

Supplementary Information for

How do genetic correlations affect species range shifts in a changing environment?

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1 Derivation of analytical approximations for $n(x, t)$ and $\bar{z}(x, t)$

1.1 Speed of the travelling wave.

Following Pease et al. (1989), and consistently with Sections 5 and 6, we propose that the solutions to the partial differential equations system formed by these equations is a travelling wave. We will first assess the speed of the travelling waves of the trait mean and of population density, by assuming they may be of different speeds, respectively k_z and k_n :

$$n(x, t) = e^{\rho t - \frac{\sigma}{2}(x - k_n t - L_n)^2} \quad (1.1)$$

$$\bar{z}(x, t) = s(x - k_z t) \quad (1.2)$$

Using these solutions and replacing the derivatives in main text equations (3) and (4) by their actual values, main text equation (3) becomes:

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$$\begin{aligned}
 0 = & x^2 \left[\frac{\sigma^2}{2} c^2 - \frac{1}{2} (\mathbf{s} - \mathbf{b})^\top \mathbf{W}^{-1} (\mathbf{s} - \mathbf{b}) \right] + x [-c k_n - c^2 L_n \sigma^2] \\
 & + t^2 \left[\frac{\sigma^2}{2} c^2 k_n^2 - \frac{1}{2} (v \mathbf{b} - k_z \mathbf{s})^\top \mathbf{W}^{-1} (v \mathbf{b} - k_z \mathbf{s}) \right] + t [c k_n^2 + c^2 k_n L_n \sigma^2] \\
 & + x t \left[-\sigma^2 c^2 k_n - (\mathbf{s} - \mathbf{b})^\top \mathbf{W}^{-1} (v \mathbf{b} - k_z \mathbf{s}) \right] + \left[-\rho + c k_n L_n + \frac{\sigma^2}{2} c^2 L_n^2 - \frac{c^2 \sigma^2}{2} + r_0 - \frac{1}{2} \text{Tr}(\mathbf{W}^{-1} \mathbf{P}) \right]
 \end{aligned}$$

and main text equation (4) becomes:

$$\begin{aligned}
 \mathbf{0} = & x [-c \sigma^2 \mathbf{s} - \mathbf{G} \mathbf{W}^{-1} (\mathbf{s} - \mathbf{b})] + t [k_n c \sigma^2 \mathbf{s} - \mathbf{G} \mathbf{W}^{-1} (v \mathbf{b} - k_z \mathbf{s})] \\
 & + [k_z \mathbf{s} + \sigma^2 c L_n \mathbf{s}]
 \end{aligned}$$

For these latter two equations to be valid whatever t and x , all coefficients of the previous two polynomes must equal 0. This leads to the following system of equations:

$$\left\{ \begin{aligned}
 0 &= \sigma^2 c^2 - (\mathbf{s} - \mathbf{b})^\top \mathbf{W}^{-1} (\mathbf{s} - \mathbf{b}) \\
 0 &= k_n + c L_n \sigma^2 \\
 0 &= \sigma^2 c^2 k_n^2 - (v \mathbf{b} - k_z \mathbf{s})^\top \mathbf{W}^{-1} (v \mathbf{b} - k_z \mathbf{s}) \\
 0 &= k_n + c L_n \sigma^2 \\
 0 &= \sigma^2 c^2 k_n + (\mathbf{s} - \mathbf{b})^\top \mathbf{W}^{-1} (v \mathbf{b} - k_z \mathbf{s}) \\
 0 &= -\rho + c k_n L_n + \frac{\sigma^2}{2} c^2 L_n^2 - \frac{c^2 \sigma^2}{2} + r_0 - \frac{1}{2} \text{Tr}(\mathbf{W}^{-1} \mathbf{P}) \\
 \mathbf{0} &= c \sigma^2 \mathbf{s} + \mathbf{G} \mathbf{W}^{-1} (\mathbf{s} - \mathbf{b}) \\
 \mathbf{0} &= k_n c \sigma^2 \mathbf{s} + \mathbf{G} \mathbf{W}^{-1} (k_z \mathbf{s} - v \mathbf{b}) \\
 0 &= k_z + \sigma^2 c L_n
 \end{aligned} \right. \quad (1.3)$$

Comparing the second (= fourth) equation in this system to the last one immediately leads to $k_z = k_n = k$. Dividing the eighth (next-to-last) equation by k and comparing it to the seventh one leads to $v/k = 1$, *i.e.* both the trait means and the population density follow a wave travelling at speed v .

The solutions for trait mean $\bar{\mathbf{z}}$ and population density n are thus (main text equations (5) and (6)):

$$\begin{aligned}
 n(x, t) &= e^{\rho t - \frac{1}{2} \frac{(x - v t - L_n)^2}{V_n}} \\
 \bar{\mathbf{z}}(x, t) &= \mathbf{s}(x - v t)
 \end{aligned} \quad (1.4) \quad (1.5)$$

NB: The solution by Pease et al. (1989) stated that $\bar{\mathbf{z}}(x, t) = \mathbf{L}_z + \mathbf{s}(x - v t)$. In our model however, it can be shown that $\mathbf{L}_z = \mathbf{0}$, because our model does not contain an intrinsically better habitat, where fitness would be maximized (also see Section 4.1).

Equations (1.3) thus collapse to the following useful set of four equations and four unknowns (c , L_n , ρ , \mathbf{s}):

$$0 = v + \sigma^2 c L_n \quad (1.6)$$

$$\mathbf{0} = \sigma^2 c \mathbf{s} + \mathbf{G} \mathbf{W}^{-1} (\mathbf{s} - \mathbf{b}) \quad (1.7)$$

$$0 = \frac{\sigma^2}{2} c^2 L_n^2 - \frac{\sigma^2}{2} c + r_0 - \frac{1}{2} \text{Tr}(\mathbf{W}^{-1} \mathbf{P}) - \rho + c v L_n \quad (1.8)$$

$$0 = \frac{\sigma^2}{2} c^2 - \frac{1}{2} (\mathbf{s} - \mathbf{b})^\top \mathbf{W}^{-1} (\mathbf{s} - \mathbf{b}) \quad (1.9)$$

Exact solutions can be derived numerically, and approximations can be derived under the assumption of large migration load, *i.e.* $\|\mathbf{G} \mathbf{W}^{-1}\| \ll \sigma \sqrt{\mathbf{b}^\top \mathbf{W}^{-1} \mathbf{b}}$, where $\|\mathbf{M}\|$ denotes the norm of matrix \mathbf{M} . As in the main text, we note $\phi = \mathbf{b}^\top \mathbf{W}^{-1} \mathbf{G} \mathbf{W}^{-1} \mathbf{b}$ and $\psi = \mathbf{b}^\top \mathbf{W}^{-1} \mathbf{b}$. The large migration load hypothesis therefore implies that $\phi \ll \sigma \psi^{3/2}$.

