dot was placed on the figure at each of these locations. We did this for every value of σ_{T1}^2 . We then did the converse of this, determining which values of σ_{T1}^2 moved our stabilizing mechanism or fitness-difference over the critical value for each σ_{T2}^2 .

Section S1 Model 1: Variation-independent mechanism

First we analyze the resource partitioning model, which represents niche partitioning at equilibrium. We assume that species compete over a variety of resources, $R_h(t)$ (for resource h at time t). Each species has a Type 1 functional response, and species j captures resources h with attack rate

$a_j(h)$. Consuming any resource allows individuals of each species to produce w offspring. Individuals die at rate δ . Thus, when there are q resources, the model for species j 's population dynamics is

$$\frac{dN_j(t)}{dt} = N_j(t) \left(\sum_{h=1}^q a_j(h)wR_h(t) - m \right). \quad (\text{S2})$$

We model resource density as growing logistically in the absence of consumers (to carrying capacity K),

$$\frac{dR_h(t)}{dt} = R_h(t) \left(1 - \frac{R_h(t)}{K} - \sum_{j=1}^2 a_j(h)N_j(t) \right). \quad (\text{S3})$$

For this analysis, we assume that resources can be divided along a one-dimensional niche axis x , such that an individual's attack rate on resource h will be similar to its attack rate on resource $h+\epsilon$ (for small ϵ). In our analysis, $a_j(h)$ was represented by either a normal or a uniform distribution. Using the formalism in MacArthur (1970), and assuming that resources all have identical attributes, we solve the mean per-capita competition coefficient as:

$$\alpha_{jk} = \int a_j(h)a_k(h)dh. \quad (\text{S4})$$

This will differ slightly, based on the form of $a_j(h)$. When we do this, we can define an intrinsic growth rate r_j which allows us to write our model as a Lotka-Volterra model:

$$\frac{dN_j(t)}{dt} = N_j(t)r_j \left(1 - \sum_{k=1}^2 \alpha_{kj}N_k(t) \right). \quad (\text{S5})$$

Section S1.1 Deriving the competition coefficients, α_{jk} , with ITV

For this section, we will assume that an individual's attack rate is based on a Gaussian distribution, such that an individual with optimal resource use μ_j on resource h as

$$a_j(h) = \frac{1}{\sqrt{2\pi\sigma_I^2}} e^{-\frac{(h-\mu_j)^2}{2\sigma_I^2}} \quad (\text{S6})$$

where σ_I determines dietary width of an individual. If species j shows ITV in μ_j , then an individual with trait T will have attack rate

$$a_j(T, h) = \frac{1}{\sqrt{2\pi\sigma_I^2}} e^{-\frac{(h-(\mu_j^*+T))^2}{2\sigma_I^2}}. \quad (\text{S7})$$

We will assume that T is normally distributed, with mean 0 and variance σ_{Tj}^2 ; we will write the pdf as $p_j(T)$. Thus, we can calculate the average resource uptake for a species as

$$a_j(h) = \int a_{jh}(T, h)p_j(T)dT \quad (\text{S8})$$

This is a normal distribution with mean μ_j^* and variance $\sigma_I^2 + \sigma_{Tj}^2$. Thus, the competition coefficients are:

$$\begin{aligned} \alpha_{jk} &= \int a_j(h)a_k(h)dh \\ &= \frac{1}{\sqrt{2\pi(2\sigma_I^2 + \sigma_{Tj}^2 + \sigma_{Tk}^2)}} e^{-\frac{(h-(\mu_j^*+T))^2}{4\sigma_I^2+2\sigma_{Tj}^2+2\sigma_{Tk}^2}}. \end{aligned} \quad (\text{S9})$$

Section S1.2 Invasion analysis

Next we derive a more general invasion analysis (i.e. one that does not depend on the form of $a_j(T, h)$). Below, however, we use equation S9 to determine specifics for the Gaussian $a_j(T, h)$. The equation governing a species is

$$\frac{1}{N_j(t)} \frac{dN_j(t)}{dt} = r_j \left(1 - \sum_{k=1}^2 \alpha_{kj} N_k(t) \right). \quad (\text{S10})$$

The right-hand side of this equation is the growth rate of the species, $r_j(t)$ (Miller and Klausmeier, 2017). If there is only resident species in the system, then it will be at equilibrium at density $N_r(t) = 1/\alpha_{rr}$. Thus, an invader's growth rate will be

$$r_i(t) = \beta_i \left(1 - \frac{\alpha_{ri}}{\alpha_{rr}} \right). \quad (\text{S11})$$

We could write this further as a resident-invader comparison, though we find it does not add any intuition (as $r_r(t) = 0$, and it is obvious what is causing the invader to have a positive or negative growth rate).

To define the sensitivity to competition, β_j , we define competition as $C_j(t) = \sum_{k=1}^2 \alpha_{kj} N_k(t)$. Thus, β_j is simply the intrinsic growth rate of a species, r_j . With this, the stabilizing mechanism in this system is

$$\overline{\Delta\rho} = 1 - \frac{1}{2} \left(\frac{\alpha_{12}}{\alpha_{11}} + \frac{\alpha_{21}}{\alpha_{22}} \right), \quad (\text{S12})$$

and the fitness advantage for species 1 is

$$\Delta\rho_1 - \overline{\Delta\rho} = \frac{1}{2} \left(\frac{\alpha_{12}}{\alpha_{11}} - \frac{\alpha_{21}}{\alpha_{22}} \right), \quad (\text{S13})$$

We can examine the effects of ITV on stability and fitness differences in the Gaussian model by substituting our derivation of α_{jk} (equation S9) into the above equations. We find that the stabilizing mechanism is

$$\overline{\Delta\rho} = 1 - \frac{\left(\sqrt{\sigma_{T1}^2 + \sigma_I^2} + \sqrt{\sigma_{T2}^2 + \sigma_I^2} \right) e^{-\frac{(\mu_1^* - \mu_2^*)^2}{2(\sigma_{T1}^2 + \sigma_{T2}^2 + 2\sigma_I^2)}}}{\sqrt{2} \sqrt{\sigma_{T1}^2 + \sigma_{T2}^2 + 2\sigma_I^2}} \quad (\text{S14})$$

and the fitness advantage for species 1 is

$$\Delta\rho_1 - \overline{\Delta\rho} = \frac{\left(\sqrt{\sigma_{T1}^2 + \sigma_I^2} - \sqrt{\sigma_{T2}^2 + \sigma_I^2} \right) e^{-\frac{(\mu_1^* - \mu_2^*)^2}{2(\sigma_{T1}^2 + \sigma_{T2}^2 + 2\sigma_I^2)}}}{\sqrt{2} \sqrt{\sigma_{T1}^2 + \sigma_{T2}^2 + 2\sigma_I^2}}. \quad (\text{S15})$$

We will explore when ITV promotes makes each positive or negative. To do this, we will take the partial derivative of each of the above equations, to see the impact of ITV in species 1. For notational simplicity, we define $\sigma_j^2 = \sigma_{Tj}^2 + \sigma_I^2$.

The partial derivative of the stabilizing mechanism is

$$\frac{\partial (\overline{\Delta\rho})}{\partial \sigma_1^2} = \frac{e^{-\frac{(\mu_1^* - \mu_2^*)^2}{2(\sigma_1^2 + \sigma_2^2)}} \left(-(\mu_1^* - \mu_2^*)^2 (\sigma_1^2 + \sqrt{\sigma_1^2} \sqrt{\sigma_2^2}) + (\sqrt{\sigma_1^2} - \sqrt{\sigma_2^2}) \sqrt{\sigma_2^2} (\sigma_1^2 + \sigma_2^2) \right)}{2\sqrt{2} \sqrt{\sigma_1^2} (\sigma_1^2 + \sigma_2^2)^{\frac{5}{2}}}. \quad (\text{S16})$$

This will be positive, meaning that ITV will increase stability, if

$$(\mu_1^* - \mu_2^*)^2 < \frac{(\sqrt{\sigma_1^2} - \sqrt{\sigma_2^2}) \sqrt{\sigma_2^2} (\sigma_1^2 + \sigma_2^2)}{\sigma_1^2 + \sqrt{\sigma_1^2} \sqrt{\sigma_2^2}}. \quad (\text{S17})$$

There are a few results to note. First, the left hand side is always non-negative, and the right hand side will only be positive if $\sigma_1^2 > \sigma_2^2$. Thus, it is always destabilizing for the species with less ITV to increase their ITV. Second, this inequality is more likely to be true when $(\mu_1^* - \mu_2^*)^2$ is small (i.e. species have similar niches) and $(\sqrt{\sigma_1^2} - \sqrt{\sigma_2^2})$ is large (i.e. species 1 has much more ITV than species 2). This describes the case of a generalist-specialist trade-off: both species have similar niches, and one species has far more ITV than the other. In this case, species are more differentiated when species 1 has more ITV. When this is not the case, however, then increasing species 1's ITV will decrease stability.

Additionally, consider the case where species are constrained to have equal ITV (i.e. $\sigma_1^2 = \sigma_2^2 = \sigma^2$). In this case, the partial derivative is

$$\frac{\partial(\overline{\Delta\rho})}{\partial\sigma_1^2} = -\frac{(\mu_1^* - \mu_2^*)^2 e^{-\frac{\mu_1^* - \mu_2^*}{2\sigma^2}}}{2(\sigma^2)^2}. \quad (\text{S18})$$

This will always be negative. Thus, uniformly increasing both species' ITV will always undermine stability, at least under these assumptions.

