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SPECIES RANGE: ADAPTATION IN SPACE AND TIME
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24 **Abstract**

26 Populations living in a spatially and temporally changing environment can survive by
adapting to the changing optimum and/or by migration towards the favourable habitat.
28 Two principal mechanisms have been proposed to explain limits to the range of a single
species in a stable environment: maladaptive gene flow from centre to the edge and lim-
30 ited genetic variance. Here we discuss both predictions for evolution with fixed variance, by
modeling joint changes in trait mean and population density, and evolution of variance in an
32 environment which varies in time and space.

34 As for a stable optimum, when genetic variance is fixed, we obtain two regimes of adap-
tation: uniform adaptation, where the population would eventually fill all available habitat
36 along the environmental gradient, and limited adaptation when the environmental gradient
is steep relative to the genetic variance. As the optimum changes in time, the uniformly
38 adapted population tracks the optimum by shifting at a uniform rate matching the environ-
mental rate of change. In contrast, a population that is only well adapted to a central region
40 adapts in the trait slower than is the rate of temporal change of the environmental optimum,
and survives by moving in space towards favourable habitat. The degree of adaption as mea-
42 sured by the gradient in trait mean relative to the spatial gradient (which also determines
the species range), and the critical gradient, above which the limited adaptation occurs, is
44 independent of the rate at which the optimum changes in time.

46 We use population genetic model with many loci to allow the genetic variance to evolve.
Now we only find equilibrium with uniform adaptation. The cline shape and number stays
48 the same as in the static model, hence the genetic variance only increases via dispersal across
the spatial gradient and agrees with the predicted value for a stable environmental gradient
50 - although higher variance would lead to a better adaptation when temporal change in the
environment is fast.

52 We explain that the outcome can be predicted by comparing the loads due to genetic
variance, dispersal and temporal change, and discuss how these parameters can be measured
54 in nature.

56 Introduction

58 Whilst many boundaries to species ranges are caused by sharp changes in the environ-
ment, or are driven by interaction with other species (see reviews of Gaston 2003, Ch. 1;
60 Bridle and Vines 2007), often there is no apparent reason for the sharp spatial limits that are
commonly observed. Some species survive remarkably well when transferred outside their
62 range (Prince and Carter 1985). More often, though, species would need to extend their niche
by adapting in one or several traits (Gaston 2003, Table 2.1). We have only a limited under-
64 standing of why such adaptation fails even when the environment changes smoothly in space.
Haldane (1956) suggested that the sharp boundary may be a result of maladaptive gene flow
66 from central populations, which prevents adaptation in less dense marginal populations - a
likely explanation for limits to adaptation due to highly asymmetrical gene flow when density
68 changes sharply due to extrinsic reasons (as in the mainland-island model of Kawecki et al.
(1997)). The second classic argument for limits to a species range is that genetic variance is
70 insufficient to allow niche extension (see Antonovics 1976). Two questions follow from this
argument: how can we quantify such limits, and what constrains the variance in the first
72 place.

74 Existing studies predicting response to a temporally changing optimum in structured
populations are rather limited. Most notably, Pease et al. (1989) analysed evolution with the
76 optimum changing in time and space, described by bivariate Gaussian fitness (in time and
space) and assuming that genetic variance is small and constant. Later, in an extension of
78 the Kirkpatrick and Barton's (1997) model allowing for species interactions, Case and Taper
(2000) briefly assessed the response of species range to a sudden change in an environment.
80 More is known about the response of a single, unstructured population: generally, the lag of
trait mean behind the optimum is proportional to the speed of movement of the optimum,
82 divided by genetic variance and strength of stabilizing selection (Charlesworth 1993; Lande
and Shannon 1996; Bürger 1999; Waxman and Peck 1999).

84

Genetic variance is crucial to understand the rate of evolution and in the long run, it is

86 important to understand how is variance maintained. Various forces will elevate the vari-
 88 ance: mutation, frequency-dependent selection, heterozygote advantage, diversifying selec-
 90 tion, some forms fluctuating selection. Genetic variance is substantially higher than we would
 expect based on simple mutation-selection balance (see Turelli 1988; Johnson and Barton
 92 2005). After about 20 generations, increasingly more genetic variance is contributed by new
 mutations (Hill 1982), rather than coming from the standing variation. In a single popula-
 94 tion, additive genetic variance maintained by mutation-selection balance, $\hat{V}_{G,m}$, reflects the
 product of genomic mutation rate ($U = 2n\mu$) and the width of stabilizing selection, V_S -
 for multiple loosely linked loci, $\hat{V}_{G,m} \approx 2UV_S$ (Turelli 1984). Laboratory studies of response
 to directional selection show that the genetic variance often stays constant for a hundred of
 96 generations (e.g. Yoo 1980; Weber et al. 2001; see reviews of Barton and Keightley 2002;
 Keightley 2004). However, unless stabilizing selection $\gamma_i = -\frac{V_P}{2V_S}$ is very weak (see King-
 98 solver et al. 2001 and the discussion), unrealistically high mutation rate or number of loci of
 small effect is required to maintain the variance that we observe (with $h^2 = 0.4$ we require
 100 $U = \frac{1}{10} \frac{V_P}{V_S}$).

102 Genetic variance can be substantially higher in a spatially heterogeneous environment:
 theoretically, if genetic variance of a quantitative trait can freely evolve in response to spa-
 104 tially variable selection, it should at any particular location increase with the extent of
 migration across the environmental gradient and the width of stabilizing selection (Barton
 106 2001). Therefore, the ability to adapt to temporal change can be significantly higher in
 species that are living in a spatially variable environment. Because migration is generally
 108 several orders of magnitude higher than mutation (the increase of genetic variance due to
 mutation, mutational variance V_m , is about 10^{-3} to 10^{-2} times random variance due to ran-
 110 dom environmental effects, V_E (Lynch and Walsh 1998), migration may significantly increase
 local genetic variance even when spatial variability is low.

112
 In spatially structured populations with limited gene flow, a cline at a single locus can
 114 be maintained by differential selection, if the population can adapt over a large enough
 range. Slatkin (1975) and Nagylaki (1976) showed that a cline will develop if the environ-
 116 ment changes over a scale which is large relative to the ratio of dispersal over the square

118 root of intensity of selection per gene, $\frac{\sigma}{\sqrt{s}}$. If the environment changes over smaller spatial
120 scales, the gene frequency responds to the selection averaged over this characteristic length.
Therefore, no cline emerges if the environment changes only over scales smaller than a few
122 characteristic lengths. It also follows that adaptation to a pocket or a marginal habitat of
different environment which is small in terms of $\frac{\sigma}{\sqrt{s}}$ is prevented (for a real world example see
Lenormand et al. 1999). Hedrick (2006) gives a nice review of current studies of adaptation
to spatially varying environments.