1.2 Solving for trait means and population density.

Solve 1.7 for \mathbf{s} (\mathbf{I} is the identity matrix).

Assumption: $[\sigma^2 c \mathbf{I} + \mathbf{G} \mathbf{W}^{-1}]$ is invertible.

$$\begin{aligned} \mathbf{s} &= [\sigma^2 c \mathbf{I} + \mathbf{G} \mathbf{W}^{-1}]^{-1} \mathbf{G} \mathbf{W}^{-1} \mathbf{b} \\ (\mathbf{s} - \mathbf{b}) &= \left(\left[\sigma^2 c \left(\mathbf{I} + \frac{\mathbf{G} \mathbf{W}^{-1}}{\sigma^2 c} \right) \right]^{-1} \mathbf{G} \mathbf{W}^{-1} - \mathbf{I} \right) \mathbf{b} \end{aligned} \quad (1.10)$$

and since $\frac{\|\mathbf{G} \mathbf{W}^{-1}\|}{\sigma \sqrt{\psi}} \ll 1$:

$$\begin{aligned} (\mathbf{s} - \mathbf{b}) &= \frac{\mathbf{G} \mathbf{W}^{-1} \mathbf{b}}{\sigma^2 c} - \mathbf{b} + o \left[\frac{\|\mathbf{G} \mathbf{W}^{-1}\|}{\sigma \sqrt{\psi}} \right] \\ (\mathbf{s} - \mathbf{b})^\top \mathbf{W}^{-1} (\mathbf{s} - \mathbf{b}) &= \mathbf{b}^\top \mathbf{W}^{-1} \mathbf{b} - \frac{2 \mathbf{b}^\top \mathbf{W}^{-1} \mathbf{G} \mathbf{W}^{-1} \mathbf{b}}{\sigma^2 c} + o \left[\frac{\|\mathbf{G} \mathbf{W}^{-1}\|}{\sigma \sqrt{\psi}} \right] \end{aligned}$$

(because \mathbf{G} and \mathbf{W}^{-1} are symmetric).

$$(\mathbf{s} - \mathbf{b})^\top \mathbf{W}^{-1} (\mathbf{s} - \mathbf{b}) = \psi - \frac{2\phi}{\sigma^2 c} + o \left[\frac{\phi}{\sigma \psi^{3/2}} \right]$$

Replace in (1.9):

$$0 = \sigma^2 c^2 - \psi + \frac{2\psi^{3/2}}{\sigma c} \frac{\phi}{\sigma \psi^{3/2}} + o \left[\frac{\phi}{\sigma \psi^{3/2}} \right]$$

The last term can be assumed to be small since it depends on ϕ , while the second one depends on ψ and $\phi \ll \psi$. Therefore, c can be written as $c = c_0 + \delta$, with

- c_0 verifying: $0 = \sigma^2 c_0^2 - \psi$ (that is, $c_0 = \pm \sqrt{\psi}/\sigma$; but only the positive root of c_0 will lead to finite ranges, hence $c_0 = \sqrt{\psi}/\sigma$),
- and $\delta \ll 1$ (δ of the order of $\phi/(\sigma \psi^{3/2})$).

Replacing in 1.9, and developing a Taylor series in ϕ/ψ and in δ gives:

$$\delta = -\frac{\phi}{\sigma^2 \psi} + o \left[\frac{\phi}{\sigma \psi^{3/2}} \right] + o[\delta]$$

Hence:

$$c = \frac{\sqrt{\psi}}{\sigma} - \frac{\phi}{\sigma^2 \psi} + o \left[\frac{\phi}{\sigma \psi^{3/2}} \right] \quad (1.11)$$

$$V_n = \frac{\sigma}{\sqrt{\psi}} + \frac{\phi}{\psi^2} + o \left[\frac{\phi}{\sigma \psi^{3/2}} \right] \quad (1.12)$$

Equation (1.10) leads to \mathbf{s} ; L_n follows from equation (1.6) and ρ from equation (1.8):

$$\mathbf{s} = \frac{\mathbf{G} \mathbf{W}^{-1} \mathbf{b}}{\sigma \sqrt{\psi}} + o \left[\frac{\|\mathbf{G} \mathbf{W}^{-1}\|}{\sigma \sqrt{\psi}} \right] \quad (1.13)$$

$$L_n = -\frac{v}{\sigma^2 c} = -\frac{v}{\sigma \sqrt{\psi}} \left(1 + \frac{\phi}{\sigma \psi^{3/2}} \right) + o \left[\frac{\phi}{\sigma \psi^{3/2}} \right] \quad (1.14)$$

$$\rho = r_0 - \frac{1}{2} \text{Tr}(\mathbf{W}^{-1} \mathbf{P}) - \frac{\sigma}{2} \sqrt{\psi} + \frac{\phi}{2\psi} - \frac{v^2}{2\sigma^2} + o \left[\frac{\phi}{\sigma \psi^{3/2}} \right] \quad (1.15)$$

2 Accuracy of the approximations derived in Section 1.

The accuracy of the approximations derived above for V_n , L_n , ρ and s was assessed for 50,000 random input parameter sets for each of $d = 2$ traits and $d = 5$ traits.

2.1 $d = 2$ traits

Matrices \mathbf{G} and \mathbf{W} were written as $\mathbf{G} = \mathbf{R}_G^T \Lambda_G \mathbf{R}_G$ and $\mathbf{W} = \mathbf{R}_W^T \Lambda_W \mathbf{R}_W$, where \mathbf{R}_{mat} are rotation matrices, with $\mathbf{R}_{\text{mat}} = \begin{pmatrix} \cos(\theta_{\text{mat}}) & -\sin(\theta_{\text{mat}}) \\ \sin(\theta_{\text{mat}}) & \cos(\theta_{\text{mat}}) \end{pmatrix}$ and Λ_{mat} are the diagonal matrices of the eigenvalues of the corresponding matrix mat . $\mathbf{b} = \lambda_{\mathbf{b}} \begin{pmatrix} \cos(\theta_{\mathbf{b}}) \\ \sin(\theta_{\mathbf{b}}) \end{pmatrix}$. 50,000 initial parameters were randomly drawn for \mathbf{b} , \mathbf{W} , \mathbf{G} , σ , and v . $r_0 = 2$ and $\mathbf{P} = 4\mathbf{G}$. $\lambda_{\mathbf{b}}$, λ_{G_i} , λ_{W_i} , σ and v were drawn from \log_{10} -uniform laws, respectively in the intervals $[10^{-3}, 10]$, $[10^{-6}, 10]$, $[10, 10^6]$, $[10^{-2}, 10^3]$, $[10^{-3}, 1]$. $\theta_{\mathbf{b}}$, θ_G , θ_W were drawn from uniform laws in $[0, 2\pi]$.

The approximations derived in Section 1 were computed, as well as the exact solutions of the system formed by equations (1.7) to (1.9).