Next, the partial derivative of species 1's fitness advantage is

$$\begin{aligned} \frac{\partial(\Delta\rho_1 - \overline{\Delta\rho})}{\partial\sigma_1^2} = & \\ & e^{-\frac{(\mu_1^* - \mu_2^*)^2}{2(\sigma_1^2 + \sigma_2^2)}} \frac{\left((\mu_1^* - \mu_2^*)^2 (\sigma_1^2 - \sqrt{\sigma_1^2} \sqrt{\sigma_2^2}) + (\sqrt{\sigma_1^2} + \sqrt{\sigma_2^2}) \sqrt{\sigma_2^2} (\sigma_1^2 + \sigma_2^2) \right)}{2\sqrt{2} \sqrt{\sigma_1^2} (\sigma_1^2 + \sigma_2^2)^{\frac{5}{2}}}. \end{aligned} \quad (\text{S19})$$

This will be positive whenever

$$\sqrt{\sigma_1^2} - \sqrt{\sigma_2^2} > -\frac{(\sqrt{\sigma_1^2} + \sqrt{\sigma_2^2}) \sqrt{\sigma_2^2} (\sigma_1^2 + \sigma_2^2)}{\sqrt{\sigma_1^2} (\mu_1^* - \mu_2^*)^2}. \quad (\text{S20})$$

The right side of this inequality will always be negative. Thus, this will always be true – and thus ITV will be advantageous for species 1 – when $\sigma_1^2 \geq \sigma_2^2$. If $\sigma_1^2 \ll \sigma_2^2$, then the above inequality is approximately

$$(\sigma_2^2)^{\frac{3}{2}} > \sqrt{\sigma_1^2} (\mu_1^* - \mu_2^*)^2. \quad (\text{S21})$$

Thus, there is an edge case where if $(\mu_1^* - \mu_2^*)^2$ is very large (i.e. both species have highly differentiated niches), that increasing ITV in species 1

could weaken its fitness. However, it appears that this situation will only happen when species 1 has a large fitness disadvantage, and it appears that it will simply equalize fitness. Thus, in nearly every case, increasing species 1's ITV increases its fitness.

Section S1.3 Alternative definitions of fitness and stability

The above results were defined in terms of the Chesson (2003) definition of fitness and stability (specifically, mean fitness difference and community average stabilizing mechanism). However, Lotka-Volterra models are often analyzed in terms of the Chesson (1990) definition. This defines relative competitive ability in terms of the fitness ratio,

$$\frac{\kappa_1}{\kappa_2} = \sqrt{\frac{\alpha_{12}\alpha_{22}}{\alpha_{21}\alpha_{11}}} \quad (\text{S22})$$

and stability in terms of the stabilizing niche difference,

$$(1 - \rho) = 1 - \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}} \quad (\text{S23})$$

Under this definition, species coexist when

$$\frac{\kappa_1}{\kappa_2} < \rho < \frac{\kappa_1}{\kappa_2}. \quad (\text{S24})$$

Plugging in our competition coefficients, equation S9, we see that the fitness ratio is

$$\frac{\kappa_1}{\kappa_2} = \sqrt{\frac{\sqrt{\sigma_{T2}^2}}{\sqrt{\sigma_{T1}^2}}}. \quad (\text{S25})$$

Thus, increasing a species' ITV (and therefore increasing its σ_j^2) will always change the fitness ratio in a way that benefits it. This result is the same as with the previous definition of fitness.

Similarly, we see that the stabilizing niche difference is

$$(1 - \rho) = 1 - \sqrt{\frac{2\sqrt{\sigma_1^2}\sqrt{\sigma_2^2}}{\sigma_1^2 + \sigma_2^2} e^{\left\{-\frac{(\mu_1^* - \mu_2^*)^2}{\sigma_1^2 + \sigma_2^2}\right\}}}. \quad (\text{S26})$$

To analyze what occurs when ITV increases for a single species, we take the derivative of this in terms of σ_{T1}^2 , and find that

$$\frac{\partial(1-\rho)}{\partial\sigma_1^2} = \frac{2(\mu_1^* - \mu_2^*)^2 - \sigma_1^2 + \sigma_2^2}{2\sqrt{2} \left(\frac{\sqrt{\sigma_1^2 \sigma_2^2}}{\sigma_1^2 + \sigma_2^2} \right)^{\frac{3}{2}} (\sigma_1^2 + \sigma_2^2)^4} \sqrt{e^{\left\{ -\frac{(\mu_1^* - \mu_2^*)^2}{\sigma_1^2 + \sigma_2^2} \right\}}}. \quad (\text{S27})$$

In the case where $\sigma_1^2 \approx \sigma_2^2$, this simplifies to

$$\frac{\partial(1-\rho)}{\partial\sigma_1^2} \approx 0. \quad (\text{S28})$$

Thus, when both species have similar levels of ITV, increasing ITV for either species will weaken stability. If species 1 has much more ITV than species 2, then

$$\frac{\partial(1-\rho)}{\partial\sigma_1^2} \approx \frac{2(\mu_1^* - \mu_2^*)^2 - \sigma_1^2}{2\sqrt{2} \left(\frac{\sqrt{\sigma_1^2 \sigma_2^2}}{\sigma_1^2} \right)^{\frac{3}{2}} (\sigma_1^2)^4} \sqrt{e^{\left\{ -\frac{(\mu_1^* - \mu_2^*)^2}{\sigma_1^2} \right\}}}. \quad (\text{S29})$$

This will be positive as long as $\sigma_1^2 < 2(\mu_1^* - \mu_2^*)^2$, and negative otherwise. Similarly, if species 2 has much more ITV, then

$$\frac{\partial(1-\rho)}{\partial\sigma_1^2} \approx \frac{2(\mu_1^* - \mu_2^*)^2 + \sigma_2^2}{2\sqrt{2} \left(\frac{\sqrt{\sigma_1^2 \sigma_2^2}}{\sigma_2^2} \right)^{\frac{3}{2}} (\sigma_2^2)^4} \sqrt{e^{\left\{ -\frac{(\mu_1^* - \mu_2^*)^2}{\sigma_2^2} \right\}}}. \quad (\text{S30})$$

This will always be positive. Thus, increasing a species' ITV will always decrease the stabilizing niche difference, except when it contributes to a generalist-specialist trade-off (i.e. when it has the higher ITV, and mean trait differences are small compared to dietary overlap). This result is the same as the case of the previous definition of stability.

$$\alpha_{jk} = \frac{1}{\sqrt{2\pi(\sigma_1^2 + \sigma_2^2)}} e^{-\frac{1}{2} \frac{(\mu_1^* - \mu_2^*)^2}{2\sigma_1^2 + 2\sigma_2^2}}. \quad (\text{S31})$$

Section S1.4 Other forms of $a_j(T, h)$ and $p_j(T)$

Above we investigated the MacArthur model when $a_j(T, h)$ and $p_j(T)$ were Gaussian functions. However, to test the generality of this situation, we

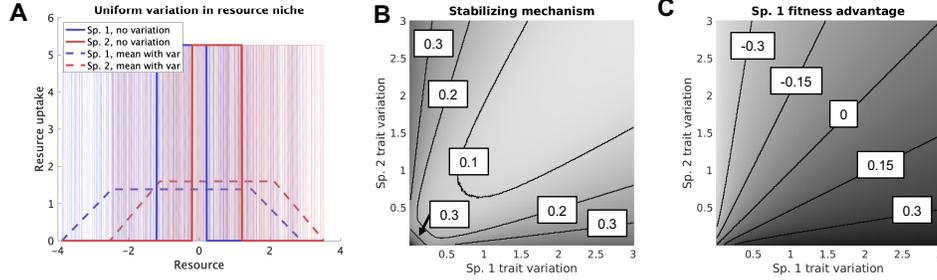


Figure S1: Variation independent mechanism with a uniform distribution. (a) We assumed that a species' uptake, $a_j(T, h)$, and their trait distribution, $p_j(T)$, were both normally distributed functions. Thus, ITV allowed a species to consume a wider variety of resources, but lowered the average attack rate on each. (b) Like with the Gaussian model, increasing the ITV of one species could increase the stabilizing mechanism by generating a generalist-specialist trade-off, but increasing ITV of both species weakened the mechanism. (c) Species with higher ITV had a fitness advantage, as they consumed more resources and therefore experience lowered intraspecific competition. Parameters: $\sigma_I^2 = 0.7$, $a_1^* = -0.5$, $a_2^* = 0.5$, .

explored other forms of $a_j(T, h)$ and $p_j(T)$ numerically. In each case, we first created a vector of the pdf of the trait distribution, $p(T)$ (a $1 \times n$ vector), and an $n \times n$ matrix $a_j(T, h)$ (where entry (T, h) is the attack rate that an individual with trait T has on resource h). Here, n was chosen to be large enough to encompass all possible resources that would be consumed. In cases where $a_j(h)$ or $p(T)$ were normal, we set all values above 3 standard deviations to 0. The vector of attack rates was then just the sum of the product $a_j(h) = p(T)a_j(T, h)$, and the competition coefficient was $\alpha_{jk} = a_j a_k^T / n$ (where a_k^T is the transpose of the vector). These two steps are thus the numerical version of equations S8 and S9. We could then calculate the stabilizing mechanisms and fitness differences using equations S12 and S13.

First, in Fig. 3 of the main text, we show $a_j(T, h)$ and $p_j(T)$ as both having Gaussian distributions, where species had different average uptakes. In that case, it was very hard for ITV to be stabilizing. However, if both species have very similar mean traits, then it is much easier for ITV in one species to create a stabilizing mechanism, fig. S2.