124

It has been shown by Kirkpatrick and Barton (1997), that it is low genetic variance
126 combined with high gene flow that can prevent adaptation to a stable environment, when
optimum varies smoothly in space. Conversely, when genetic variance is unconstrained, no
128 limit to species range arises (Barton 2001). Kirkpatrick and Barton's (1997) study follows
jointly population dynamics and the evolution of trait mean due to adaptation to a static
130 spatial gradient. They find two classes of solutions at equilibrium: uniform adaptation when
the trait mean matches the optimum perfectly on the whole range, and the solution, where
132 the gradient in trait mean is shallower than the environmental optimum, hence maladaptation
increases away from the centre, leading to a limited range. Limited adaptation arises
134 as the gradient steepens relative to genetic variance. Both solutions are stable when the
available habitat is infinite, but if an expanding population reaches the margins of the suit-
136 able habitat, uniform adaptation collapses from the margins (Kirkpatrick and Barton 1997,
Appendix) towards limited adaptation, where gradient in trait mean is shallower than envi-
138 ronmental gradient. Barton (2001) extended the model by allowing the genetic variance to
evolve. Then, the population could always adapt to the environmental gradient by increasing
140 its variance, and there is no equilibrium with a limited range. However, population density
steadily decreases with increasing variation around the optimum - eventually, as gradient
142 steepens, population goes extinct on the whole range.

144 Here, we extend the above models to allow the environmental optimum to vary both
in time and space. By continuity with the static case, we would expect that when genetic
146 variance is fixed, there would still be two solutions, either with uniform adaptation, or with
adaptation only over a limited range. When the optimum changes in time, we suppose the

148 population would track the changing optimum both by adaptation and migration (unless the
environment changes too fast in either space or time, leading to extinction). In relation to the
150 static case, we are interested in whether the gradient in trait mean changes, which would lead
to a change in size of species range, and if there is any change to the critical gradient, above
152 which the limited adaptation occurs. We address the evolution of genetic variance with a
population genetic model, assuming that the quantitative trait under selection is determined
154 by n_l loci with approximately additive effects and/or under weak selection. Then genetic
variance increases as a function of migration across the spatial gradient and perfect adap-
156 tation (in trait mean) to arbitrarily steep gradients is possible, until the population density
decreases to zero due to loss of fitness caused by variation around the optimum. Now the sole
158 solution we found has a uniform population density. We address whether now genetic
variance also increases with the rate at which the optimum changes in time; and whether
160 the temporal change can drive limits to the species range (rather than just cause a uniform
decrease in density) when the variance can freely evolve.

162

Evolution in a spatially and temporally changing environment

164

In the first section, we study a quantitative trait using a phenotypic model with fixed
166 genetic variance, using three different forms of density-dependence: simple regulation, where
population density is a function of the average growth rate, and two models of joint regulation
168 of trait mean and population density, which we call logarithmic and logistic. In the second
part, we address the evolution of variance by finding the uniform solution for the population
170 genetic model, and numerically iterating the evolution of allele frequencies.

172 **Adaptation to a linear environmental gradient, that moves in time - pheno- typic model**

174

Following Pease et al. (1989), the change of the mean phenotype \bar{z} can be written as:

$$\frac{\partial \bar{z}}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 \bar{z}}{\partial x^2} + \sigma^2 \frac{\partial \ln(n)}{\partial x} \frac{\partial \bar{z}}{\partial x} + V_A \frac{\partial \bar{r}}{\partial \bar{z}} \quad (1)$$

176 The equation describes the effect of migration and selection on a population with density
 n with quantitative trait (z) under selection. The first term represents migration, approxi-
178 mated by diffusion with variance σ^2 . The second term describes gene flow from populations
which vary in population density, n . The third term describes the effect of selection on a nor-
180 mally distributed character z with additive genetic variance V_A (Lande 1976, \bar{r} is the mean
(Malthusian) fitness, \bar{r} in continuous time $\sim \log(\bar{W})$ in discrete time): $\frac{\partial \bar{z}}{\partial t} = h^2 V_P \frac{\partial \bar{r}}{\partial \bar{z}} = V_A \frac{\partial \bar{r}}{\partial \bar{z}}$
182 - here V_A is additive genetic variance, V_P the phenotypic variance and h^2 is the narrow sense
heritability $h^2 \equiv \frac{V_A}{V_P}$. The predicted effect of selection on phenotype will be accurate only for
184 weak selection as strong selection will generally distort Gaussian distribution of phenotypes
(see Bulmer 1980, Ch. 9; ? ?): in this study, we would expect deviations namely when
186 temporal change induces high fitness cost - due to directional nature of this selection.

188 **Simple population regulation**

190 We start by following change in the trait mean, whilst population density is a function
of mean fitness of the population. Throughout the paper, we assume that there is an optimal

192 value $\theta[x, t]$ for the trait $z[x, t]$, which is changing at a steady rate through space (x) and
 193 time (t):

$$\theta[x, t] = bx - kt, \quad (2)$$

194 where b is the gradient of optimum in space and k is the rate of change of the optimum in
 195 time. The habitat is one-dimensional, and the position on it is denoted by x .

196

The fitness

$$r[z] = r_\theta - \frac{(z - \theta[x, t])^2}{2V_S} \quad (3)$$

198 is a function of the adaptation of phenotype z at position x at time t and r_θ is the fitness
 199 when mean phenotype is perfectly adapted. V_S is the variance of stabilizing selection around
 200 the optimum, the strength of stabilizing selection is $\frac{1}{V_S}$. As the phenotypic variance $V_P \equiv$
 $\overline{(z - \bar{z})^2} = \overline{z^2} - \bar{z}^2 = \overline{(z - \theta)^2} - (\bar{z} - \theta)^2$ for any θ , the average fitness gives the intrinsic rate
 202 of increase of the population:

$$\bar{r}[\bar{z}] = r_\theta - \frac{(\bar{z}[x] - \theta[x, t])^2}{2V_S} - \frac{V_P[x]}{2V_S} \quad (4)$$

204 In the simple regulation we assume that local population density simply grows with the
 205 average fitness $\bar{r}[\bar{z}]$:

$$n = Ke^{\gamma \bar{r}}, \quad (5)$$

206 where K reflects the carrying capacity and $1/\gamma$ is the intensity of density-dependent regula-
 207 tion.

208 It follows from the above equations that, just as for a fixed environmental gradient (Kirk-
 209 patrick and Barton 1997, Eq. 1), the mean phenotype changes as:

$$\frac{\partial \bar{z}}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 \bar{z}}{\partial x^2} + \frac{-\bar{z} + bx - kt}{V_S} (V_A - \sigma^2 \gamma \frac{\partial \bar{z}}{\partial x} (b - \frac{\partial \bar{z}}{\partial x})) \quad (6)$$

210 We can immediately see a solution where the population adapts as the optimum moves:
 211 the trait mean is $\bar{z} = \beta x - kt + a$, $\beta = b$. Substituting this into Eq. 6 reveals that the lag a of
 212 the trait mean behind the optimum is $a = \frac{kV_S}{V_A}$. (If there is no variance in the trait, $V_A = 0$,
 213 a solution only exists for an optimum fixed in time, $k = 0$.) Population density is uniform
 214 in space, at $n = Ke^{\gamma(r_\theta - \frac{V_P}{2V_S} - \frac{k^2 V_S}{2V_A^2})}$. High genetic variance allows population to maintain

its trait mean closer to the changing optimum, but population growth rate also decreases
 216 with phenotypic variance (by $\frac{V_E}{2V_S}$), and so there is an optimal variance when population has
 the highest density: $V_A = \sqrt[3]{2k^2h^2V_S^2}$. With simple regulation, there is no other solution in
 218 which the population adapts to changing conditions.

220 Before embarking on a detailed discussion of the results, and for comparison with more
 realistic models, it is useful to reduce the number of parameters by re-scaling time, distance
 222 and trait. Following Barton (2001) we therefore introduce:

$$T = r^*t, X = x\sqrt{\frac{2r^*}{\sigma^2}}, Z = \frac{z}{\sqrt{r^*V_S}} \quad (7)$$

where r^* is the strength of density dependence at equilibrium (for simple regulation, $r^* = 1/\gamma$
 224 as explained later in the logarithmic model with joint regulation of trait and density).