Except for s , the absolute value of the relative error of our approximations, as compared to the exact value, were below 5% as long as $\|\mathbf{G}\mathbf{W}^{-1}\|/\sigma\sqrt{\psi} < 0.1$ (for s , all approximations were accurate at 5% level for $\|\mathbf{G}\mathbf{W}^{-1}\|/\sigma\sqrt{\psi} < 0.01$).

2.2 $d = 5$ traits

For $d = 5$, using rotation matrices was too cumbersome. Matrix \mathbf{W} was written as a variance-covariance matrix, and vector \mathbf{b} and matrices \mathbf{W} and \mathbf{G} were drawn randomly element-wise, with diagonal coefficients and off-diagonal coefficients written as Var_{ii} and $\kappa_{ij}\sqrt{Var_{ii}Var_{jj}}$. As previously, 50,000 parameters were drawn for \mathbf{b} , \mathbf{W} , \mathbf{G} , σ , v ; \mathbf{P} was set to $4\mathbf{G}$ was set to 0.5 and $r_0 = 2$. \mathbf{b}_i , \mathbf{G}_{ii} , \mathbf{W}_{ii} , σ and v were drawn from \log_{10} -uniform laws, respectively in the intervals $[10^{-1}, 10]$, $[10^{-6}, 10]$, $[10, 10^6]$, $[10^{-2}, 1]$, $[10^{-1}, 1]$ and all κ_{ij} were drawn from uniform laws in interval $[-0.5, 0.5]$. All computations were carried on using *Mathematica 7.0*.

Figure 2.1 shows the results of these comparisons for $d = 5$ traits, for variables V_n and s . For all four parameters, approximations are valid in the same domain as when $d = 2$ traits.

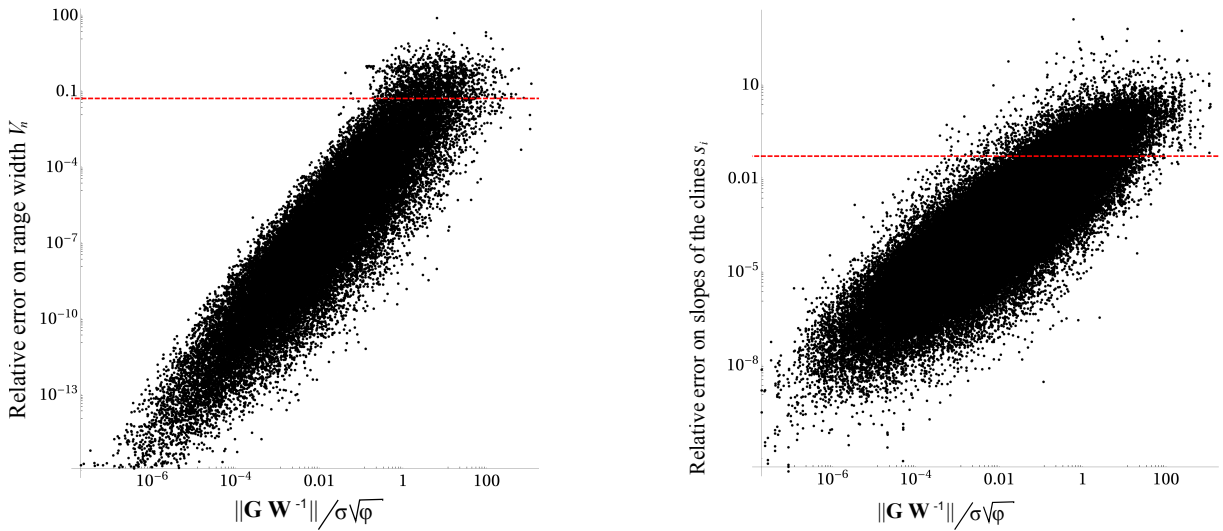


Figure 2.1: $d = 5$. Absolute value of the relative error of the approximations for V_n (left panel) and the slopes of all traits (right panel) as a function of $\epsilon = \frac{\|\mathbf{G}\mathbf{W}^{-1}\|}{\sigma\sqrt{\psi}}$, for 50,000 random initial values of \mathbf{b} , \mathbf{G} , \mathbf{W} , v , σ . The red dashed line represents 5% relative error.

3 Eigendecomposition of ϕ and ψ .

$$\begin{aligned}\phi &= \boldsymbol{\beta}_x^\top \mathbf{G} \boldsymbol{\beta}_x \\ &= \text{Tr}(\boldsymbol{\beta}_x^\top \mathbf{G} \boldsymbol{\beta}_x) \\ &= \text{Tr}(\boldsymbol{\beta}_x \boldsymbol{\beta}_x^\top \mathbf{G})\end{aligned}$$

Let $\mathbf{G} = \mathbf{Q} \boldsymbol{\Lambda}_{\mathbf{G}} \mathbf{Q}^\top$, where $\mathbf{Q} = (\mathbf{e}_{\mathbf{G}_1} \mid \dots \mid \mathbf{e}_{\mathbf{G}_d})$ is orthonormal (because \mathbf{G} is symmetric), and $\boldsymbol{\Lambda}_{\mathbf{G}}$ is the $d \times d$ diagonal matrix containing the eigenvalues of \mathbf{G} in decreasing order of magnitude.

$$\phi = \text{Tr}\left((\mathbf{Q}^\top \boldsymbol{\beta}_x)(\mathbf{Q}^\top \boldsymbol{\beta}_x)^\top \boldsymbol{\Lambda}_{\mathbf{G}}\right)$$

which is the projection of \mathbf{G} on the basis formed by $(\mathbf{Q}^\top \boldsymbol{\beta}_x)(\mathbf{Q}^\top \boldsymbol{\beta}_x)^\top$. Hence we obtain main text equation (14):

$$\phi = \|\boldsymbol{\beta}_x\|^2 \sum_{i=1}^d \lambda_{\mathbf{G}_i} \cos^2(\mathbf{e}_{\mathbf{G}_i}, \boldsymbol{\beta}_x) \quad (3.1)$$

Note that $\sum_{i=1}^d \cos^2(\mathbf{e}_{\mathbf{G}_i}, \boldsymbol{\beta}_x) = 1$ since the $\mathbf{e}_{\mathbf{G}_i}$ form an orthonormal basis of \mathbb{R}^d , so that:

$$\|\boldsymbol{\beta}_x\|^2 \min[\lambda_{\mathbf{G}_i}] \leq \phi \leq \|\boldsymbol{\beta}_x\|^2 \max[\lambda_{\mathbf{G}_i}] \quad (3.2)$$

Since all variables describing adaptation and demography positively covary with ϕ , and ϕ is bounded above by $\|\boldsymbol{\beta}_x\|^2 \max[\lambda_{\mathbf{G}_i}]$, a species will exhibit better adaptation, wider ranges and larger growth rates when fitness relies on few traits with large genetic variance, than upon numerous traits sharing the same total amount of variance.