We also investigated the case where $a_j(T, h)$ and $p(T)$ were uniformly

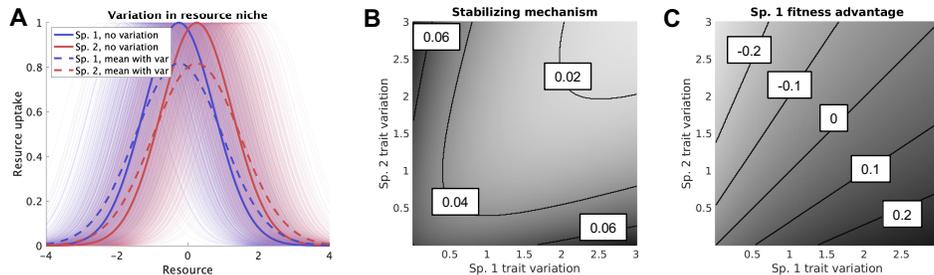


Figure S2: Variation independent mechanism when species have similar mean uptake. (a) We assumed that both species had very similar mean uptake ($\mu_1^* \approx \mu_2^*$). (b) In this case, there was a broad range in which ITV in one species could generate a generalist-specialist trade-off, promoting coexistence. (c) Species with higher ITV still had a fitness advantage. Parameters: $\sigma_I^2 = 0.7$, $\mu_1^* = -0.5$, $a_2^* = 0.5$.

distributed. We defined an individual's uptake as

$$a_j(T, h) = \begin{cases} \frac{1}{2\sigma_I^2} & \text{for } |a_j^* + T - h| \leq \sigma_I^2 \\ 0 & \text{for } |a_j^* + T - h| > \sigma_I^2 \end{cases}. \quad (\text{S32})$$

An example is shown in fig. S1. We found that the results were qualitatively similar to the case where they are normally distributed. We found that increasing both species ITV weakens the stabilizing mechanism. ITV in just one species will weaken the stabilizing mechanism when trait means differ substantially, and it strengthens the stabilizing mechanism when trait means are sufficiently similar. ITV in both species always weakens the stabilizing mechanism. Finally, ITV will always give a species a fitness advantage.

Section S2 Model 2: The storage effect

Section S2.1 Putting ITV into the lottery model

We first derive $\lambda_j(T, t)$, the amount that an individual with trait T is expected to contribute to the population at time $t + 1$ via survival and reproduction. Every individual survives with probability $1 - \delta$. Let K be the total number of territories. An individual will produce $Y_j(T, t)$ offspring in year t , and therefore send $Y_j(T, t)/K$ offspring to each territory. That territory will be vacated with probability δ , otherwise, the offspring will not capture

the site. If the site is vacant, then the offspring must compete with all other offspring for that site. To calculate the number of individuals competing for a site, let us define $I_j(T, k, t)$ as 1 if a given site k has an individual of species j with trait T at time t , and 0 otherwise. Then, the number of offspring competing for a site will be

$$\sum_j \sum_T \sum_k Y_j(T, t) I_j(T, k, t), \quad (\text{S33})$$

where the leftmost summation is over both species, the middle summation is over all possible traits, and the rightmost summation is over all sites. Let's defined $N_j(T, t)$ as the fraction of sites occupied by an individual of species j . Thus,

$$\sum_j \sum_T \sum_k Y_j(T, t) I_j(T, k, t) = \sum_j \sum_T Y_j(T, t) N_j(T, t). \quad (\text{S34})$$

The pdf of the trait is $p(T) = N_j(T, t)/N_j(t)$, therefore

$$\sum_j \sum_T \sum_k Y_j(T, t) I_j(T, k, t) = \sum_j \sum_T Y_j(T, t) p(T) N_j(t). \quad (\text{S35})$$

If we define $\overline{Y_j(t)} = \int Y_j(T, t) p(T) dT$ as the mean value of $Y_j(T, t)$, then this is simply

$$\begin{aligned} \sum_j \sum_T \sum_k Y_j(T, t) I_j(T, k, t) &= \sum_j \overline{Y_j(t)} N_j(t) \\ &= C(t) \end{aligned} \quad (\text{S36})$$

(where $C(t) = \sum_j \overline{Y_j(t)} N_j(t)$ now uses average fecundity). Thus, the chance that a seed captures of an individual captures a given site is $\frac{Y_j(T, t)}{KC(t)}$ (and this is summed across all K sites). Therefore,

$$\lambda_j(T, t) = 1 - \delta + \frac{\delta Y_j(T, t)}{C(t)}. \quad (\text{S37})$$

Once we have our equation for $\lambda_j(T, t)$, it is fairly easy to calculate the species-average growth rate:

$$\begin{aligned} \lambda_j(t) &= \int \lambda_j(T, t) p(T) dT \\ &= \int \left(1 - \delta + \frac{\delta Y_j(T, t)}{C(t)} \right) p(T) dT \\ &= 1 - \delta + \frac{\delta \overline{Y_j(t)}}{C(t)} \end{aligned} \quad (\text{S38})$$

Thus, we see that the impact of ITV is purely caused by how it changes $Y_j(t)$ (and with it $C(t)$) on any given time step.

Section S2.2 Invasion analysis

For our invasion analysis, we will use the variable transformation

$$\begin{aligned}\mathcal{Y}_j(t) &= \ln \{Y_j(t)\} \\ \mathcal{C}(t) &= \ln \{C(t)\}.\end{aligned}\tag{S39}$$

Our equation then becomes

$$\lambda_j(t) = 1 - \delta + \delta e^{\mathcal{Y}_j(t) - \mathcal{C}(t)}.\tag{S40}$$

We make this change of variables as it substantially simplifies our calculations below (if we did not, then most terms would need to be scaled by a power of $\mathbf{E}[Y_j(t)]$).

We want to figure out the long term rate of increase of each species, $\mathbf{E}[r_j(t)] = \mathbf{E}[\ln\{\lambda_j(t)\}]$. Because $\mathbf{E}[\ln\{\lambda_j(t)\}]$ is nonlinear, there is not a good way to do this exactly. Instead, we determine what $\ln\{\lambda_j(t)\}$ would be at values near $\mathcal{Y}_j(t) = \mathbf{E}[\mathcal{Y}_j(t)]$ and $\mathcal{C}(t) = \mathbf{E}[\mathcal{Y}_j(t)]$ (that is not a typo, $\mathcal{C}(t)$ should be near the mean of $\mathcal{Y}_j(t)$, as doing this makes $\ln\{\lambda_j(t)\} = 0$). We first do a second-order Taylor series approximation, i.e.

$$\begin{aligned}r_j(t) &\approx r_j(t)|_{\mathcal{Y}=\mathcal{C}=\mathbf{E}[\mathcal{Y}]} + (\mathcal{Y}_j(t) - \mathbf{E}[\mathcal{Y}_j(t)]) \frac{\partial r_j(t)}{\partial \mathcal{Y}_j(t)} + (\mathcal{Y}_j(t) - \mathbf{E}[\mathcal{Y}_j(t)]) \frac{\partial r_j(t)}{\partial \mathcal{C}(t)} \\ &+ \frac{1}{2} (\mathcal{Y}_j(t) - \mathbf{E}[\mathcal{Y}_j(t)])^2 \frac{\partial^2 r_j(t)}{\partial \mathcal{Y}_j(t)^2} + \frac{1}{2} (\mathcal{C}(t) - \mathbf{E}[\mathcal{Y}_j(t)])^2 \frac{\partial^2 r_j(t)}{\partial \mathcal{C}(t)^2} \\ &+ (\mathcal{Y}_j(t) - \mathbf{E}[\mathcal{Y}_j(t)]) (\mathcal{C}(t) - \mathbf{E}[\mathcal{Y}_j(t)]) \frac{\partial^2 r_j(t)}{\partial \mathcal{Y}_j(t) \partial \mathcal{C}(t)}.\end{aligned}\tag{S41}$$

This simplifies to

$$\begin{aligned}r_j(t) &\approx 0 + (\mathcal{Y}_j(t) - \mathbf{E}[\mathcal{Y}_j(t)]) \delta - (\mathcal{C}(t) - \mathbf{E}[\mathcal{Y}_j(t)]) \delta \\ &+ \frac{1}{2} (\mathcal{Y}_j(t) - \mathbf{E}[\mathcal{Y}_j(t)])^2 \delta(1 - \delta) + \frac{1}{2} (\mathcal{C}(t) - \mathbf{E}[\mathcal{Y}_j(t)])^2 \delta(1 - \delta) \\ &- (\mathcal{Y}_j(t) - \mathbf{E}[\mathcal{Y}_j(t)]) (\mathcal{C}(t) - \mathbf{E}[\mathcal{Y}_j(t)]) \delta(1 - \delta).\end{aligned}\tag{S42}$$

For this to be an accurate representation, we must assume that $\mathbf{var}(\mathcal{Y}_1(t))$, $\mathbf{var}(\mathcal{Y}_2(t))$, and $\mathbf{E}[\mathcal{Y}_1(t)] - \mathbf{E}[\mathcal{Y}_2(t)]$ are all $O(\epsilon)$, where ϵ is a small number (see Chesson, 1994, for details).

Next, we calculate the average of equation S42. By definition, the long term average of $\mathcal{Y}_j(t) - \mathbf{E}[\mathcal{Y}_j(t)]$ is 0, and the long term average of $(\mathcal{Y}_j(t) - \mathbf{E}[\mathcal{Y}_j(t)])^2$ is the variance of $\mathcal{Y}_j(t)$, $\mathbf{var}(\mathcal{Y}_j(t))$. The mean of $(\mathcal{C}(t) - \mathbf{E}[\mathcal{Y}_j(t)])^2$ is $\mathbf{var}(\mathcal{Y}_j(t)) + (\mathbf{E}[\mathcal{C}(t)] - \mathbf{E}[\mathcal{Y}_j(t)])^2$; and, under our assumptions size assumptions, $(\mathbf{E}[\mathcal{C}(t)] - \mathbf{E}[\mathcal{Y}_j(t)])^2$ will be $O(\sigma^4)$, and can thus be ignored. Thus,

$$\begin{aligned} \mathbf{E}[r_j(t)] &\approx 0 + 0 - \left(\overline{\mathcal{C}(t)} - \mathbf{E}[\mathcal{Y}_j(t)]\right) \delta \\ &\quad + \frac{1}{2} \mathbf{var}(\mathcal{Y}_j(t)) \delta(1 - \delta) + \frac{1}{2} \mathbf{var}(\mathcal{C}(t)) \delta(1 - \delta) \\ &\quad - \mathbf{cov}(\mathcal{Y}_j(t), \mathcal{C}(t)) \delta(1 - \delta). \end{aligned} \quad (\text{S43})$$