We then have three parameters A , B and k^* .

$$A = \frac{V_A}{r^*V_S}, B = \frac{b\sigma}{r^*\sqrt{2V_S}}, k^* = \frac{k}{\sqrt{r^*^3V_S}} \quad (8)$$

226 The scaled growth rate is

$$\bar{R} = \frac{\bar{r}}{r^*} = \frac{r_\theta}{r^*} - \frac{1}{2}(\bar{Z} - BX + k^*T)^2 - \frac{A}{2h^2} \quad (9)$$

The scaled parameters A , B and k^* describe the decrease of fitness due to the standing
 228 genetic variance, the spatial gradient and the temporal change in the optimum. Specifically,
 $A r^*/2$ is the standing genetic load, $B^2 r^{*2}$ is the load due to dispersal across the spatial
 230 gradient and $k^{*2} r^*/2$ is the load due to temporal change in the optimum over the character-
 istic time $\Delta t = 1/r^*$. Relative to the time $T = r^*t$, we get the loads of $A/2$, B^2 and (over
 232 $\Delta T = 1$), $k^{*2}/2$. Note that the lag load is described by the scaled variable $a^* = \frac{a}{\sqrt{r^*V_S}}$: at
 equilibrium, the lag load caused by the temporally changing optimum is $\frac{1}{2}a^{*2}r^*$.

234

Now, the re-scaled trait mean then changes as follows:

$$\frac{\partial \bar{Z}}{\partial T} = \frac{\partial^2 \bar{Z}}{\partial X^2} + (BX - k^*T - \bar{Z})(A - 2\frac{\partial \bar{Z}}{\partial X}(B - \frac{\partial \bar{Z}}{\partial X})) \quad (10)$$

236 As in the case of environmental gradient fixed in time (Kirkpatrick and Barton 1997),
 we get two locally stable equilibrium solutions for the trait mean $\bar{Z} = \beta^* X - q^* T + a^*$ -
 238 one with uniform adaptation, where the gradient in trait mean matches the environmental
 gradient, $\beta^* = B$, and hence the range is unlimited, and another where adaptation is con-
 240 strained by genetic variance, the gradient in trait mean is shallower than the environmental
 gradient, $\beta^* < B$ and species' range is limited. With simple regulation, however, adaptation
 242 to temporal change only occurs for the uniform solution. (This is not the case for the joint
 regulation, assessed later.) As the optimum changes over time, the trait mean changes at the
 244 same rate as the optimum ($q^* = k^*$) and lags behind the optimum uniformly by $a^* = \frac{k^*}{A}$.
 Population density is uniform at $n = e^{\bar{R}} = e^{r_0 - \frac{1}{2}(\frac{k^{*2}}{A^2} + \frac{A}{h^2})}$, where $r_0 \equiv \frac{r_0}{r^*}$.

246
 In the second solution, the population is adapted on a limited range and the gradient in
 248 trait mean $\beta^* = \beta_-^* = \frac{B}{2}(1 - \sqrt{1 - \frac{2A}{B^2}})$ is shallower than the environmental gradient (see
 Fig 1, thin lines). Such a solution only exists if the environment changes sufficiently sharply
 250 relative to the genetic variance, $B > \sqrt{2A}$ (see Fig 2, thin line). The population density is
 highest where the line $\bar{Z} = \beta^* X + a^*$ intersects the trait optimum (on the infinite range, the
 252 shift a^* of the trait mean is arbitrary) and the population density $n = e^{r_0 - \frac{1}{2}((B - \beta^*)^2 X^2 + \frac{A}{h^2})}$
 declines as a Gaussian from the center of the range, with variance given by the difference
 254 between gradient in trait mean and environmental gradient, $\beta - \beta^*$. As the optimum changes
 in time, the trait mean stays constant: $q^* = 0$, hence locally the population becomes extinct:
 256 the population density (given by the simple regulation) simply tracks the changing optimum
 in space, moving at speed $c^* = \frac{k^*}{B - \beta^*}$, as long as there is a suitable habitat available.

258
 On an infinite (spatial) range, both above solutions (with $\beta^* = \beta_-^*$ and $\beta^* = B$) are locally
 260 stable whenever they exist ($B > \sqrt{2A}$). The third, unstable solution, $\beta_+^* = \frac{B}{2}(1 + \sqrt{1 - \frac{2A}{B^2}})$
 (see Fig 1, dashed line), determines the global stability. If the space is effectively infinite and
 262 the initial gradient in trait mean, β_0^* , is above the unstable solution with intermediate gradi-
 ent, β_+^* , the population always evolves towards uniform adaptation. Conversely, if $\beta_0^* < \beta_+^*$,
 264 the trait mean evolves towards the solution with shallow gradient, $\beta_-^* = \frac{B}{2}(1 - \sqrt{1 - \frac{2A}{B^2}})$, and
 the range is limited at equilibrium. The gradients and hence the stability are independent of
 266 the rate at which the optimum moves in time. When available habitat is limited and there is

no gene flow over the margins, however, adaptation collapses from the margins towards the
 268 trait mean with the shallow gradient, β_-^* , whenever solution with limited adaptation exists
 (see Appendix: Stability, Simple regulation. No gene flow over the margins is represented
 270 by reflecting or absorbing boundary conditions - when in the first case migrants intending to
 migrate over the margins move back to range or in the second case, die.) This corresponds to
 272 similar results for local stability under static environmental gradient (Kirkpatrick and Barton
 1997, Table 17.1 and Appendix).

274

Joint population regulation

276

Logarithmic model

278

It is more realistic to assume that there is a joint regulation of trait mean (Eq. 1) and
 280 population density. The population grows locally at rate r and migration is approximated
 by diffusion with variance σ^2 :

$$\frac{\partial n}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 n}{\partial x^2} + \bar{r}n \quad (11)$$

282 where the growth rate $r[n, z]$ and the intrinsic rate of increase, $\bar{r}[n, \bar{z}]$, both depend on the
 population density and adaptation in the trait:

$$r = r_e[n] + r_g[z], \bar{r} = r_e[n] + \bar{r}_g[\bar{z}], \quad (12)$$

284 As before, fitness depends on adaptation in the trait as follows:

$$r_g := -\frac{(z - \theta[x, t])^2}{2V_s}, \bar{r}_g := -\frac{(\bar{z} - \theta[x, t])^2}{2V_s} - \frac{V_P}{2V_S} \quad (13)$$

First, we assess the logarithmic model, where the growth rate r_e declines logarithmically
 286 as the carrying capacity is approached, $r_e = r_\theta - \frac{1}{\gamma} \log(\frac{n}{K})$:

$$\bar{r} = r_\theta - \frac{1}{\gamma} \log(\frac{n}{K}) - \frac{(\bar{z} - \theta[x, t])^2}{2V_S} - \frac{V_P}{2V_S} \quad (14)$$

With logarithmic density dependence, the fitness is very high for low densities ($n \ll K$),
 288 followed by fast regulation. We use the logarithmic model because it converges to the
 simple regulation near equilibrium ($n \rightarrow K$). (Neglecting migration, at equilibrium we

290 have $\bar{r} = r_e + \bar{r}_g = 0$, and hence using the above formula for logarithmic r_e we recover
 $n = Ke^{\gamma(r_\theta + \bar{r}_g)}$ - as for the simple regulation.) We can now see that $r^* = 1/\gamma$ is the strength
 292 of density dependence, defined as $r^* \equiv -n \frac{d\bar{r}}{dn} |_{n=\hat{n}_m}$ (Kirkpatrick and Barton 1997, where \hat{n}_m
 is the density at carrying capacity, i.e. spatially homogenous equilibrium when the optimum
 294 is stable in time).