Decomposition of $\psi = \mathbf{b}^\top \mathbf{W}^{-1} \mathbf{b}$ is performed as above, and leads to main text equation (15).

4 Comparison with earlier models.

In this section, we compare the results of the model by Pease et al. (1989), the logistic models of Kirkpatrick and Barton (1997) and Polechová et al. (2009), and ours. A summary of the correspondence between notations used in these models and ours can be found in Table 1.

The logarithmic model of Polechová et al. (2009) leads to analytic approximations, but logarithmic regulation assumes growth rates that increase without limit as the density decreases. As a result, a population under logarithmic regulation cannot go extinct, whatever the steepness of the cline or the speed of the shift (Polechová et al., 2009). Logarithmic density regulation leads to a travelling wave for the population density, and that wave travels across space faster than the gradient moves. This generates a non-constant lag between the peak of population density and the location of optimal fitness. For these reasons, the analytical results obtained for a logarithmic model of population density regulation cannot be compared to ours.

For simplicity, in this section we assume $b > 0$ and hence $\sqrt{b^2} = b$ (all comparisons remain valid if $b < 0$).

Parameter	Notation in P89	Notation in KB97	Our model	This section
Genetic variance	G	V_A	\mathbf{G}	G
Malthusian fitness	$\ln(\bar{W})$	\bar{r}	\bar{r}	\bar{r}
Width of stabilizing selection	$w_{22}(1-\rho^2)$	V_S	\mathbf{W}	V_S
Slope of environmental gradient	$\rho \sqrt{\frac{w_{22}}{w_{11}}}$	b	\mathbf{b}	b
Maximum growth rate	r_0	r^*	$r_0 - \frac{1}{2} \text{Tr}(\mathbf{W}^{-1} \mathbf{P})$	$r_0 - \frac{V_P}{2V_S}$
Standing genetic load	$\frac{G}{w_{22}(1-\rho^2)}$	Ar^*	$\mathbf{G} \mathbf{W}^{-1}$	$\frac{G}{V_S} \dagger$
Dispersal load	$\frac{\sigma^2}{2w_{11}} \frac{\rho^2}{1-\rho^2}$	Br^*	$\frac{1}{2} \sigma^2 \mathbf{b}^T \mathbf{W}^{-1} \mathbf{b} = \frac{1}{2} \sigma^2 \psi$	$\frac{b \sigma}{\sqrt{2V_S}} \dagger$
Intensity of selection	-	I_S	$\text{Tr}(\mathbf{W}^{-1} \mathbf{P})$	$\frac{V_P}{V_S}$
Adveective migration	$M(x, t) = -m(x - vt)$	-	-	$m = 0$
Weight of adaptation in \bar{r}	ρ (here noted p)	-	-	$p = 1$

Table 1: Correspondence of notations between models. P89 stands for Pease et al. (1989) and KB97 for Kirkpatrick and Barton (1997); †: see (5) in Polechová et al. (2009)

4.1 Reformulation of Pease et al.'s fitness function (1989).

The model by Pease et al. (1989) defines fitness as (their equation (3), in their notation):

$$\ln(\bar{w}) = r_{max} - \frac{(x - vt)^2}{2w_{11}(1-\rho^2)} + \frac{\rho \bar{z}(x - vt)}{(1-\rho^2)\sqrt{w_{11}w_{22}}} - \frac{\bar{z}^2}{2w_{22}(1-\rho^2)} \quad (4.1)$$

To avoid conflict between notation, we will write their ρ as p . Notation ρ will denote population growth rate, as elsewhere in this document and in the main text. Their fitness equation can be written as:

$$\bar{r} = r_0 - \frac{V_P}{2V_S} - \frac{1}{2V_S} [\bar{z} - b(x - vt)]^2 - \frac{1}{2V_S} \frac{(1-p^2)}{p^2} [b(x - vt)]^2 \quad (4.2)$$

where $V_S = w_{22}(1-p^2)$ and $b = p \sqrt{\frac{w_{22}}{w_{11}}}$.

(Note that the notation r_{max} by Pease et al. (1989) encompasses the phenotypic variance, such as: $r_{max} = r_0 - \frac{V_P}{2V_S}$.)

With this writing, it appears evident that fitness relies on adaptation and on an extrinsic factor, habitat quality. Term $-(\bar{z} - b(x - vt))^2 / 2V_S$ is the loss of fitness due to maladaptation for one trait. Term $(1-p^2) [b(x - vt)]^2 / (2p^2 V_S)$ quantifies the loss of fitness due to living in non-optimal habitats: whatever the value of \bar{z} , the population growth rate is maximized at $x = vt$. Factor p (ρ in Pease et al.'s notation) describes the relative weights of adaptation and habitat quality in defining fitness. When p is small (say $p = 0$), the trait's optimal value is 0 everywhere, and fitness mostly relies on the geographic position, θ . On the other hand, a large p (say $p = 1$) ensures that habitat quality does not impact fitness: fitness only relies on adaptation (that is, on $|\bar{z} - b(x - vt)|$). This last term in the fitness equation (4.2) can also be interpreted as the fitness loss due to a second trait (uncorrelated to the first trait) with no genetic variance. When $p = 1$, equation 4.2 corresponds to the one-trait version of equation (2) in the main text.

In this section, we will consider $m = 0$ (no advective migration), $p = 1$ (no habitat preference: fitness determined by adaptation only).

With this formulation, the trait optimum is a linear gradient shifting in space ($\theta = b(x - vt)$), just like in our model, and in the one by Polechová et al. (2009).

4.2 Unlimited ranges.

Equation (2.9) in Pease et al. (1989) gives: $c \approx \frac{1}{\sigma} \sqrt{\frac{b^2}{V_S}} - \frac{G}{\sigma^2 V_S}$, and the width of the range becomes infinite whenever $c \leq 0$, that is (if $b > 0$): $b < \frac{G}{\sigma \sqrt{V_S}}$. Like the models by Kirkpatrick and Barton

(1997) and Polechová et al. (2009) (and ours), the model by Pease et al. (1989) therefore admits a regime of perfect adaptation with an infinite range, when the slope of the environmental gradient is lower than some value.

The same expressions are obtained by Kirkpatrick and Barton (1997) (page 11, once corrected the scaling of A as mentioned by Polechová et al., 2009, p. 193).

In our model, unlimited ranges occur whenever $c \leq 0$, *i.e.* (equation 1.11 in Section 1): $\sigma\psi^{3/2} \leq \phi$. With only one trait, we recover the same formula as Pease et al. (1989) and those found in the logistic regulation models of Kirkpatrick and Barton (1997) and Polechová et al. (2009).

4.3 Width of the range.

When $d = 1$ trait, equation 1.11 gives exactly the same formula as Pease et al. (1989) (their equation (2.9)), and is also similar to the expression of the width of the range given by Kirkpatrick and Barton (1997) (whose equation (17) should read: $R = \frac{4\sigma P^{1/4}}{\sqrt{b\sqrt{I_S}\sigma - h^2 I_S \sqrt{P}}}$).