If we define $\beta_j = \delta$, then this simplifies to

$$\begin{aligned} \frac{\mathbf{E}[r_j(t)]}{\beta_j} &\approx 0 + 0 - \left(\overline{\mathcal{C}(t)} - \mathbf{E}[\mathcal{Y}_j(t)]\right) \\ &\quad + \frac{1}{2} \mathbf{var}(\mathcal{Y}_j(t)) (1 - \beta) + \frac{1}{2} \mathbf{var}(\mathcal{C}(t)) (1 - \delta) \\ &\quad - \mathbf{cov}(\mathcal{Y}_j(t), \mathcal{C}(t)) (1 - \delta). \end{aligned} \quad (\text{S44})$$

To calculate the invader growth rate of invader species i (when species r is the resident), we will calculate

$$\mathbf{E}[r_i(t)] = \mathbf{E}[r_i(t)] - \frac{\beta_i}{\beta_r} \mathbf{E}[r_r(t)]. \quad (\text{S45})$$

Then, by equation S44, this is

$$\begin{aligned} \frac{\mathbf{E}[r_i(t)]}{\beta_i} &\approx \mathbf{E}[\mathcal{Y}_i(t)] - \mathbf{E}[\mathcal{Y}_r(t)] \\ &\quad + \frac{1 - \delta}{2} (\mathbf{var}(\mathcal{Y}_i(t)) - \mathbf{var}(\mathcal{Y}_r(t))) \\ &\quad + 0 \\ &\quad - (1 - \delta) (\mathbf{cov}(\mathcal{Y}_i(t), \mathcal{C}(t)) - \mathbf{cov}(\mathcal{Y}_r(t), \mathcal{C}(t))) \end{aligned} \quad (\text{S46})$$

(note the third term is 0 because $\mathcal{C}(t)$ will be the same for both species).

The first term is often the most important part of the fitness effect. Its average across species will be 0, as $\mathbf{E}[\mathcal{Y}_j(t)]$ only depends on a species' trait distribution (and thus will not change with its abundance). Therefore, species 1's fitness advantage is simply $\mathbf{E}[\mathcal{Y}_1(t)] - \mathbf{E}[\mathcal{Y}_2(t)]$. Thus, species 1 will have an advantage if it produces more seeds on average than its competitor. ITV can affect this by changing fecundity in any given year, and

either increasing or decreasing it on average overall. For similar reasons, the second term will also have a small impact on the fitness effect and no stabilizing effect. It gives an advantage to the species with the higher variance in yield.

The last term is the storage effect, and will generally be the only mechanism that can be stabilizing. By our definition of $\mathcal{C}(t)$, $\mathcal{C}(t) = \mathcal{Y}_r(t)$. Thus, we find $\mathbf{cov}(\mathcal{Y}_r(t), \mathcal{C}(t)) = \mathbf{var}(\mathcal{Y}_r(t))$, and $\mathbf{cov}(\mathcal{Y}_r(t), \mathcal{C}(t)) = \rho_{ir}(\mathbf{var}(\mathcal{Y}_r(t)) \mathbf{var}(\mathcal{Y}_i(t)))^{1/2}$ (where ρ_{ir} is the correlation between the $\mathcal{Y}_j(t)$'s). Thus, this term will be positive for both species (unless $\rho_{ir} = 1$), and therefore contribute to the stabilizing mechanism. The important intuitive thing is this: the stabilizing effect will be stronger when $\mathbf{var}(\mathcal{Y}_j(t))$ is large, and when ρ_{ir} is small or negative. Thus, ITV in both species will decrease both of these factors, as they reduce variation in $\mathcal{Y}_j(t)$ and cause species to have a more similar response.

Section S2.3 Further analysis

In the text, we considered a trait T that affects fecundity, such that

$$\begin{aligned} Y_j(T, t) &= (1 + f(T)) \left(Y_{\text{gain}-j} e^{-\frac{(E(t) - \mu_j)^2}{w}} + Y_{\text{min}-j} \right) \\ &= (1 + f(T)) Y(0, t). \end{aligned} \quad (\text{S47})$$

In equation == of the main text, we gave an approximation for how ITV would change $\mathbf{E}[Y_j(t)]$ when fecundity is adjusted according to a nonlinear function $f(T)$. When $|T|$ is not too large, $f(T)$ can be approximated using a Taylor series

$$f(T) \approx f(0) + T \frac{df(0)}{dT} + T^2 \frac{d^2f(0)}{dT^2}. \quad (\text{S48})$$

The mean of T is 0, and the variance is $\sigma_{T_j}^2$. Thus,

$$\begin{aligned} \overline{f(T)} &\approx f(0) + \overline{T} \frac{df(0)}{dT} + \overline{T^2} \frac{d^2f(0)}{dT^2} \\ &= f(0) + \sigma_{T_j}^2 \frac{d^2f(0)}{dT^2} \end{aligned} \quad (\text{S49})$$

and

$$\overline{Y_j(t)} \approx \left(1 + \sigma_{T_j}^2 \frac{d^2f(0)}{dT^2} \right) Y_j(0, t). \quad (\text{S50})$$

For our analysis with $\mathcal{Y}_j(t)$, we can use similar methods. $\mathcal{Y}_j(t)$ is simply

$$\mathcal{Y}_j(T, t) = \ln \{Y_j(T, t)\} = \ln \{1 + f(T)\} + \ln \{Y_j(0, t)\}. \quad (\text{S51})$$

Thus, using the above methods, we find that

$$\overline{\mathcal{Y}_j(t)} \approx \sigma_{T_j}^2 \left(\left(\frac{df(0)}{dT} \right)^2 - \frac{d^2 f(0)}{dT^2} \right) + \mathcal{Y}_j(0, t). \quad (\text{S52})$$

Based on our analytical work in equation S46, this has a couple obvious implications. First, the fitness-difference that results from differences in mean fecundity becomes

$$\begin{aligned} \Delta\rho_i &= \mathbf{E}[\mathcal{Y}_i(t)] - \mathbf{E}[\mathcal{Y}_r(t)] \\ &\approx \mathcal{Y}_i(0, t) - \mathcal{Y}_r(0, t) + (\sigma_{T_i}^2 - \sigma_{T_r}^2) \left(\left(\frac{df(0)}{dT} \right)^2 - \frac{d^2 f(0)}{dT^2} \right) \end{aligned} \quad (\text{S53})$$

Thus, if $\left(\left(\frac{df(0)}{dT} \right)^2 - \frac{d^2 f(0)}{dT^2} \right)$ is positive (i.e. $f(T)$ is convex up or only slightly concave down), then ITV gives species a fitness advantage, and if it is negative, then ITV gives species a fitness disadvantage.

Second, this will have no impact on the stabilizing mechanism. The fecundity in any given year will be boosted by $\sigma_{T_j}^2 \left(\left(\frac{df(0)}{dT} \right)^2 - \frac{d^2 f(0)}{dT^2} \right)$. This is constant relative to t , therefore

$$\mathbf{cov} \left(\overline{\mathcal{Y}_j(t)}, \overline{\mathcal{Y}_k(t)} \right) = \mathbf{cov} \left(\mathcal{Y}_j(0, t), \mathcal{Y}_k(0, t) \right) \quad (\text{S54})$$

As such, ITV should have no impact on ΔI .

We tested our results with simulations. We modeled $f(T) = \exp -T^2/2 - 1$, fig. S3. We modeled populations by generating 1000 individuals, each with different traits. Trait were determined using the Box-Muller method (Box and Muller, 1958): we generated two uniform distributions, U_1 and U_2 ; then, species traits were $T = \sqrt{-2 \ln \{U_1\}} \cos(2\pi U_2)$. Environmental conditions, $E(t)$, were also generated using these methods (doing this allowed us to remove stochasticity produced by randomly choosing conditions). Then, each time step, we calculated the fecundity for each individual in the population, and averaged this over the population to determine $\overline{Y_j(t)}$. In an invasion analysis, $C(t) = \overline{Y_r(t)}$. Thus, we calculated the invader's growth rate as

$$\mathbf{E}[r_i] = \ln \left\{ \overline{1 - \delta + \delta \frac{\overline{Y_i(t)}}{\overline{Y_r(t)}}} \right\}. \quad (\text{S55})$$

Similar methods were used for both types of traits, the only difference was how the trait affected fecundity.

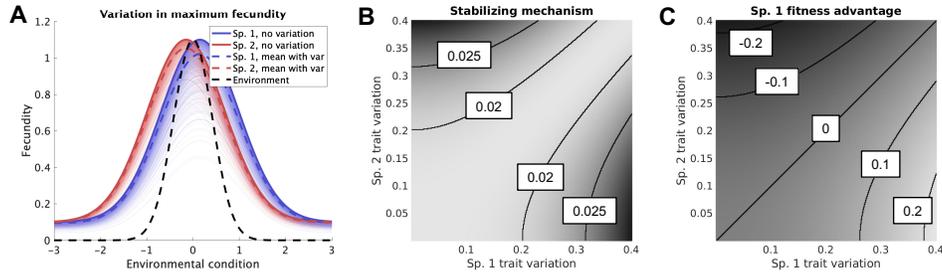


Figure S3: Storage effect when the trait affects fecundity. (a) We assumed that a species with trait T had fecundity $Y_j(0, T) \exp\{-T^2/2\}$. Thus, ITV reduced a species' average yield. (b) ITV had a slightly negative impact on the stabilizing mechanism, as it seemed to slightly weaken variation in fecundity. (c) ITV had a large negative impact on a species' fitness. Parameters: $\delta = 0.4$, $\mu_1 = 0.15$, $\mu_2 = -0.15$, $w = 1/\sqrt{2}$, $Y_{\min} = 0.3$, $Y_{\text{gain}}^* = 1$. $E(t)$ was a normal distribution with mean 0 and variance 0.4.