296 It is clearer to describe all solutions when the model is re-scaled as was done for simple
 regulation (Eq. 7). In addition, we scale the population density so that it is equal to one
 298 when trait mean matches the gradient: $N = \frac{n}{K^*}$, $K^* = Ke^{\gamma(r_\theta - \frac{V_P}{2V_S})} = Ke^{r_0 - \frac{A}{2h^2}}$. (Note
 that in Kirkpatrick and Barton 1997 and Barton 2001, $r_0 \equiv \frac{r_\theta}{r^*}$ is in the logarithmic model
 300 set to zero.)

302 Then (from Eqs. 1 and 11) for joint regulation of trait mean and logarithmic density-
 dependence we obtain:

$$\frac{\partial \bar{Z}}{\partial T} = \frac{\partial^2 \bar{Z}}{\partial X^2} + \frac{2}{N} \frac{\partial N}{\partial X} \frac{\partial \bar{Z}}{\partial X} - A(\bar{Z} - BX + k^*T) \quad (15)$$

$$\frac{\partial N}{\partial T} = \frac{\partial^2 N}{\partial X^2} + \bar{R}N \quad (16)$$

$$\bar{R} = \frac{\bar{r}}{r^*} = -\log(N) - \frac{1}{2}(\bar{Z} - BX + k^*T)^2$$

306 These equations correspond to Eqs. 8 and 9 for fixed environmental gradient ($k^* = 0$) in
 Barton (2001).

308 We search for an equilibrium solution in the form of a traveling wave: $\bar{Z} - \theta^* = f[U] + a^*$,
 310 where U transforms the spatial coordinate according to the changing optimum: $U = X - c^*T$
 and c^* describes the speed of the traveling wave. Now the lag of trait mean behind the opti-
 312 mum, $\theta^* = BX - k^*T$, is a function of a single variable, U . We assume that the population
 density would have a form $N = n_1^* e^{-U^2 \frac{\zeta^*}{2}}$, and the variance along U , $\frac{1}{\zeta^*}$, is constant.

314 In the extension from the simple to joint regulation, and as when the environmental gra-
 316 dient is fixed in time (Kirkpatrick and Barton 1997), we again find two classes of solutions: a
 uniform adaptation and, when spatial gradient is steep ($B > B_c$), an adaptation on a limited

318 range. Both solutions can be described jointly by the following formulae.

320 At equilibrium of joint regulation with logarithmic environmental growth rate, the scaled lag of the trait mean behind the optimum is

$$a^* = \frac{k^*}{A + \frac{2B^2}{A}\phi(1-\phi)} \quad (17)$$

322 where $\phi \equiv \frac{\beta^*}{B}$ describes the degree of adaptation in the gradient of trait mean. The population density at equilibrium is

$$N = e^{-\zeta^* - \frac{a^{*2}}{2} - U^2 \frac{\zeta^*}{2}}, \quad (18)$$

324 where $\zeta^* = \frac{A(1-\phi)}{2\phi}$ is the inverse of the variance of population density along U . The trait mean $\bar{Z} = \beta^* X - q^* t + a^*$ adapts at speed $q^* = k^* - c^*(B - \beta^*) = a^* A$. The speed c^* of movement of the traveling wave is $c^* = \frac{2a^* B \phi}{A}$ for $\phi \neq 1$. When the gradients match ($\phi = 1$), the solution is uniform with respect to U and $c^* = \frac{k^*}{B}$.

328

The solution with uniform adaptation, where the gradient in trait mean, β^* , and environmental gradient, B are equal ($\phi = 1$), always exists. At this equilibrium, the trait mean $\bar{Z} = BX - q^* T + a^*$ changes at the same rate as the optimum ($q^* = k^*$) and lags behind it by $a^* = \frac{k^*}{A}$. In the original units, the lag is $a = \frac{kV_S}{V_A}$ - as expected for a single population (e.g. Lande and Shannon, 1996).

334

The population density is uniform in space, $N = e^{-\frac{a^{*2}}{2}}$ - see Fig 3, left. Note that N is the scaled population density, so that $N = 1$ for a uniformly adapted population when the environmental optimum is stable in time. In the logarithmic model, N is always greater than zero, but we can reasonably assume that very small populations with density $N \leq N_{tr}$ are effectively extinct. If loss of fitness due to temporal change in the optimum is too high, $k^* > A\sqrt{2\log(\frac{1}{N_{tr}})}$, population (in term of scaled density N) goes extinct - see Fig A 6. In terms of the original units, population density is $n = Ke^{r_0 - \frac{a^{*2}}{2} - \frac{A}{2h^2}} = Ke^{\gamma(r_0 - \frac{k^2 V_S}{2V_A^2} - \frac{V_A}{2h^2 V_S})}$. Hence when the abundance of resource described by K is fixed, the fitness \bar{r} as well as the population density n are highest when $V_A = \sqrt[3]{2k^2 h^2 V_S^2}$ - as with the simple regulation.

344

When the environmental gradient is steep ($B > B_c$), the population may alternatively
 346 adapt only on a limited range (see Fig 3, right), with gradient in trait mean $\beta_-^* \approx \frac{A}{\sqrt{2}} < B$.
 The cubic equation for the relative gradient in the trait mean ($\phi \equiv \frac{\beta_-^*}{B}$) is $2B^2\phi^2(1 - \phi) =$
 348 $A^2(1 - \phi) + A\phi$ (see Fig 1). It follows that the solution with limited range exists when
 $B > B_c = \frac{1}{4}\sqrt{20A + 8A^2 + (1 + 8A)^{3/2}} - 1$; approximately for small A when $B > \sqrt{2A}$, or
 350 $V_A < \frac{1}{4}\gamma\sigma^2b^2$ in the original units (see Fig. 2). Note that the gradient in trait mean is inde-
 pendent of the speed of movement of the optimum, k^* , and the approximate formula is the
 352 same as the exact result for gradient in trait mean under simple population regulation (Eq. 3).

354 Populations with limited adaptation ($\phi < 1$) adapt slower than is the rate at which the
 optimum changes in time (k^*) - the (scaled) trait mean changes at a rate determined by
 356 $q^* = \frac{k^*A^2}{A^2 + 2B^2\phi(1-\phi)}$. The rate of adaptation always increases with the standing genetic load
 (\tilde{A}) and migration across the gradient (B) and is close to $q^* \approx \frac{k^*A}{1+A}$, unless $B \rightarrow B_c \approx \sqrt{2A}$,
 358 where the rate of adaptation drops off sharply (see Fig. 4, first row; approximations are A
 small). Therefore, when the population lives on a limited range, the trait mean is always
 360 adapting slower than is the rate the environment changes in time, and the difference between
 the rates k^* and q^* decreases with A . The dependence on the effective gradient B is insignifi-
 362 cant unless B is close to B_c , when the rate of adaptation a^* increases sharply (Fig. 4, second
 row). The scaled lag of trait mean behind the optimum is simply $a^* = \frac{q^*}{A}$. The population
 364 is centered at $X = c^*T$, $c^* = \frac{2B\phi k^*}{A^2 + 2B^2\phi(1-\phi)}$: the rate at which the population moves in space
 is close to $c^* \approx \frac{k^*}{B}(1 + \frac{A}{2B^2})$, increasing as the fitness effect of variance (A) increases, and
 366 decreasing as the effective gradient B gets steeper; again, the dependency gets stronger as
 $B \rightarrow B_c$ (Fig. 4, third row).