4.4 Slope of the trait.

Equation (1.13) gives, for one trait and $b > 0$: $s \approx \frac{G}{\sigma\sqrt{V_S}}$, which is identical to Equation (2.8) in Pease et al. (once notations have been changed according to Table 1), and to the results found by Kirkpatrick and Barton (1997) (whose equation on page 10 should read: $slope = \frac{\sqrt{V_P I_S} h^2}{\sigma}$).

4.5 Lag of trait mean.

This variable is due to the existence of preferential migration towards a given location in Pease et al. (1989); it has little relevance in our model (where it can be shown to be zero).

4.6 Lag of the mode of population density.

This parameter is an arbitrary constant (implicitly zero) in Kirkpatrick and Barton (1997) where it has no relevance since the gradient does not shift.

Equation (1.14) gives, for one trait: $L_n \approx -\frac{v\sqrt{V_S}}{\sigma b} \left(1 + \frac{G}{\sigma b\sqrt{V_S}}\right)$, which is identical to equation (8) in Pease et al., once notations are converted according to Table 1.

4.7 Population growth rate and critical speed of change.

With one trait, our equations for ρ and v_c are identical to equations (6) and (7) in Pease et al. once notations are converted according to Table 1, and $p = 1$ and $m = 0$.

5 Numerical integration of the system formed by main text equations (3) and (4)

5.1 Rewriting the partial differential equations governing the system - with logistic density regulation

In order to avoid numerical problems with population densities growing towards infinity or becoming extremely small, the fitness function is modified **in this section and in the next one only** by introducing logistic density regulation (as in Kirkpatrick and Barton, 1997 and Polechová et al., 2009). Using variable $u = x - vt$, main text equation (2) becomes:

$$\bar{r}(\bar{\mathbf{z}}, x, t) = r_0 \left(1 - \frac{n}{K}\right) - \frac{1}{2} \text{Tr}(\mathbf{W}^{-1} \mathbf{P}) - \frac{1}{2} (\bar{\mathbf{z}} - \mathbf{b}u)^{\top} \mathbf{W}^{-1} (\bar{\mathbf{z}} - \mathbf{b}u) \quad (5.1)$$

where K is the local carrying capacity, assumed constant across space.

Main text equations (3) and (4) can thus be rewritten as:

$$\begin{cases} \frac{\partial \ln(n)}{\partial t} = v \frac{\partial \ln(n)}{\partial u} + \frac{\sigma^2}{2} \frac{\partial^2 \ln(n)}{\partial u^2} + r_{max} \left(1 - \frac{n}{K}\right) - \frac{1}{2} \text{Tr}(\mathbf{W}^{-1} \mathbf{P}) - \frac{1}{2} (\bar{\mathbf{z}} - \mathbf{b}u)^{\top} \mathbf{W}^{-1} (\bar{\mathbf{z}} - \mathbf{b}u) \\ \frac{\partial \bar{\mathbf{z}}}{\partial t} = v \frac{\partial \bar{\mathbf{z}}}{\partial u} + \frac{\sigma^2}{2} \frac{\partial^2 \bar{\mathbf{z}}}{\partial u^2} + \sigma^2 \frac{\partial \ln(n)}{\partial u} \frac{\partial \bar{\mathbf{z}}}{\partial u} + \mathbf{G} \mathbf{W}^{-1} (\bar{\mathbf{z}} - \mathbf{b}u) \end{cases} \quad (5.2)$$

These equations can be numerically integrated, using the finite differences method.

Note that the variable change does not induce any assumption as to the speed of the travelling wave.

5.2 Shape of the numerically integrated solutions.

Numerical integration was performed for $d = 2$ traits, with $du = 1$ and $dt = 0.01$ on a table of width 240 (the length of axis u). Initial conditions were: $n(u, 0) = 1$, $\bar{\mathbf{z}}(u, 0) = \mathbf{0}$. The size of the range of the species was computed as the number of cells on u with a population density exceeding 1 % of the maximal density ($= 1$). Iteration was stopped after the size of the range had remained constant for 500 iterations (see Figure (6.1)a for an example).

For a variety of parameters, the trait means were observed to develop linear clines, while the population density took a Gaussian shape (see Figure (6.2) for examples).

The size of the range was always inferior to the window size, and the peak of population density was encompassed in the window, showing that the population tracks the location of maximal fitness at a speed numerically not distinguishable from v . Section (6) below analyses the speed at which trait means and population density travel in the logistic regulation case and show it must be v in most sensible cases.

5.3 Comparing the width of the range obtained by finite differences integration or through the exact solution with an *a priori* on the shape of the solution

1000 input parameters (*i.e.* \mathbf{b} , \mathbf{W} , \mathbf{G} , \mathbf{P} , σ , v) were generated randomly. Both components of vector \mathbf{b} were drawn from a uniform law in $[-1, 1]$. For both variance-covariance matrices (\mathbf{G} and \mathbf{W}), diagonal terms Var_{ii} were drawn from \log_{10} -uniform laws, resp. in intervals $[10^{-4}, 10^{-1}]$ and $[10, 10^4]$, and off-diagonal terms (covariances) were written as $\kappa_{ij} \sqrt{Var_{ii} Var_{jj}}$, with κ_{ij} drawn from a uniform law in $[-0.5, 0.5]$. σ was drawn from a \log_{10} -uniform law in $[1, 10]$. v and K were constant, with $v = 0.01$ and $K = 1000$, and \mathbf{P} was proportional to \mathbf{G} , with $\mathbf{P} = 4\mathbf{G}$. r_0 was chosen so that $\rho = 0$ if there were no regulation of population density (as given by the exact solving of equations 1.6-(1.9)).

In this section and the following (section (6)), we defined the size of the range as the width of the region where density was above 1% of its maximal value. For all 1000 sets of input parameters, we compared the size of the range obtained:

- through the finite differences integration. The iteration process was stopped when the width of the range was constant for 500 iterations. The size of the range corresponded to the number of positions along axis x where population density was > 0.01 .

- using the exact solution based on the hypotheses that $n(u) = e^{-\frac{(u-L_n)^2}{2V_n}}$ and $\bar{z}(u, t) = s u$ (see Section 1 below), forcing the final growth rate of the population to be null. When density has a Gaussian shape, the size of the region where density is $> 1\%$ of the maximal density is approximately $6.07\sqrt{V_n}$.

The width of the space over which the finite differences integration was carried on (240 u units) was based on the observation that the exact width without density regulation (*i.e.* computed from equations (1.6) to (1.9) below) was never $> 220 u$ units with our 1000 initial parameter sets.

The sizes of the ranges obtained by the two methods were almost identical (see Figure 5.1), suggesting that the only solution to equations (5.2) is the one we derive in Section 1 below.