We found that ITV had a small impact on the stabilizing mechanism. This appeared to happen because ITV lowered $\overline{f(T)}$, which reduced the variance of $\overline{Y_j(t)}$, which must have slightly weakened temporal partitioning. However, the main impact was on the fitness difference, where increasing ITV reduced a species' fitness. Thus, we are confident in claiming that at least the main impact is to change relative fitness, rather than reduce the stabilizing mechanism.

In the main text that when the trait affect a species' optimal conditions for reproduction, ITV would reduce a species' fitness if they were mostly adapted to the environment, but it could increase a species' fitness if they were mostly maladapted. We show an example of the later in fig. S4. This appears most likely to occur when a species' average resource uptake is very different from the environmental average. Interestingly, in the case in fig. S4, too much ITV will reduce a species' fitness, as they start generating individuals on the other extreme end of maladaptation.

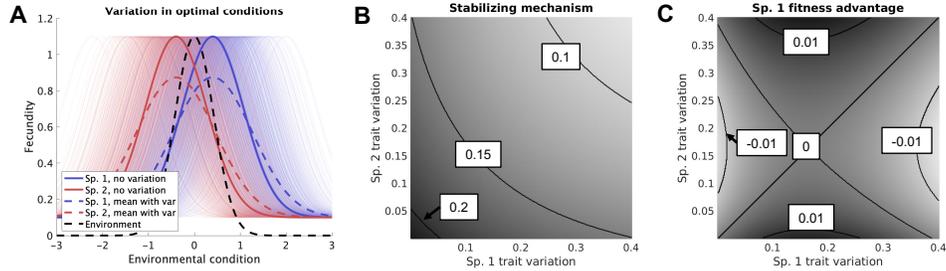


Figure S4: Storage effect when the trait affects optimal conditions for reproduction. (a) We assumed that an individual's trait determined what environmental conditions were optimal for it to reproduce. However, we also assumed that the average optimal condition for each species was more than a standard deviation away from the average environmental conditions (b) ITV had a negative impact on the stabilizing mechanism, as it is a trade-off trait. (c) However, here ITV boosted a species' relative fitness. Parameters: $\delta = 0.4$, $\mu_1^* = 0.4$, $\mu_2^* = -0.4$, $w = 1/\sqrt{2}$, $Y_{\min} = 0.3$, $Y_j^* = 1$. $E(t)$ was a normal distribution with mean 0 and variance $1/\sqrt{2}$.

Section S3 Model 3: The fitness-density covariance

Section S3.1 Invasion analysis

As with the lottery model, we will work with the transformed variables

$$\begin{aligned}\mathcal{Y}_j(x) &= \ln \{Y_j(x)\} \\ \mathcal{C}_j(x) &= \ln \{C(x)_j\}.\end{aligned}\tag{S56}$$

Note that this time we write the transformed variable as $\mathcal{C}_j(x)$, rather than just $\mathcal{C}(x)$, as it may differ between species (because of differences in α_j). Our equation then becomes

$$\lambda_j(x) = \sum_{x=1}^2 \nu_j(x, t) e^{\mathcal{Y}_j(x) - \mathcal{C}_j(x)}.\tag{S57}$$

First, we calculate $\lambda_j(x)$ as the growth rate at each site, weighted by the number of individuals at each site

$$\lambda_j(x) = \mathbf{E}[\nu_j(x, t)] \mathbf{E}\left[e^{\mathcal{Y}_j(x) - \mathcal{C}_j(x)}\right] + \mathbf{cov}\left(\nu_j(x, t), e^{\mathcal{Y}_j(x) - \mathcal{C}_j(x)}\right)\tag{S58}$$

(where $\mathbf{E}[\cdot]$ is now a spatial mean). By our definition of $\nu_j(x, t)$, its average is 1. Thus,

$$\lambda_j(x) = \mathbf{E} \left[e^{\mathcal{Y}_j(x) - \mathcal{C}_j(x)} \right] + \mathbf{cov} \left(\nu_j(x, t), e^{\mathcal{Y}_j(x) - \mathcal{C}_j(x)} \right). \quad (\text{S59})$$

For this analysis, we will approximate $e^{\mathcal{Y}_j(x) - \mathcal{C}_j(x)}$ using a first-order Taylor series around the point $\mathcal{Y}_j(x) = \mathcal{C}_j(x) = \mathbf{E}[\mathcal{Y}_j(x)]$,

$$e^{\mathcal{Y}_j(x) - \mathcal{C}_j(x)} \approx 1 + (\mathcal{Y}_j(x) - \mathbf{E}[\mathcal{Y}_j(x)]) - (\mathcal{C}_j(x) - \mathbf{E}[\mathcal{Y}_j(x)]). \quad (\text{S60})$$

Note, we could use a second-order Taylor series, which would reveal a spatial relative nonlinearity and a spatial storage effect (Chesson, 2000). We stopped with the first-order model, as previous work has suggested that a fitness-density covariance is the main mechanism (Uriarte and Menge, 2018). Substituting equation S60 into S59, we find that

$$\begin{aligned} \lambda_j(x) &\approx 1 + \mathbf{E}[(\mathcal{Y}_j(x) - \mathbf{E}[\mathcal{Y}_j(x)]) - (\mathcal{C}_j(x) - \mathbf{E}[\mathcal{Y}_j(x)])] \\ &\quad + \mathbf{cov}(\nu_j(x, t), 1 + (\mathcal{Y}_j(x) - \mathbf{E}[\mathcal{Y}_j(x)]) - (\mathcal{C}_j(x) - \mathbf{E}[\mathcal{Y}_j(x)])) \\ &= 1 - \mathbf{E}[\mathcal{C}_j(x)] + \mathbf{E}[\mathcal{Y}_j(x)] \\ &\quad + \mathbf{cov}(\nu_j(x, t), \mathcal{Y}_j(x)) - \mathbf{cov}(\nu_j(x, t), \mathcal{C}_j(x)). \end{aligned} \quad (\text{S61})$$

For our invasion analysis, we will define $\beta_j = 1$. We focus on $\lambda_j - 1$, rather than just λ_j , because it centers it around 0 (i.e. so that < 0 mean declining and > 0 means increasing). When we do this, we can write the invader growth rate as

$$\begin{aligned} \lambda_i(x) - 1 &= (\lambda_i(x) - 1) - (\lambda_r(x) - 1) \\ &\approx \mathbf{E}[\mathcal{Y}_i(x)] - \mathbf{E}[\mathcal{Y}_r(x)] \\ &\quad - (\mathbf{E}[\mathcal{C}_i(x)] - \mathbf{E}[\mathcal{C}_r(x)]) \\ &\quad + \mathbf{cov}(\nu_i(x, t), \mathcal{Y}_i(x)) - \mathbf{cov}(\nu_r(x, t), \mathcal{Y}_r(x)) \\ &\quad - (\mathbf{cov}(\nu_i(x, t), \mathcal{C}_i(x)) - \mathbf{cov}(\nu_i(x, t), \mathcal{C}_r(x))). \end{aligned} \quad (\text{S62})$$

The first term is similar to the storage effect model: it is a comparison of the average fecundity over sites. Its average across species will be 0, thus it has no stabilizing effect. Instead, species 1 will have a fitness advantage of $\mathbf{E}[\mathcal{Y}_1(x)] - \mathbf{E}[\mathcal{Y}_2(x)]$ (which will be negative if it is less fecund than its average competitor). The second term is new. It represents differences in species' sensitivity to competition. If both species have the same α_j , then this term will be 0. Otherwise, it will be positive for the species who is

less susceptible to competition, and negative for the species who is more susceptible.

The third and fourth terms of equation S70 are fitness-density covariances. The third term determines how much of the population is in its optimal site (based on fecundity). It will be stabilizing if the invader can concentrate itself in optimal sites more than the resident. The last term determines how much a population is in the sites with high competition. This will be stabilizing whenever the invader and resident become separated – the invader can be at high relative density (high ν) without being at high absolute density (leading to high C), whereas the resident cannot; therefore, the covariance will be more positive for the resident.

Section S3.2 Analysis of this model with ITV

We first consider the case where ITV affects sensitivity to competition, such that $\alpha_j(T) = (1 + T)\alpha_j^*$. This will affect how susceptible a population is to competition, on average. We can write the impact of $\mathcal{C}_j(x, t)$ using Taylor approximations, (we will use $N(x) = N_1(x, t) + N_2(x, t)$ for short)

$$\begin{aligned}\overline{\mathcal{C}_j(x)} &= \overline{\ln \left\{ 1 + \alpha_j^*(1 + T)N(x) \right\}} \\ &\approx \mathcal{C}_j(0, x) - \frac{\left(\alpha_j^* N(x) \right)^2}{1 + \alpha_j^* N(x)} \sigma_{Tj}^2.\end{aligned}\tag{S63}$$

This is complicated, but has an important implication: ITV decreases the negative impact a species has to competition.

Plugging our approximation for $\overline{\mathcal{C}_j(x)}$ into equation S70, we find that it is now

$$\begin{aligned}\lambda_i(x) - 1 &\approx \mathbf{E} [\mathcal{Y}_i(x)] - \mathbf{E} [\mathcal{Y}_r(x)] \\ &\quad - (\mathbf{E} [\mathcal{C}_i(0, x)] - \mathbf{E} [\mathcal{C}_r(0, x)]) \\ &\quad + \mathbf{E} \left[\frac{(\alpha_i^* N(x))^2}{1 + \alpha_i^* N(x)} \sigma_{Ti}^2 \right] - \mathbf{E} \left[\frac{(\alpha_r^* N(x))^2}{1 + \alpha_r^* N(x)} \sigma_{Tr}^2 \right] \\ &\quad + \mathbf{cov} (\nu_i(x, t), \mathcal{Y}_i(x)) - \mathbf{cov} (\nu_r(x, t), \mathcal{Y}_r(x)) \\ &\quad - (\mathbf{cov} (\nu_i(x, t), \mathcal{C}(0, x)) - \mathbf{cov} (\nu_r(x, t), \mathcal{C}(0, x))) \\ &\quad + \mathbf{cov} \left(\nu_i(x, t), \frac{(\alpha_i^* N(x))^2}{1 + \alpha_i^* N(x)} \sigma_{Ti}^2 \right) - \mathbf{cov} \left(\nu_r(x, t), \frac{(\alpha_r^* N(x))^2}{1 + \alpha_r^* N(x)} \sigma_{Tr}^2 \right)\end{aligned}\tag{S64}$$

This equation has two novel terms. The third term shows how ITV affects a species' average susceptibility to competition. The species with more ITV will have a fitness advantage, as it can produce more offspring on every site. The last term is now the covariance between density and $\frac{(\alpha_i^* N(x))^2}{1+\alpha_i^* N(x)} \sigma_{Ti}^2$; this term will tend to be very small, and simply state that a species will have an advantage if there are more individuals where it is least susceptible to competition.