368
 For a population adapted on a limited range, the degree of adaptation ($\phi \equiv \frac{\beta_-^*}{B}$) increases
 370 only slowly as the gradient steepens, and the density declines - both in the centre, where
 when the environmental optimum is static, trait mean would match the optimum perfectly,
 372 and as the difference between the trait mean and environment increases with the distance
 from the centre. A population living on a limited range goes extinct when the environmental
 374 gradient is steeper than $B_e = \frac{A - 2 \log(N_{tr})}{\sqrt{2}}$ for $k^* = 0$ (as it follows from the formula for
 the scaled population density, Eq. 18). The rate the gradient changes in time has only a

376 minor effect, B_e decreases by $-\frac{k^{*2}}{4\sqrt{2}}(\frac{1}{\log(N_{tr})^2} + \frac{A}{\log(N_{tr})^3}) + O(A^2, k^4)$ - see Fig A 6. Note
 that for a given variance ($A = \gamma\frac{V_A}{V_S}$ fixed), the species range as determined by $\zeta^* = \frac{A(1-\phi)}{2\phi}$
 378 is independent of the rate at which the environment changes in time - the width as given by
 (say) 2 standard deviations of $N(X)$ is $\frac{2}{\sqrt{\zeta^*}}$.

380

Logistic density dependence

382

It is useful to understand how robust is the model against different assumptions about
 384 density dependent regulation. The logarithmic model leads to high growth rates at low
 densities, and so we also assess the "logistic" model, with the environmental growth rate
 386 defined as $r_e = r_m(1 - \frac{n}{K})$. The scaled average growth rate for the logistic model is

$$\bar{R} = \frac{\bar{r}}{r^*} = 1 - N - \frac{1}{2}(\bar{Z} - BX + k^*T)^2$$

where time $T = r^*t$ is scaled by $r^* = r_m - \frac{V_P}{2V_S}$. Scaling is the same as for the logarithmic
 388 model, described by Eq. 7 and $N = \frac{n}{K^*}$, with new parameters as in Eq. 8. Again, r^* is
 the strength of density dependence at spatially homogeneous equilibrium if the mean was
 390 perfectly adapted ($a^* = 0, \beta^* = B$), as defined in the description of logistic model. In the
 logistic model, scaled carrying capacity is $K^* = K\frac{r^*}{r_m}$. The variance scaled by its effect on
 392 fitness is $A = \frac{h^2V_P}{r^*V_S}$, hence $K^* = K(1 - \frac{A}{A+2h^2})$.

394

We do not have an exact solution for the logistic model, but can obtain an approximation.
 The population density at equilibrium is close to $N = (1 - \zeta^* - \frac{a^{*2}}{2})e^{-U^2\frac{\zeta^*}{2}}$, the approximate
 396 formulas for a^* , c^* and ζ^* at equilibrium are the same as in the logarithmic model (see Eq. 17
 and below), only the gradient in trait mean differs: now the relative gradient ϕ follows equa-
 398 tion $2B^2\phi^2(1 - \phi) = \frac{A^2}{2}(1 - \phi) + A\phi(1 - \frac{a^{*2}}{2})$, hence depends on the rate of temporal change
 of the optimum as the lag a^* is a function of k^* . (To obtain this result, population density
 400 in the equation describing density regulation (Eq. 16) is approximated by $N \approx n_1^*(1 - U^2\frac{\zeta^*}{2})$.)

402

Again, the population range would expand without limits if the scaled environmental
 gradient B is below a critical gradient B_c . Its value is intermediate between the models with
 404 simple and logarithmic regulation and agrees with the prediction for the simple regulation

to first order in A , $B_c = \sqrt{2A} + O(A^{3/2})$ (see Fig 2). For steeper gradients, both uniform
406 adaptation on the whole range and adaptation on a limited range with shallower gradient in
trait mean are possible.

408

For the equilibrium with uniform adaptation, scaled population density $N = 1 - \frac{k^*2}{2A^2}$
410 declines significantly as k^* increases and the population goes extinct if selection due to
temporal change is large relative to the standing genetic load scaled by the strength of
412 density-dependence, $k^* > \sqrt{2A}$. Re-scaling to the original units, $n = \frac{r^*}{r_m} KN = \frac{K}{r_m}(r_m -$
 $\frac{V_P}{2V_S})(1 - \frac{k^2 V_S}{2r^* V_A^2})$: a uniformly adapted population would go extinct if the temporal change in
414 the optimum is greater than $k_e = \sqrt{\frac{2r^*}{V_S}} h^2 V_P$ so that the lag of trait mean behind the opti-
mum becomes larger than $a = \sqrt{2V_S r^*}$, same as for unstructured population (see Lynch and
416 Lande, 1993, Eq. 11). The genetic variance, when the fitness \bar{r} of the population is highest,
does not depend on the environmental growth rate and stays as for the simple regulation at
418 $V_A = \sqrt[3]{2k^2 h^2 V_S^2}$. However, highest fitness does not coincide with highest population density,
which requires genetic variance $V_A = khV_S$ - the density initially sharply increases with V_A
420 but drops to zero when phenotypic load is too high, $\frac{V_P}{2V_S} > r_m$.

422 As the gradient B steepens relative to the scaled variance, A , another solution emerges.
The population living on a limited range can migrate towards favourable habitat, but its
424 total population density reflects the rate at which the environment changes in space: the
difference between the optimal gradient and the gradient in trait mean increases with B (see
426 Fig. 5), hence population away from the very centre becomes more maladapted and the
density drops to zero - population goes extinct approximately when $B_e > \frac{A+2}{\sqrt{2}} - \frac{k^*2}{4\sqrt{2}}(1 - A +$
428 $\frac{3}{4}A^2) + O(k^*3) + k^2 O(A^3)$. (We use that for B large, $\beta^* \approx \frac{A}{\sqrt{2}}$.) The "extinction" gradient,
 B_e , slowly decreases with the rate optimum changes in time (k) and agrees well to the limit
430 for logarithmic regulation when $N_{tr} = e^{-1}$. Re-scaling to original units we obtain that such
an "imperfectly" adapted population goes extinct for $b_e \approx \frac{1}{\sqrt{V_S \sigma}}(2r_m V_S + V_P(h^2 - 1))$ when
432 environment is stable in time. Note that this formula corrects the typographical error in
Kirkpatrick and Barton (1997, Eq. 16), as their scaling uses genetic load A rather than $A/2$
434 stated in their Eq. 11a (as mentioned earlier by Case and Taper, 2001). When the optimum
changes in time, extinction gradient for population constrained by its genetic variance be-

436 comes $b_e \frac{\sigma}{\sqrt{V_S}} \approx 2r_m + \frac{V_P}{V_S}(h^2 - 1) - \frac{1}{4}k^2(r_m - \frac{V_P}{V_S}(\frac{1}{2} + h^2)) + O(V_P^3, h^4)$.