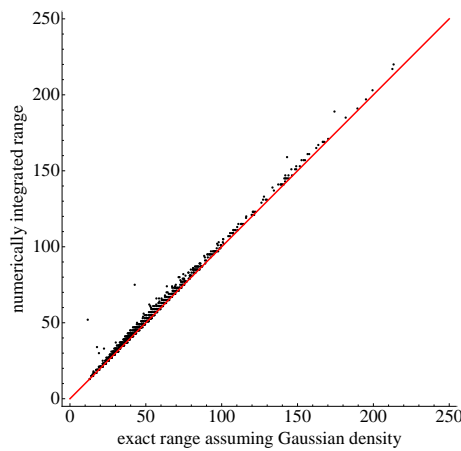


Figure 5.1: Size of the species' range for 1000 sets of input parameters, estimated by numerical integration (ordinates) or exactly under the hypotheses of Gaussian distribution of population density and linear clines in the means of the traits (abscissas). The red line has slope 1.

5.4 Influence of logistic density regulation on the critical rate of change.

The critical rate of change v_c , above which the population growth rate became negative, was computed for 100 random sets of \mathbf{b} , \mathbf{W} , \mathbf{G} , \mathbf{P} , and σ obtained as described above, using the exact solution as derived from equations (1.6) to (1.9) below.

To determine the critical rate of change with logistic density regulation, v'_c , we performed a numerical integration of the above equations. The numerical integration was performed for 50,000 iterations with $du = 1$, $dt = 0.01$ over a table of length 240 (as above), for different values of v , starting with $\bar{z} = \mathbf{0}$ and $n(u, 0) = e^{-5}$. We then determined the local growth rates as the difference in population density between iterations #50,000 and #49,999, for each value of u .

If the local growth rate was negative for all cells in the range, v was considered to be an upper bound of v'_c . If the growth rate was positive in at least part of the range, v was declared to be a lower bound of v'_c .

For all 100 parameter sets, $0.95 v_c < v'_c < 1.2 v_c$. Logistic density regulation therefore does not seem to strongly affect the critical rate of change inferred in our model.

6 Speed of the shifts in trait means and in population density with logistic density regulation.

In this section, we examine whether the speed of the shift in trait means and that of the shift in the center of the population is affected by various factors (using numerical integration, section (6.1)), and provide analytical elements showing that these speeds should not differ from v in most sensible cases (section (6.2)).

6.1 Numerical integration.

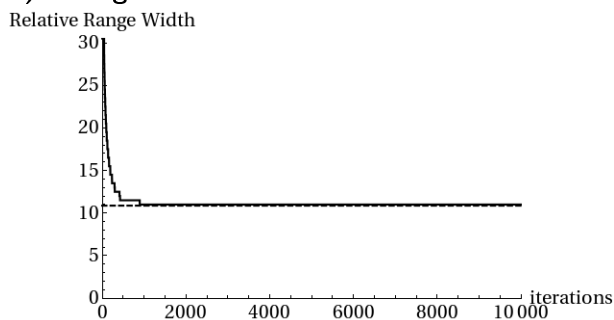
In this section, we carry numerical integration of main text equations (3) and (4), with equation (3) modified to include logistic density regulation as in Section 5, with a single set of parameters (these are reproducible with other sets of parameters) to show that:

1. The width of the species range converges to the value predicted with no regulation of population density (Figure (6.1)a), although in some cases, it may then expand without limit (Figure (6.1)b; see section (6.2.2) below for an explanation). Note that when genetic variance and r_0 are low (as in the previous section) only the first case is encountered.
2. The speed of the travelling wave for population density is undistinguishable from v (Figure (6.2)a) regardless of the magnitude of genetic variance (Figure (6.2)b), the speed of the environmental change (Figure (6.2)c) and initial conditions (Figure (6.2)d). However, lags in trait means may appear (Figure (6.2), d), and diminish over time (Figure (6.2)d) or not [or slowly] (Figure (6.2)c).

Parameters used in the following figures are: two traits, $\mathbf{b} = \begin{pmatrix} 1 \\ 0.5 \end{pmatrix}$, $\mathbf{G} = \begin{pmatrix} 0.05 & \sqrt{2}/100 \\ \sqrt{2}/100 & 0.1 \end{pmatrix}$, $\mathbf{W} = \begin{pmatrix} 10 & 4 \\ 4 & 40 \end{pmatrix}$, heritabilities $h^2 = 0.25$ for both traits; $\sigma = 1$, $v = 0.01$, $K = 1000$ and r_0 such as $\rho = 0$ if there were no regulation of population density (as given by the exact solving of equations 1.6-(1.9)). Unless otherwise stated, initial conditions were: $n(x, 0) = K$, $\bar{z}_1(x, 0) = \bar{z}_2(x, 0) = 0$. Integration was performed using the finite differences method over a window of 61 units of space, sliding at speed v , with $dx = 1$, $dt = 0.01$.

“Larger genetic variance” corresponds to $\mathbf{G} = \begin{pmatrix} 5 & 5\sqrt{5} \\ 5\sqrt{5} & 1 \end{pmatrix}$; “faster speed of change” corresponds to $v = 1$.

a) Low genetic variance



b) Large genetic variance

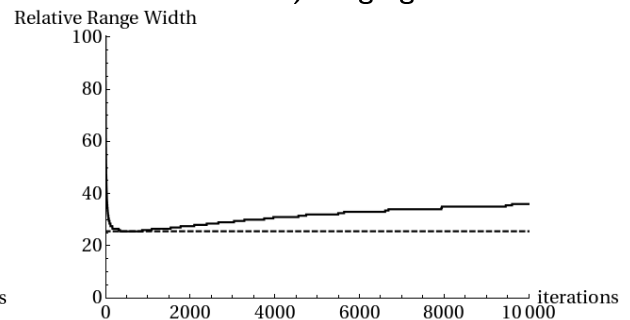


Figure 6.1: Evolution of the width of the range over time (for 100 time units; continuous line); predicted width with no regulation (dashed line). (a) With parameters defined above; (b) with larger genetic variance.

With low genetic variance (a), the width of the range converges to the value predicted with no regulation. So does it at first when genetic variance is larger (b); then the population starts to enlarge its range without limit. (Note the integration was carried over a wider window in (b) to show this phenomenon).