The biggest impact of ITV on stability will likely be on changing the distribution of species $\nu_j(x, t)$. If ITV causes species to become more segregated, it could in theory raise the stabilizing mechanism. However, simulations suggest that the opposite is true: it weakens stability (likely by making species less segregated), Fig. X of the main text.

We tested multiple ways that ITV could affect coexistence. We first considered the possibility that the trait affected the optimal conditions for reproduction, μ_j , fig. S5. We assumed that there was an environmental condition at each patch, $E(1)$ and $E(2)$. We then modeled an individual's fecundity in habitat x as

$$Y_j(x) = Y_{\max} \exp \left\{ -\frac{(E(x) - \mu_j)^2}{w} \right\} + Y_{\min}. \quad (\text{S65})$$

This is an identical model to the optimal conditions for reproduction in the storage effect model. We assumed that the trait T affected an individual's optimal condition, such that

$$\mu_j(T) = \mu_j^*(1 + T) \quad (\text{S66})$$

(where $T > -1$). Therefore, an individual's growth rate at site $E(x)$ would be

$$Y_j(x, T) = Y_{\max} \exp \left\{ -\frac{(E(x) - \mu_j^* - T)^2}{w} \right\} + Y_{\min-j}. \quad (\text{S67})$$

This a niche trait: a high-T individual is better at competing in high- $E(x)$ patch, but worse at competing in low- $E(x)$ patches. ITV in this trait will reduce a species' average reproductive output in patches where $E(x) < \mu_j^*$, but increase a species' average reproductive output in patches where $E(x)$ is close to μ_j^* . Thus, ITV makes a species more of a generalist in its habitat niche (Fig.S5a).

Our results were very similar to those of the storage effect model, and here we provide intuition as to why. The trait's impact on Y_j is a Gaussian distribution, thus we know that second derivative of $Y_j(T, x)$ will be negative

when $(E(x) - \mu_j^* - T)^2 < w$, and positive elsewhere, and it will generally be at its most negative when $E(x) - \mu_j^* - T = 0$. This will not quite be true for $\mathcal{Y}_j(T, x)$, as it is the natural log of $Y_j(T, x)$, though this gives us a start for building intuition. First, ITV is likely to counteract the fitness-density covariance in the fourth and fifth terms. Species are more likely to become segregated, and will benefit more from segregation, if they partition habitat. ITV weakens this partitioning, by making a species' growth rate more even across both patches. Thus, as with the storage effect model, ITV will reduce the stabilizing mechanism. The one exception is when there was a generalist-specialist trade-off (fig. S5b). It appeared that the conditions for a generalist-specialist trade-off to occur were somewhat limited, as there were only two environmental conditions; therefore, it seemed to only occur if both species were best adapted to the same patch. Second, we found that ITV could promote or weaken a species' fitness. ITV will reduce a species' fecundity in locations where it is a strong competitor, and increase its fecundity in locations where it is a weak competitor. The net impact of this across both patches will determine whether $\mathbf{E} \left[\frac{\partial^2 \mathcal{Y}_j(0, x)}{\partial T^2} \right]$ is positive or negative (and therefore whether ITV improves or weakens a species relative fitness). Fig. S5 is an example of the later: ITV makes the species marginally better in its worst habitat and much worse in its best habitat (fig. S5c), therefore, ITV tends to reduce a species' fitness.

Second, we examined how the stabilizing mechanisms and fitness differences would change if fecundity dependent on some environmental condition

$$Y_j(x, T) = Y_j^* \exp \left\{ -\frac{(E(x) - \mu_j^* - T)^2}{w} \right\} + Y_{\min-j}. \quad (\text{S68})$$

The average yield of a population at T will be

$$\overline{\mathcal{Y}_j(T, x)} \approx Y_j(0, x) + \sigma_{Tj}^2 \frac{\partial^2 \mathcal{Y}_j(0, x)}{\partial T^2}. \quad (\text{S69})$$

(the second derivative of $\mathcal{Y}_j(T, x)$ is too complicated to be worth writing, but we discuss its important properties below). Putting this into our invader

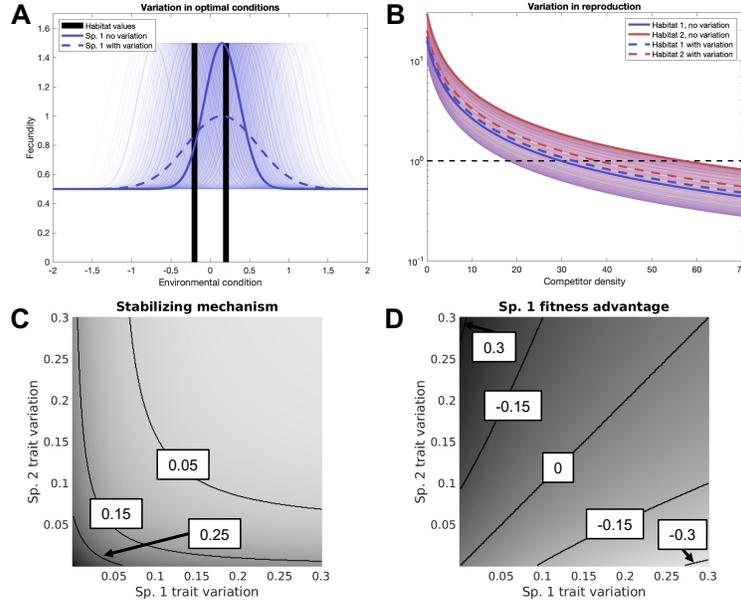


Figure S5: Fitness-density covarianace when the trait affects optimal conditions for reproduction. (a) We assumed that a species with trait T its optimal conditions for reproduction. Because there were only two patches (the black lines), only two of those possible conditions were experienced. (b) Here we show the growth rate of individuals of species 1 in each patch. The red line is its growth rate at different competitor densities in its best habitat, while the blue line is its growth rate at different densities in its worse habitat. ITV tends to increase its total reproduction in the worse habitat, but reduce it in the best habitat. (c) We find that ITV had a strongly negative impact on the stabilizing mechanism. (d) Additionally, ITV reduces a species' relative fitness. Parameters: $d = 2$, $\alpha_1 = \alpha_2 = 0.5$, $\mu_1 = 0.15$, $\mu_2 = -0.15$, $w = 1/\sqrt{2}$, $Y_{\min} = 10$, $Y_{\text{gain}} = 20$, $E(1) = -0.2$, $E(2) = 0.2$.

growth rate approximation, equation S70, we find that

$$\begin{aligned}
\lambda_i(x) - 1 &\approx \mathbf{E}[\mathcal{Y}_i(0, x)] - \mathbf{E}[\mathcal{Y}_r(0, x)] \\
&+ \sigma_{T_i}^2 \mathbf{E}\left[\frac{\partial^2 \mathcal{Y}_r(0, x)}{\partial T^2}\right] - \sigma_{T_r}^2 \mathbf{E}\left[\frac{\partial^2 \mathcal{Y}_r(0, x)}{\partial T^2}\right] \\
&- (\mathbf{E}[\mathcal{C}_i(x)] - \mathbf{E}[\mathcal{C}_r(x)]) \\
&+ \mathbf{cov}\left(\nu_i(x, t), \mathcal{Y}_i(0, x) + \sigma_{T_i}^2 \frac{\partial^2 \mathcal{Y}_i(0, x)}{\partial T^2}\right) \\
&- \mathbf{cov}\left(\nu_r(x, t), \mathcal{Y}_r(0, x) + \sigma_{T_r}^2 \frac{\partial^2 \mathcal{Y}_r(0, x)}{\partial T^2}\right) \\
&- (\mathbf{cov}(\nu_i(x, t), \mathcal{C}(x)) - \mathbf{cov}(\nu_r(x, t), \mathcal{C}(x))).
\end{aligned} \tag{S70}$$

The main impact of ITV would be on on the mean effect; this will not vary with resident and invader states, and will therefore mainly produce fitness differences. Depending on the curvature, it could have a slight effect on the first fitness-density covariance term, $\mathbf{cov}\left(\nu_i(x, t), \mathcal{Y}_j(0, x) + \sigma_{T_j}^2 \frac{\partial^2 \mathcal{Y}_j(0, x)}{\partial T^2}\right)$. However, we expect that this impact would be small. Simply, the impact would be related to $\sigma_{T_j}^2 \mathbf{cov}\left(\nu_j(x, t), \frac{\partial^2 \mathcal{Y}_j(0, x)}{\partial T^2}\right)$. For this to make a difference, $\frac{\partial^2 \mathcal{Y}_j(0, x)}{\partial T^2}$ would need to differ significantly between patches (which seems like it will be much smaller than between-patch differences in $\mathcal{Y}_j(0, x)$), and also it would need to differ between species. It is also possible that ITV could impact the stabilizing mechanism indirectly by altering $\nu_j(x, t)$, however, again, because it is boosting a species' ability to compete in both patches, this impact is likely to be small. This is indeed what we found using simulations, fig. S6.