438 In comparison to the static case, though gradients in trait mean stay nearly the same
whenever they exist, the faster moving optimum lead to zero densities sooner for uniform
440 adaptation (see Fig. 6). Also, though stability of the uniform solution on the infinite range
does not change, on finite range we see that uniform adaptation is less prone to collapse from
442 the margins when optimum changes very slowly (as the advantage of marginal phenotypes
does not build up over time). However, starting from little adaptation, solution tends to
444 evolve towards limited spread (see Fig. 5.)

446 Before moving onto the evolutionary dynamics of populations when variance can evolve
freely, we give a brief summary of the results for fixed variance. As for a stable optimum, two
448 regimes of adaptation exist at equilibrium: uniform adaptation, where the population would
eventually fill all available habitat along the environmental gradient, and limited adaptation,
450 where the environmental gradient is steep relative to (fixed) genetic variance. As the opti-
mum changes in time, the uniformly adapted population tracks the optimum by shifting at a
452 uniform rate, matching its rate of change. In contrast, a population that is only well adapted
at the centre, adapts in the trait slower than is the rate of temporal change of the optimum,
454 and survives by moving in space towards favourable habitat. The degree of adaption as mea-
sured by the gradient in trait mean relative to the spatial gradient (which also determines
456 the species range), and the critical gradient, above which the limited adaptation occurs, is
independent of the rate at which the optimum changes in time.

458

460 **Adaptation to a linear environmental gradient moving in time - Population genetic model**

462 In order to relax the assumption of fixed genetic variance, we need to use a model with
explicit determination of a trait; for comparison to the previous models, the trait distribu-
464 tion should be (close to) a Gaussian. For an optimum stable in time, Barton (2001) analysed
three such models: assuming weak selection, a continuum of alleles model with many alleles
466 with Gaussian distribution of effects (Crow and Kimura 1964; Kimura 1965), the two alleles

model, where the trait under selection is encoded by many additive independent bi-allelic loci
 468 with equivalent effects (Wright 1935) and Fisher's infinitesimal model (Fisher 1918; Bulmer
 1980), where adaptation occurs via changes in linkage disequilibrium.

470

Here we only assess the two alleles model, where the trait under selection is determined
 472 by n_l diploid loci of additive effect with two alleles (with frequencies q_i , p_i , and effects
 $-\alpha_i/2$, $\alpha_i/2$). The trait mean is $\bar{z} = \sum_{i=1}^n \alpha_i(p_i - q_i)$ and variance at linkage equilibrium is
 474 $V_A = 2 \sum_{i=1}^n \alpha_i^2 p_i q_i$. Substituting to Eqs. 1, 12 and 13 gives

$$\frac{\partial \sum_{i=1}^n \alpha_i \partial p_i}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 \sum_{i=1}^n \alpha_i \partial^2 p_i}{\partial x^2} + \sigma^2 \frac{\partial \log(n)}{\partial x} \frac{\partial \sum_{i=1}^n \alpha_i \partial p_i}{\partial x} + 2 \sum_{i=1}^n \alpha_i^2 p_i q_i \left(\frac{p_i - q_i}{2V_S} - \frac{\bar{z} - \theta}{V_S} \right) - \mu(p_i - q_i), \quad (19)$$

where μ is the mutation rate, which is assumed to be symmetric. Now the genetic vari-
 476 ance changes with allele frequency, so we get an extra term $\frac{p_i - q_i}{2V_S}$ arising from $\frac{\partial \bar{z}}{\partial z}$ (using that
 $\frac{\partial}{\partial \bar{z}} = \sum_{i=1}^n \frac{1}{2\alpha_i} \frac{\partial}{\partial p_i}$).

478

The cline shape in a static environment ($k = 0$) has been derived by Barton (1999, 2001),
 480 assuming that clines have the same form and are distributed in space so that the trait mean
 matches the gradient. Then, allele frequencies change as

$$\frac{\partial p_i}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 p_i}{\partial x^2} + \sigma^2 \frac{\partial \log(n)}{\partial x} \frac{\partial p_i}{\partial x} + \frac{\alpha^2}{2V_S} p_i q_i (p_i - q_i - 2\delta) - \mu(p_i - q_i), \quad (20)$$

482 where $\delta \equiv \frac{\bar{z} - \theta}{\alpha}$. Barton (2001, p. 378-382) showed that at spatially uniform equilibrium
 with no mutation, allele frequency (centered at $x = 0$) has a form of $\hat{p}[x] = \frac{1}{1 + \exp(-\frac{x}{w})}$ (we
 484 set $\alpha_i = \alpha$); where the width of the cline is $w = 4\sqrt{\frac{\sigma^2 V_S}{\alpha^2}}$. The variance contribution due to
 one locus is $V_{G, n_l=1} = 2\alpha\sqrt{\sigma^2 V_S}$, obtained by integrating the variance formula over space,
 486 with $p \rightarrow \hat{p}[x]$. As there need to be $\frac{b}{2\alpha}$ clines per unit distance (as each cline shifts the trait
 mean by 2α) to match the spatially variable optimum θ , we get $\hat{V}_G = b\sqrt{\sigma^2 V_S}$. In the scaled
 488 model (see Appendix: Scaling for the population genetic model), that is $V \equiv \frac{V_A}{r^* V_S} = B\sqrt{2}$.

490 As the optimum changes in time, allele frequencies will need to move in space. We are
 again looking for a traveling wave solution, where the allele frequency, $p[x, t] = p[u]$, is solely
 492 a function of a new variable $u = x - ct$ (and $\frac{\partial}{\partial x} = \frac{d}{du}$, $\frac{\partial}{\partial t} = -c \frac{d}{du}$):

$$-c \frac{dp_i}{du} = \frac{\sigma^2}{2} \frac{d^2 p_i}{du^2} + \sigma^2 \frac{d \log(n)}{du} \frac{dp_i}{du} + \frac{\alpha_i^2}{2V_S} p_i q_i (p_i - q_i - 2\delta) - \mu(p_i - q_i), \quad (21)$$

and where the allele frequency (which was at the time $t = 0$ centered on $u = 0$) has a form
of $p[u] = \frac{1}{1 + \exp(-\frac{u}{w})}$. Then $\frac{dp}{du} = \frac{4}{w} pq$ and $\frac{d^2 p}{du^2} = (\frac{4}{w})^2 pq(p - q)$, so with no mutation, there
is a spatially uniform solution for a given δ , where $w = 4\sqrt{\frac{\sigma^2 V_S}{\alpha^2}}$ and $\frac{c}{\delta} = \frac{w\alpha^2}{4V_S}$. The cline
width, w , is independent of the rate of movement of the traveling wave as $u = x - ct$ only
shifts the clines along x . For the uniform solution, where the rate of change in the trait mean
matches the change in the optimum, we must have $c = \frac{k}{b}$, and hence the lag of trait mean
behind the optimum is $a = \frac{k\sqrt{V_S}}{b\sigma}$. The number of clines required to match the optimum
at any particular time stays the same as in the static case at $\frac{b}{2\alpha}$, and hence the resulting
variance stays at $\hat{V}_G = b\sqrt{\sigma^2 V_S}$ (without mutation and under linkage equilibrium) - and so
as in the static case Barton (2001, p. 378-9), it is independent of allelic effect or numbers of
genes. The lag of the trait mean is therefore $a = \frac{kV_S}{V_G}$, in agreement with the prediction for
the phenotypic model.