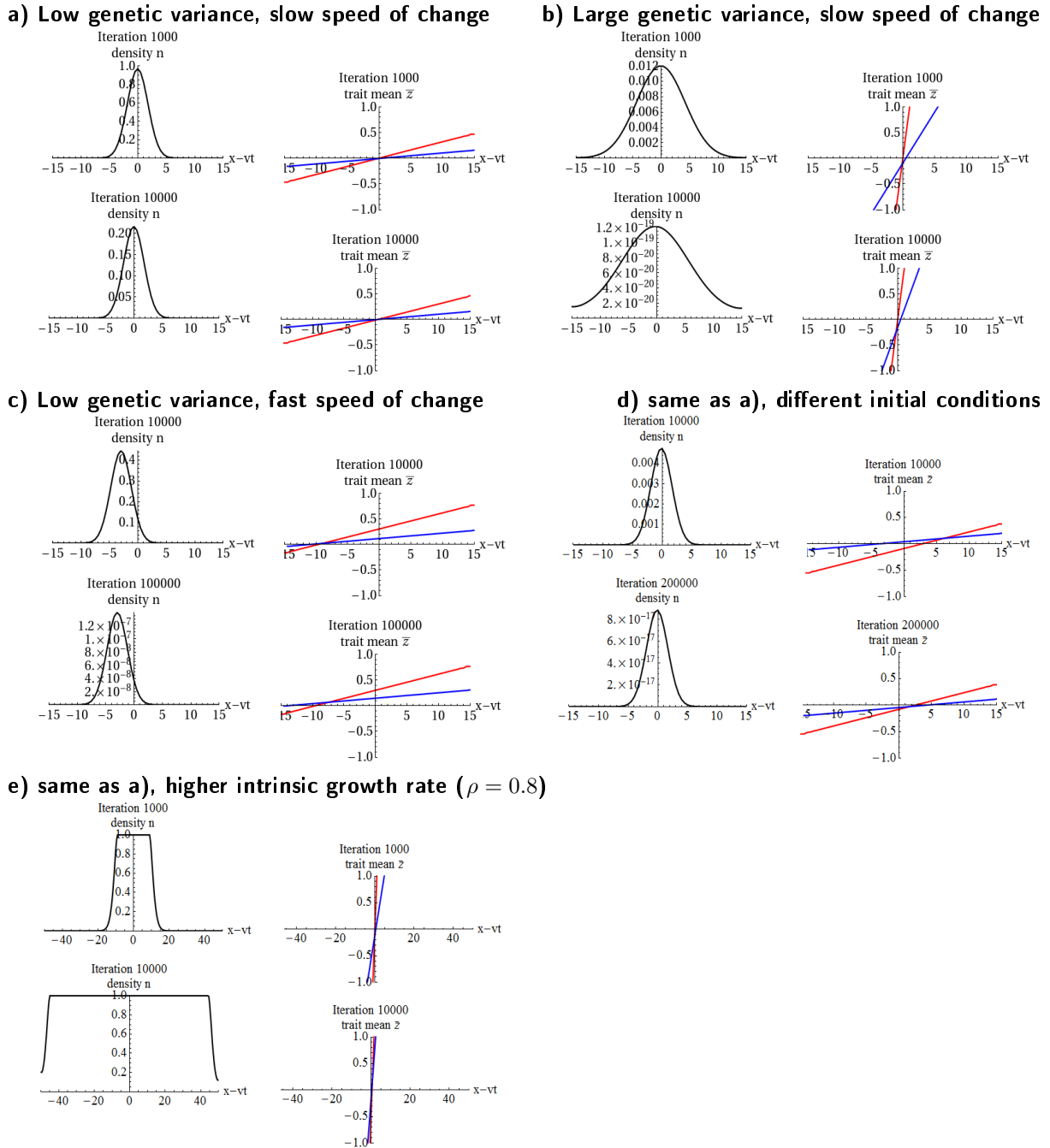


Figure 6.2: Plots of population density (left panels) and trait means (right panels, one color per trait) at different times during the numerical integration process (top vs. lower panels). (a) with parameters defined above, (b) with larger genetic variance, (c) with faster speed of change, (d) with different initial conditions (initial density $n(x, 0) = 0.02$, initial trait values $\bar{z}_1(x, 0) = -0.1$, $\bar{z}_2(x, 0) = 0.1$).

Regardless of the amount of genetic variance, both the trait means and the wave of population density travel at a speed undistinguishable from v (a,b). With faster change (larger v , panel c), their speed is unmodified but the trait means lag behind their optimum. The lag of population density corresponds to the predicted lag with no regulation, $L_n \approx -3.2$. Modifying the initial conditions does not change the speed of the travelling wave, but the trait means may show lags (positive or negative) during the transitory regime, which eventually reduce to zero (panel d). When growth rates are high, the population reaches the carrying capacity over a stretch of space, enduring perfect adaptation and allowing the population to expand in both directions (panel e; see section (6.2.2) below).

6.2 Analytical proof that sensible cases advance at speed v

Let us rewrite model PDEs with logistic density-dependent growth rate, following Polechová et al. (2009) (in this subsection the analysis is restricted to one trait):

$$\partial_t n = \frac{\sigma^2}{2} \partial_{xx} n + r_0 n(1-n) - \frac{n}{2V_S} (\bar{z} - b(x-vt))^2 \quad (6.1)$$

$$\partial_t \bar{z} = \frac{\sigma^2}{2} \partial_{xx} \bar{z} + \frac{\sigma^2}{n} \partial_x n \cdot \partial_x \bar{z} - \frac{V_G}{V_S} [\bar{z} - b(x-vt)] \quad (6.2)$$

In equation (6.1), r_0 incorporates both the basic growth rate and the standing load, and the carrying capacity, corrected for the standing load, has been used to scale n .

The following sections detail several elements that prove that population density and trait mean must advance at speed v in all “sensible cases”. This is done so:

1. if we look for steady state solutions with given speeds k_z and k_n , consistency relations imply that these speeds equal v ;
2. with solutions that are not steady states, n will depend on t besides depending on $x - k_n t$. With positive local growth rate, one intuitively expects this situation to generate plateaus of n , where n is constant and equal to the carrying capacity over some area. We prove that when this happens, \bar{z} tends towards perfect adaptation with a constant lag. When this lag is not too large, this situation in turn allows population density to increase in both spatial directions, *i.e.* to effectively mimic the pattern of advancing advantageous alleles in continuous space (Fisher, 1937);
3. when solutions do not expand in both directions, approximations of PDEs at the boundaries of population distribution yield solutions similar to those found in the absence of regulation, hence indicating that both boundaries of the bubble of population density advance at speed v .