We tested the above claims using simulations. We initialized the resident's population to $Y_r(x, 0)/\alpha_r$ in each population. We then simulated the population for 2000 generations. Each population was represented by 1000 individuals with uniformly distributed traits. Each time step, we calculated the average fecundity of an individual with each trait at each site, and used the mean across individuals as the fecundity for that site. We then dispersed the population. The invader's density was set to 0, however, its relative density ($\nu_i(x)$) still changed over time: the per-capita growth rate at site x and time t was

$$\Delta \nu_i(x, t) = \frac{\overline{Y_i(x, t)}}{Y_r(x, t)} + \frac{1}{\nu_i(x, t)} d(\nu_i(y, t) - \nu_i(x, t)), \tag{S71}$$

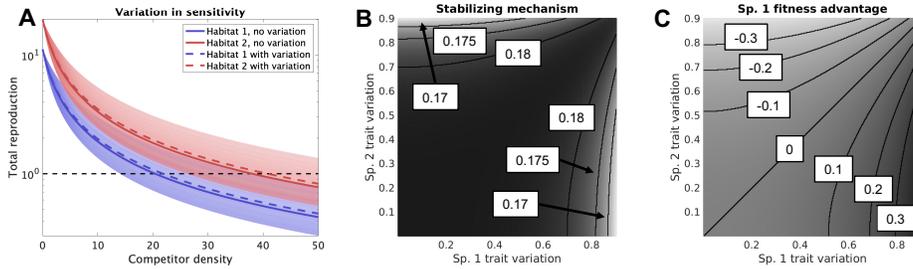


Figure S6: Fitness-density covariance model with trait that affects sensitivity to competition. (a) Here we show an individual's reproduction in patch 1 and 2, at different levels of competitor density. This trait is a non-compensatory trait, as individuals with a lower α_j produce more offspring in both patches. ITV increases a species' average reproduction, as individuals low α_j have a disproportionately high reproduction. (b) ITV had minimal impact on the stabilizing mechanism. Species with more variation benefitted everywhere, and thus it had little impact on how habitat was partitioned. If one species had much higher ITV than the other, this was slightly destabilizing, as it likely gave invaders an advantage in their non-optimal habitat, reducing the benefit of habitat partitioning. (c) However, ITV increased a species' relative fitness, as a species with high trait variation was less susceptible to competition on average. Parameters: $d = 2$, $\alpha_1^* = \alpha_2^* = 0.5$, $Y_1(1) = 27.6$, $Y_1(2) = 17.6$, $Y_2(1) = 17.6$, $Y_2(2) = 27.6$.

and so the actual relative density at time $t + 1$ was then

$$\nu_i(x, t + 1) = \frac{\Delta \nu_i(x, t)}{\Delta \nu_i(x, t) + \Delta \nu_i(y, t)}. \quad (\text{S72})$$

We allowed the populations to equilibrate for 1000 generations, and then recorded the invader's average growth rate over the next 1000 generations.

Section S4 Model 4: Relative nonlinearities

Finally, we examine the Monod model. A species' growth rate is

$$\begin{aligned} r_j(t) &= f_j(R(t)) - \delta \\ &= \frac{a_j R(t)}{1 + a_j R(t) h_j} - \delta \end{aligned} \quad (\text{S73})$$

where a_j is the species' attack rate, h_j is its handling time, δ is its death rate, and $R(t)$ is the density of resources. We will treat the dynamics of the resource implicitly.

Section S4.1 Invasion analysis

We will first solve this model without ITV, and then show how our results will be essentially the same with ITV. We first write this as a Taylor series expansion around the resource level ($R(t)$) that will allow the species to be at equilibrium,

$$R_j^* = \frac{\delta}{a_j(1 - h_j\delta)}. \quad (\text{S74})$$

The Taylor approximation is

$$\begin{aligned} r_j(t) &\approx r_j(t)|_{R(t)=R_j^*} + (R(t) - R_j^*) \frac{dr_j(t)}{dR(t)} + \frac{1}{2} (R(t) - R_j^*)^2 \frac{d^2r_j(t)}{dR(t)^2} \\ &= 0 + (R(t) - R_j^*) \frac{a_j}{(1 + a_jR_j^*h_j)^2} - (R(t) - R_j^*)^2 \frac{a_j^2h_j}{(1 + a_jR_j^*h_j)^3}. \end{aligned} \quad (\text{S75})$$

Defining $\mathbf{E}[R(t)]$ and σ_R^2 as the temporal mean and variance of $R(t)$, the temporal mean growth rate is

$$\begin{aligned} \mathbf{E}[r_j(t)] &\approx r_j(t)|_{R(t)=R_j^*} + (\mathbf{E}[R(t)] - R_j^*) \frac{dr_j(t)}{dR(t)} + \frac{1}{2}\sigma_R^2 \frac{d^2r_j(t)}{dR(t)^2} \\ &= 0 + (\mathbf{E}[R(t)] - R_j^*) \frac{a_j}{(1 + a_jR_j^*h_j)^2} - \sigma_R^2 \frac{a_j^2h_j}{(1 + a_jR_j^*h_j)^3}. \end{aligned} \quad (\text{S76})$$

Note that $\mathbf{E}[R(t)]$ likely differs slightly from R_j^* . If we define the sensitivity to competition as the derivative of the functional response,

$$\begin{aligned} \beta_j &= \frac{df_j(R_j^*)}{dR(t)} \\ &= \frac{a_j}{(1 + a_jR_j^*h_j)^2}, \end{aligned} \quad (\text{S77})$$

then,

$$\begin{aligned} \frac{\mathbf{E}[r_j(t)]}{\beta_j} &\approx \mathbf{E}[R(t)] - R_j^* - \frac{\sigma_R^2}{\beta_j} \frac{d^2r_j(t)}{dR(t)^2} \\ &\approx \mathbf{E}[R(t)] - R_j^* - \sigma_R^2 \frac{a_jh_j}{1 + a_jR_j^*h_j}. \end{aligned} \quad (\text{S78})$$

Writing this as an invader-resident comparison, it is

$$\begin{aligned}
\frac{\mathbf{E}[r_i(t)]}{\beta_i} &= \frac{\mathbf{E}[r_i(t)]}{\beta_i} - \frac{\mathbf{E}[r_r(t)]}{\beta_r} \\
&\approx - (R_i^* - R_r^*) - \sigma_R^2 \left(\frac{1}{\beta_i} \frac{d^2 r_i(t)}{dR(t)^2} - \frac{1}{\beta_r} \frac{d^2 r_r(t)}{dR(t)^2} \right) \\
&= - (R_i^* - R_r^*) - \sigma_R^2 \left(\frac{a_i h_i}{1 + a_i R_i^* h_i} - \frac{a_r h_r}{1 + a_r R_r^* h_r} \right).
\end{aligned} \tag{S79}$$

There are two terms in the above equation. The first term is an R^* comparison: in a stable environment, the species that can persist at the lowest resource level will win competition (Hsu et al., 1977). The value of each species' R_j^* does not depend on its density, therefore this term will only produce fitness differences. The second term gives the amount that a species' growth rate is reduced by resource fluctuations. The species with the larger handling time will often be penalized more, and this penalty will be stronger the higher variation is. This term could be stabilizing if the amount of resource variation R_j^* changes, depending on which species in the resident. As previous work has shown (Armstrong and McGehee, 1980; Chesson, 1994), this can promote coexistence if the species who is least harmed by variation also tends to increase resource variation when they are abundant.

Section S4.2 Inserting ITV into the Monod model

Our model considered three forms of ITV: variation in attack rate a_j , variation in handling time h_j , and variation in both. For simplicity, we will work out the later case (as variation in a_j alone can be calculated by setting variation in h_j to 0). An individual with a particular attack time α and handling time η will have a growth rate of

$$\begin{aligned}
r_j(\alpha, \eta, t) &= f_j(\alpha, \eta, R(t)) - \delta \\
&= \frac{\alpha_j R(t)}{1 + \alpha R(t) \eta} - \delta.
\end{aligned} \tag{S80}$$

Thus, the growth rate of the population is

$$\begin{aligned}
r_j(t) &= \int \int (f_j(\alpha, \eta, R(t)) - \delta p_j(\alpha, \eta)) d\alpha d\eta \\
&= \left(\int \int \frac{\alpha R(t)}{1 + \alpha R(t) \eta} p_j(\alpha, \eta) d\alpha d\eta \right) - \delta.
\end{aligned} \tag{S81}$$

Thus, if we define a_j and h_j as the mean of α and η across individuals in species j , $\sigma_{\alpha j}^2$ and $\sigma_{\eta j}^2$ as the variance of α and η , and $\sigma_{\alpha\eta j}^2$ as their covariance, then we can approximate the growth rate of species j as

$$\overline{r_j(t)} \approx f_j(a_j, h_j, R(t)) + \frac{1}{2}\sigma_{\alpha j}^2 \frac{\partial^2 r_j(t)}{\partial \alpha^2} + \frac{1}{2}\sigma_{\eta j}^2 \frac{\partial^2 r_j(t)}{\partial \eta^2} + \sigma_{\alpha\eta j}^2 \frac{\partial^2 r_j(t)}{\partial \alpha \partial \eta} - \delta. \quad (\text{S82})$$

Thus, if we define the population-level approximate growth rate as

$$\tilde{f}_j(R(t)) = f_j(a_j, h_j, R(t)) + \frac{1}{2}\sigma_{\alpha j}^2 \frac{\partial^2 r_j(t)}{\partial \alpha^2} + \frac{1}{2}\sigma_{\eta j}^2 \frac{\partial^2 r_j(t)}{\partial \eta^2} + \sigma_{\alpha\eta j}^2 \frac{\partial^2 r_j(t)}{\partial \alpha \partial \eta}, \quad (\text{S83})$$

then we can write the population-level growth rate as

$$r_j(t) \approx \tilde{f}_j(R(t)) - \delta. \quad (\text{S84})$$

Note that under the trade-off scenario, ITV could likely altered the mean values of a_j and h_j . This occurred because there was a nonlinear relationship between the location on the trade-off axis. However, the above results could still be defined in terms of the variance of the trait T , and could be used to calculate a similar $\tilde{f}_j(R(t))$.