We can test the robustness of the predictions by iterating the two-allele model numerically,
following joint evolution in clines (and hence mean and variance) and population density, as
described by Eq. 22 (Appendix) and 16. Initially, the population has no spatial adaptation:
allele frequencies at time zero are uniform in space and almost fixed to zero or one, with
uniform distribution of deviations ranging from zero to 0.01. Over time, allele frequencies
diversify across the range to match the optimum (see Fig. 8)

The population evolves to be uniformly adapted, with gradient in trait mean matching
the optimum and lagging behind by $a^* = \frac{k^*}{A}$ ($a = \frac{kV_S}{V_A}$ in the original units), matching the
predictions for phenotypic model (see Fig. 7 and 9, top). Scaled genetic variance V stays very
close to the prediction (above), $V = B\sqrt{2}$ (Fig. 7 and 9, middle). As genetic variance does
not increase above the static equilibrium when optimum changes faster in time, population
density decreases towards zero when the loss of fitness due to temporal change is too large
relative to the standing genetic variance (Fig. 7 and 9, bottom). The rate of decrease of
population density is the only outcome which quantitatively differs between the logistic and

logarithmic model - for logistic model, population density declines faster with k^* , leading to
522 extinction at $k^* \geq \sqrt{2}A$.

524 Discussion

526 In an environment which varies both in time and space, populations can survive by adapt-
ing in trait mean or by moving to a more favourable habitat. Here we extend Kirkpatrick
528 and Barton's (1997) model with static optimum to let the environment vary in time as well
as in space. We show that a temporally changing environment does not have a significant
530 effect on the degree of adaptation as measured by the gradient in trait mean, and hence the
species range: instead we see a steady decrease of population density as the rate at which the
532 optimum changes in time increases. In natural populations, however, we could still expect a
range reduction arising from the Allee effect and possibly other forces which are not analysed
534 in this paper - most important, genetic drift (see Butlin et al. 2003; Alleaume-Benharira
et al. 2006). As in the static case, we see two kinds of response: a population, which is
536 uniformly adapted in space, tracks the optimum by shifting at a uniform rate matching the
environmental rate of change, and a population, where only the central range is well adapted,
538 both adapts in the trait and moves in space towards favourable habitat. Below we attempt
to explain when one or the other regime is likely, and when a population is likely to fail to
540 track the change by adaptation and/or migration.

542 We ignore many complications in the phenotypic and genetic models presented in this
paper: namely epistasis between loci, possible adaptation in genotype-by-environment in-
544 teractions (Nussey et al. 2005). We also only explicitly assess evolution of one trait at a
time; although we can think of genetic variance being constrained due to another trait (see
546 Grant and Grant 1995; Etterson and Shaw 2001) for examples of effect of interaction between
loci). However, the nature of the Gaussian distribution of phenotypes which follows from our
548 assumptions is quite robust and allows for analytical predictions, whose sensitivity towards
specific complex scenarios can be tested.

550

Whether a population can adapt to an unlimited range depends on the dimensionless

552 parameters A , B ; its ability to respond to change through time depends on the scaled pa-
 554 rameter k^* . These three parameters can be thought of as three kinds of genetic loads, each
 556 scaled relative to the strength of density dependence, r^* . $Ar^*/2$ is the standing genetic load,
 i.e. loss of fitness due to genetic variance around the optimum; B^2r^{*2} is the loss of fitness
 558 when an optimally adapted population shifts by one dispersal range; and similarly, $k^{*2}r^*/2$
 is the loss of fitness when an optimally adapted population shifts through the characteristic
 time $1/r^*$.

560 Below, we first outline the general results and then relate them to the real world by dis-
 cussing estimates of the scaled parameters.

562

Evolution with constant genetic variance

564

First, we focus on predictions based on the assumption that genetic variance can be
 566 treated as constant. In this case the equilibrium with uniform adaptation always exists, and
 as the effective spatial environmental gradient, $B = \frac{b\sigma}{r^*\sqrt{2V_S}}$, increases relative to the scaled
 568 variance, $A = \frac{h^2V_P}{r^*V_S}$, we the equilibrium with limited adaptation as well. The critical gradient
 does not change significantly with the rate at which the optimum moves in time, and is close
 570 to $B_c = \sqrt{2A}$ (see Fig. 2), as shown previously for a static optimum by Barton (2001),
 Kirkpatrick and Barton (1997). When they exist, both solutions are locally stable on infinite
 572 range. When habitat is limited, uniform adaptation tends to collapse from the margins when
 environmental gradient is steeper than the critical value B_c (see Figs. 2). In the original
 574 units, limited adaptation emerges approximately when the critical gradient $\frac{b\sigma}{\sqrt{h^2V_P}} > 2\sqrt{r^*}$:
 when the change in spatial optimum over one dispersal range, $b\sigma$, relative to the standard
 576 deviation of genetic variance, $\sqrt{V_A}$, is smaller than twice the square root of the strength of
 density dependence, $2\sqrt{r^*}$. Optimum changing slowly in time extends the local stability of
 578 uniformly adapted population as the optimum for marginal populations changes over time, so
 edge effects are less important. Population adapted on a limited range can however sustain
 580 faster temporal change in the optimum than is possible for a uniformly adapted population
 (see Fig. 6).

582

Uniform adaptation

584

For uniform adaptation, the spatial gradients in the trait mean and the environment
586 are equal, as are the rates of temporal change and adaptation in trait mean. The scaled
trait mean, \bar{Z} , lags behind the optimum by a^* , leading to a load of $\frac{1}{2}a^{*2}r^*$. This load dif-
588 fers markedly between the uniform adaptation where gradients match, $\beta^* = B$, and limited
adaptation, where the gradient in trait mean is shallower than the spatial environmental
590 gradient, $\beta^* < B$. At the uniform equilibrium, the scaled lag of the trait mean behind the
optimum increases linearly with the scaled rate of temporal change (k^*): $a^* = \frac{k^*}{A}$. In the
592 original units, we recover $a = \frac{kV_S}{V_A}$, which is the same as for unstructured populations, and
robust against the choice of growth rate (Lande and Shannon 1996; Bürger 1999; Waxman
594 and Peck 1999, and similar in Charlesworth 1993).

596 At equilibrium, population density declines with the scaled lag of trait mean behind the
optimum, a^{*2} , as a Gaussian for the logarithmic model: $\hat{N} = e^{-\frac{1}{2}\frac{k^{*2}}{A^2}}$, and quadratically
598 for the logistic one ($\hat{N} = 1 - \frac{1}{2}\frac{k^{*2}}{A^2}$). A uniformly adapted population fails to survive when
selection due to the optimum changing in time, k^* , is large relative to the genetic load scaled
600 by the strength of density dependence, A . The critical rates of change of the optimum at
which the population goes extinct are $k_e^* = A\sqrt{2\log(1/N_{tr})}$ (where N_{tr} is the density when
602 the population is no longer viable) and $k_e^* \approx A\sqrt{2}$, for the logarithmic and logistic model,
respectively. When we scale back to the original units, for the logistic model we recover
604 $k_e = \sqrt{\frac{2r^*}{V_S}}h^2V_P$, which agrees with the result for an unstructured population (see (Lynch
and Lande, 1993, Eq. 11). Note that since A as a function of additive genetic variance
606 V_A only enters as a parameter, we do not get an explicit dependence of scaled population
density N on the environmental gradient; but when we scale back to the population density
608 $n = \frac{N}{K^*}$, we uncover the trade-off between the standing load caused by genetic variance vs.
the increased ability of the population to adapt when additive genetic variance is higher. The
610 "optimal" genetic variance (when the fitness is highest) is $V_A = \sqrt[3]{2k^2h^2V_S^2}$ - again the same
as predicted for an unstructured population by Lande and Shannon (1996).