6.2.1 General steady state solutions

We now look for general bounded solutions to equations (6.1) and (6.2) such that $n = n(x - k_n t)$ and $\bar{z} = \bar{z}(x - k_z t)$. Let $\theta = x - vt$, $\theta_n = x - k_n t$, $\varphi_n = k_n x + t$, $\theta_z = x - k_z t$, $\varphi_z = k_z x + t$. By construction, directions given by isopleths of θ_i and φ_i (with i equal to either n or z) are orthogonal. Replacing $\partial_{\theta_n} n$ by n' and $\partial_{\theta_z} \bar{z}$ by z' , and using relationship among derivatives (e.g. $\partial_t n = -k_n n'$), yields the following equations:

$$k_n n' + \frac{\sigma^2 n''}{2} + r_0 n [1-n] = \frac{1}{2V_S} \left[\bar{z} - b \left(\frac{1+k_n v}{1+k_n^2} \theta_n + \frac{k_n - v}{1+k_n^2} \varphi_n \right) \right]^2 \quad (6.3)$$

$$k_z z' + \frac{\sigma^2 z''}{2} = \frac{V_G}{V_S} \left[\bar{z} - b \left(\frac{1+k_z v}{1+k_z^2} \theta_z + \frac{k_z - v}{1+k_z^2} \varphi_z \right) \right] - \sigma^2 [\log(n)]' z' \quad (6.4)$$

The left-hand side of equation (6.3) is independent of φ_n , and the left-hand side of equation (6.4) is independent of φ_z . Taking the derivative of equation (6.3) with respect to φ_n and the derivative of equation (6.4) with respect to φ_z , we obtain the following relationships:

$$[\bar{z} - b\theta] [(k_n - k_z) z' - (k_n - v) b] = 0 \quad (6.5)$$

$$(k_z - k_n) V_S \sigma^2 z' [\log(n)]'' + (k_z - v) b V_G = 0 \quad (6.6)$$

From equations (6.5) and (6.6) several cases can arise, some of which are inconsistent with equations (6.3) and (6.4) and imperfect adaptation:

1. $k_n = k_z = v$
2. $k_n = v \neq k_z$. Equation (6.5) implies that \bar{z} is constant with regard to θ_z , and is not consistent with equation (6.4).

3. $k_z = v \neq k_n$. Equation (6.5) yields $\bar{z} = z_0 + b\theta$. Equation (6.6) implies that $\log(n) = y_1 + y_0\theta_n$, so that n must grow to infinity with either high or low θ_n (inconsistent with a bounded steady state solution), or be constant. With constant n , we recover the case for perfect adaptation, in which k_n is not defined.
4. $k_z = k_n \neq v$. Equation (6.5) yields $\bar{z} = b\theta$ which is a contradiction with the fact that $\bar{z} = \bar{z}(\theta_z)$.
5. $k_z \neq k_n \neq v$.

We now focus on investigating case 5. Equations (6.5) and (6.6) yield:

$$\bar{z} = \frac{(k_n - v)b}{k_n - k_z}\theta_z + z_0 \quad (6.7)$$

$$\log(n) = \frac{(k_z - v)V_G}{2V_S\sigma^2(k_n - v)}\theta_n^2 + y_0\theta_n + y_1 \quad (6.8)$$

A simple rewriting of equation (6.3) yields:

$$n = 1 - \frac{1}{2r_0V_S}[\bar{z} - b\theta]^2 + \frac{1}{r_0}\left(\frac{k_n n'}{n} + \frac{\sigma^2 n''}{2n}\right) \quad (6.9)$$

i.e., from equation (6.8), an exponential function of θ_n must be equal to a quadratic function of θ_n , which is generically impossible. Hence, case 5 is not generically possible.

Conclusion: Steady-state bounded solutions of equations (6.1) and (6.2) necessarily advance at speed v .

6.2.2 Dynamics of distribution center

Adaptation on a population plateau

When n is approximately flat, *i.e.* $\partial_x n \approx 0$, equation (6.2) becomes:

$$\partial_t \bar{z} \approx \frac{\sigma^2}{2}\partial_{xx}\bar{z} - \frac{V_G}{V_S}[\bar{z} - b(x - vt)] \quad (6.10)$$

Equation (6.10) can be easily solved using a Fourier transform of \bar{z} , yielding:

$$\bar{z}(x, t) = \frac{bvV_S}{V_G} + b(x - vt) + \frac{e^{-V_G t/V_S}}{\sqrt{2t\sigma}} \int_{-\infty}^{\infty} \left[z_0(y) - by - \frac{bvV_S}{V_G} \right] e^{-\pi(x-y)^2/(2\sigma^2 t)} dy \quad (6.11)$$

As $t \rightarrow \infty$, \bar{z} forms a cline with a slope equal to the environmental slope, b , similarly to what happens with perfect adaptation, but with a constant lag bvV_S/V_G . The last term in equation (6.11) corresponds to a diffusive noise that tends towards 0 as time passes, and starts so that $\bar{z}(x, 0) = z_0(x)$, *i.e.* the initial condition for trait mean. If $z_0(x) = 0$ for all x , equation (6.11) reads as:

$$\bar{z}(x, t) = \frac{bvV_S}{V_G} \left(1 - e^{-V_G t/V_S}\right) + b \left[x \left(1 - e^{-V_G t/V_S}\right) - vt \right] \quad (6.12)$$

In equation (6.12), the “instantaneous speed” of the cline in trait means is:

$$k(t) = v / \left(1 - e^{-V_G t/V_S}\right) \quad (6.13)$$

which tends towards v as time passes.

Population dynamics with perfect adaptation

When $\bar{z}(x, t) \approx \frac{bvV_S}{V_G} + b[x - vt]$, as will be the case with equation (6.12) given enough time, equation (6.1) becomes the classic Fisher (1937) equation for the dynamics of advantageous alleles:

$$\partial_t n = \frac{\sigma^2}{2} \partial_{xx} n + r_1 n(1 - n) \quad (6.14)$$

with $r_1 = r_0 - \frac{b^2 v^2 V_S}{2V_G^2}$ and n is scaled by the appropriate carrying capacity. Equation (6.14) admits two solutions: either $r_1 < 0$, i.e. the population collapses, or $r_1 > 0$ and the population advances in both directions at speed $k_F = \sigma \sqrt{2 \left[r_0 - \frac{b^2 v^2 V_S}{2V_G^2} \right]}$.

6.2.3 Dynamics of distribution boundaries

When $n \approx 0$, the dynamics of n can be approximated by the following PDE:

$$\partial_t n \approx \frac{\sigma^2}{2} \partial_{xx} n + r_0 n - \frac{n}{2V_S} (\bar{z} - b(x - vt))^2 \quad (6.15)$$

Getting from equation (6.1) to equation (6.15) at the boundaries of the species' distribution is the equivalent of the approximation carried out by Kirkpatrick and Barton (1997) to obtain an approximation for the shape of the population density under the logistic density-dependent static model (their equations [12-14]).

Solving the system of PDEs formed by equations (6.2) and (6.15) leads to the same types of solutions as those given in the Section (1.1) - which are, in fact, strict analogues to equations [12-14] in Kirkpatrick and Barton (1997). In particular, it leads to $k_z = k_n = v$ (Section (1.1)), i.e. away from the "center" of its distribution, population density behaves as if it followed a travelling wave of speed v , and average trait values develop on spatio-temporal clines that move at speed v .

Conclusion: Whatever the form of the general solution to equations (6.1) and (6.2), when boundaries advance in the same direction (i.e. there is no "wave of advance" phenomenon), boundaries of population densities behave as if there were no density-dependence and, hence, advance at speed v .

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