We can use this in our previous analysis. We will define \tilde{R}_j^* as the value for which $\tilde{f}_j(R(t)) = \delta$. Then, substituting $\tilde{f}_j(R(t))$ for $f_j(R(t))$ into our approximation for $\mathbf{E}[r_j(t)]$ (equation S76), we find that

$$\mathbf{E}[\overline{r_j(t)}] \approx \left(\mathbf{E}[R(t)] - \tilde{R}_j^* \right) \frac{d\tilde{f}_j(\tilde{R}_j^*)}{dR(t)} + \frac{1}{2}\sigma_R^2 \frac{d^2 \tilde{f}_j(\tilde{R}_j^*)}{dR(t)^2}. \quad (\text{S85})$$

By defining $\tilde{\beta}_j$ as the derivative of the functional response (akin to equation S86),

$$\tilde{\beta}_j = \frac{d\tilde{f}_j(\tilde{R}_j^*)}{dR(t)}, \quad (\text{S86})$$

we can calculate the growth rate of an invader (akin to equation S79) as approximately

$$\frac{\mathbf{E}[\overline{r_i(t)}]}{\tilde{\beta}_i} \approx - \left(\tilde{R}_i^* - \tilde{R}_r^* \right) - \sigma_R^2 \left(\frac{1}{\tilde{\beta}_i} \frac{d\tilde{f}_i(\tilde{R}_i^*)}{dR(t)^2} - \frac{1}{\tilde{\beta}_r} \frac{d\tilde{f}_r(\tilde{R}_r^*)}{dR(t)^2} \right). \quad (\text{S87})$$

Thus, we see that our result is qualitatively the same as before.

The above result shows that ITV can affect coexistence in three ways. First, it could alter a species' minimum resource requirement at equilibrium,

affecting its relative fitness. Second, it could alter the impact of variation, altering both the fitness-difference and the stabilizing mechanism. However, we are slightly skeptical as to how important this is, as it will be proportional to $\sigma_R^2 \sigma_{\alpha_j}^2$ or $\sigma_R^2 \sigma_{\eta_j}^2$, and thus are likely only important when there is an extreme amount of both resource variation and ITV. Third, it could alter the amount that resources fluctuate, potentially altering both the fitness-difference and the stabilizing mechanism.

Section S4.3 Simulating the Monod model

We simulated the Monod model using a fourth-order Runge-Kutta method. Each resource was initiated at a density of $\bar{R}_{\text{in}}/\delta$. The resident's population was set to $N_r(0) = 1$, and the invader's population was set to $N_i(0) = 0$. We modeled each population as containing a large number of individuals with different traits. To model variation in attack rate or handling time, we assumed that individual's trait T was uniformly distributed over many individuals. To model variation in the trade-off function, we assumed each population contained 1000 individuals whose trait T was normally distributed (generated using the Box-Muller method, Box and Muller, 1958). In either case, each time step we calculated the resource uptake of every individual in the population, and used this average as the species' mean resource uptake at that time period. We calculated the growth rate of the invader at each time step in order to calculate the mean growth rate of the invader (though its population stayed at 0). We simulated the community for 500 units of time, and calculated the invader's average growth rate as its mean growth rate over the last oscillation (i.e. the last τ units of time, where τ was the period of R_{in}).

At the end of each simulation, we calculated the equilibrium resource density, R_i^* , for the invader. We did this using a bisection method: we chose a minimum and maximum possible value of R , R_{min} and R_{max} respectively, such that $f_i(R_{\text{min}}) < \delta$ and $f_i(R_{\text{max}}) > \delta$ (i.e. resource uptake was above and below replacement). We then calculated the growth rate at $R_{\text{test}} = (R_{\text{max}} + R_{\text{min}})/2$. If $f_i(R_{\text{test}}) < \delta$, then we set a new R_{min} to $R_{\text{min}} = R_{\text{test}}$; otherwise we set R_{min} to $R_{\text{max}} = R_{\text{test}}$. We repeated this 15 times.

First we examine the case where the trait T affects an individual's handling time,

$$h_j(T) = h_j^*(1 + T) \tag{S88}$$

(where $T > 1$). As with attack rate, handling time is a hierarchical trait: low- T individuals will be able to consume food faster. h_j has a concave up effect on resource uptake (Fig. S7a). As such, ITV raises average resource

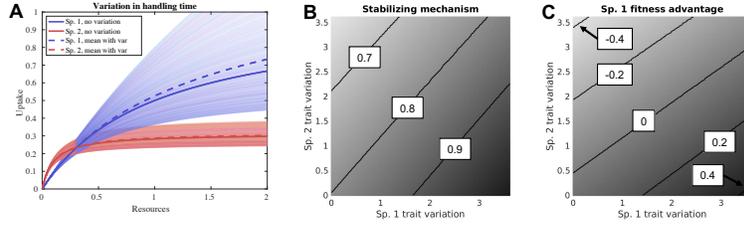


Figure S7: Relative nonlinearity with the trait affecting an individual’s handling time. (a) Here we show as individual’s resource uptake a different levels of resource density. This trait is a non-compensatory trait, as an individual with a low handling time will allow it to take up resources faster at any resource level. ITV increased a species’ average resource uptake rate, as individuals with a low handling time take up disproportionately more resources. (b) ITV in species 1 (the opportunist) increases the stabilizing mechanism, though ITV in species 2 (the gleaner) reduces it. These species coexist when there was low resource variation when species 1 was the resident, but high variation when species 2 was the resident. In either case, ITV allows a species to reduce resource variation. Thus, ITV in species 1 increases the difference in the variation niche, and ITV in species 2 reduces it. (c) In either case, ITV increases a species’ relative fitness, as it increases the species’ average ability to take up resources. Parameters: $\delta = 0.2$, $\overline{R}_{in} = 6$, $A = 5.5$, $\tau = 0.5$, $a_1 = 1$, $a_2 = 3$, $h_1^* = 1$, $h_2^* = 3.2$.

uptake for a species by reducing the number of individuals who are handling-time limited. Thus, as a concave-up, hierarchical trait, ITV in handling time improves a species’ fitness (Fig. S7c). As with attack rate, handling time is one element of a between-species trade-off, and therefore ITV affects the stabilizing mechanism. However, variation in handling time has the opposite impact that variation in attack rates did? ITV in the opportunist’s increases stability, whereas ITV in the gleaner decreases stability (Fig. S7b). The reason is analogous to before. ITV increases a species’ ability to acquire resources when resources are abundant, but also makes it more able to reduce resource fluctuations. Thus, an opportunist with a high ITV benefits from resource variation, making it less like the gleaner; whereas a gleaner with a high ITV also benefits from high resource variation, making it more like the opportunist. Thus, like before, ITV that makes the functional response lines more different increases stability, and ITV that makes the lines more similar decreases stability.

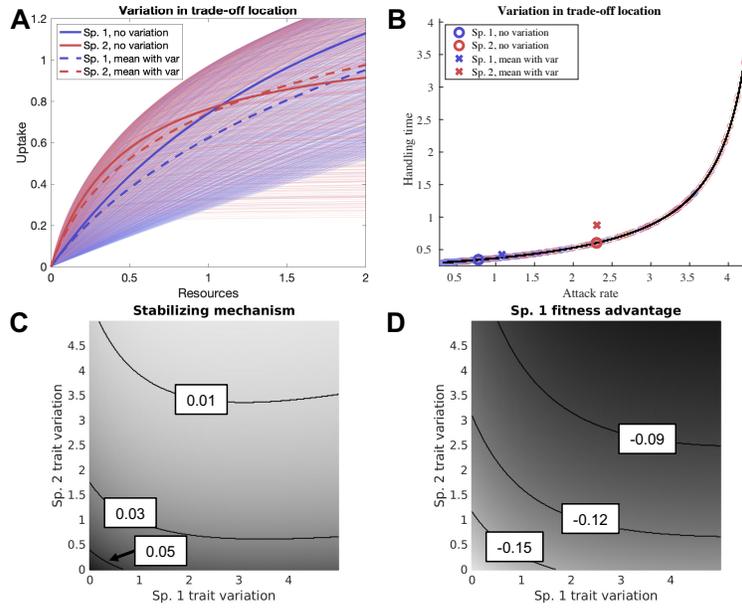


Figure S8: Relative nonlinearity with the trait affecting an individual's location on a trade-off axis. (a) We assumed that handling time and attack rate traded off, and that both species were on the same trade-off curve (though had different mean values along that curve). Above we show the curve we used for this simulation. (b) Here we show the resource uptake of each species at different levels of resource uptake. ITV tended to alter the shapes of the curves. (c) ITV tended to weaken the stabilizing mechanism by making species more similar; this result held up through all simulations that we ran. (d) In this parameter set, ITV in either species helped species 1's fitness. Parameters: $\delta = 0.2$, $\overline{R_{in}} = 6$, $A = 5.5$, $\tau = 0.5$, $\mu_1^* = 2$, $\mu_2^* = 0$, $a_1 = 0.3$, $a_2 = 4$, $h_1 = 0.3$, $h_2 = 4$, $h_3 = -2.5$.

Next we show the results of the case where the trait affected an individual’s location on the attack-rate-handling-time trade-off, fig. S8. As stated in the main text, an individual’s attack rate and handling time are determined by their trait $\mu_j(T) = \mu_j^* + T$, such that

$$\begin{aligned} a_j(T) &= a_1 + \frac{a_2}{1 + e^{\mu_j(T)}} \\ h_j(T) &= h_1 + \frac{h_2}{1 + e^{\mu_j(T)-h_3}} \end{aligned} \tag{S89}$$

Interestingly, because of the nonlinearities in the trade-off function, the averages of a_j and h_j are not the population median (and actually do not exist on the trade-off curve, fig. S8a). We found that in this case, ITV tended to weaken the stabilizing mechanism. Whether it improved or weakened a species’ fitness depended on its location on the trade-off axis. And, in some cases, it could have different impacts on different species, such as in fig. S8d, where ITV in either species helps species 1.

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