612

Adaptation on limited range

614

As the environmental gradient, B , steepens relative to the scaled genetic variance, A ,
 616 another equilibrium emerges: now the gradient in trait mean is much shallower than the
 environmental gradient, the (initial) position of the population in space is arbitrary (see
 618 Fig 3, right), and population density decreases away from the center, leading to a limited
 species' range. The population tracks favourable conditions both in space and time - the
 620 rate at which the trait mean changes is slower than the change in optimum: approximately,
 $q^* \approx \frac{k^*A}{1+A}$. The centre of population density moves in space at a rate $c^* \approx \frac{k^*}{B}(1 + \frac{A}{2B^2})$ (see
 622 Fig. 4) - hence as the rate of temporal change increases, the decline of density is much slower
 than for uniform adaptation (when favourable habitat is available). We can find the critical
 624 rate of change of environment in time and space when the population goes extinct: for the
 logistic model, that is $B_e \approx \frac{A+2}{\sqrt{2}} - \frac{k^{*2}}{4\sqrt{2}}(1 - A + \frac{3}{4}A^2)$; in terms of the original units that is
 626 $b_e \frac{\sigma}{\sqrt{V_S}} \approx 2r_m + \frac{V_P}{V_S}(h^2 - 1) - \frac{1}{4}k^2(r_m - \frac{V_P}{V_S}(\frac{1}{2} + h^2))$: the extinction gradient increases with
 the genetic load $Ar^*/2 = \frac{h^2V_P}{2V_S}$ - both due to the static term, and as the decrease due to
 628 temporal change (last term) is smaller.

630 Evolution of variance

632 The equilibrium variance, which determines the rate of response to selection (Fisher
 (1930)), depends on the shape of fitness as a function of phenotype and space. When op-
 634 timum moves in time, the equilibrium variance must be also dependent on fitness form;
 therefore below, we discuss studies of moving optimum of a Gaussian, or approximate Gaus-
 636 sian ($\approx 1 - \frac{(z-\theta)^2}{2V_S}$), fitness as used in our model, extended with spatial gradient.

638 We can get an idea about the optimal distribution of phenotypes in a single unstructured
 population by analysing the dynamics of cumulants describing the phenotypic distribution:
 640 1993's (1993 and 2000, Ch.VII/7.3) studies predict that unless mutation is infinitesimally
 small, the genetic variance would increase with skewness of the underlying distribution,
 642 which arises from directional selection (Bürger 2000, Eq. 7.20, p.327). It is less clear how
 often this is the case in finite sexual populations: individual-based simulations by Bürger
 644 and Lynch (1995) and Bürger (1999 and 2000, Ch.VII/7.3), demonstrate sharp increase and

a maintenance of higher variance as the optimum changes in time (Bürger and Lynch 1995, Fig 7.4) - unless effective population size is very small (Bürger and Lynch 1995, Fig 7.5; genomic mutation rate $U = 10^{-2}$). Consistently with the expectation that the total number of mutations in the population would limit the adaptation, Waxman and Peck (1999) show that in infinite sexually reproducing population (assessed via simulations of genotype frequencies), high variance evolves even for much lower mutation rates. Note that in unstructured populations, mutation is essential to maintain nonzero variance, which is not the case when selection varies in space.

In a static environment, variance can be maintained by gene flow across spatial gradient. When environmental optimum changes in both time and space, higher variance could evolve. We approximate the trait with the "two-allele" model Barton (2001), following frequencies of n_l clines of additive bi-allelic loci. For a static environment, the study of Barton (2001) shows that in this case, gene flow across spatial gradient, $b\sigma$, maintains a variance of $V_A = b\sigma\sqrt{V_S}$. Uniform equilibrium, where clines are scattered in the space and have the same form, can be found analytically: as environment changes in time, the shape of the cline stays the same as in the static case (Barton 2001), but the cline moves in space at a rate $c = k/b$ (in scaled units, $c^* = k^*/B$). As neither the shape of the cline nor the number of polymorphic clines changes as the optimum moves in time (and we assume that alleles are at linkage equilibrium), the predicted variance stays the same as for the static case.

The above predictions can be tested by numerically iterating the two-allele model over time, so that the shape, spacing and number of (variable) allele frequencies are not constrained. The solutions confirm that the variance stays at the same level as maintained by gene flow across the environmental gradient in the static case, even though as k^* increases, population density gradually drops to zero (see Fig 7), and better adaptation would be possible if V_A was higher. The variance does not increase above the static equilibrium even when we add mutation to the model. We can imagine that if population was age structured (see Charlesworth 1980), then the spatial gradient can be thought of as blurred with standard deviation as a function of change of the environment over the average generation time, $k\Delta t$, which would lead to an increase of variance. Also, individual-based model may bring a

676 different result, for two reasons: first, we could follow genotype frequencies, so that linkage
 equilibrium could build up. Second, genetic drift can have a qualitative effect on the results
 678 regarding species range (see Butlin et al. 2003; Bridle et al. in prep.) - as such, however,
 this is the scope for a separate paper and we do not elaborate on the topic here.

680

Because genetic variance of an additive trait tends to evolve towards $\hat{V} = \sqrt{2B}$; in terms
 682 of the original units $\hat{V}_A = b\sigma\sqrt{V_S}$, spatial gradient facilitates adaptability in time: we can
 clearly see from the formula for the fitness maximum at $V_A = \sqrt[3]{2k^2h^2V_S^2}$ that the popula-
 684 tion grows fastest when $b\sigma \approx \sqrt[3]{\frac{2k^2h^2}{V_S}}$, which also gives the highest population density for
 logarithmic growth rate. Under the logistic model, phenotypic load must be smaller than
 686 the maximum growth rate ($\frac{V_P}{2V_S} < r_m$) to maintain positive population density, which leads
 to extinction for steep spatial gradients when variance can evolve ($B_e \approx \sqrt{2}h^2r_m/r^*$); and
 688 the density is highest for $b\sigma = hk$. When environment changes in time, the "extinction" in
 terms of the scaled density, N , occurs approximately for $k^* > \sqrt{2}A$ in the logistic model and
 690 for $k^* > \sqrt{2}A \log(1/N_{tr})$ in the logarithmic one: therefore for uniformly adapted population,
 we would expect extinction at $k_e^* \approx 2B$ and $k_e^* = 2B \log(1/N_{tr})$, respectively. In terms of
 692 the original units, a population with logistic environmental growth rate and unconstrained
 variance would go extinct when the rate of change of the optimum in time is greater than
 694 $k_e \approx b\sigma\sqrt{2(r_m - \frac{b\sigma}{2h^2\sqrt{V_S}})} = b\sigma\sqrt{2r^*}$.

696 Parameters in nature

698 What are plausible values for the parameters A, B, k^* and r^* ? First, consider A , a mea-
 sure of the load due to genetic variance around the optimum. Since Lande and Arnold (1983)
 700 renewed interest in the quantitative genetics of wild populations, there have been hundreds
 of studies of the strength of stabilising selection, and of additive genetic variation, in nature.
 702 The observed distribution (Kingsolver et al. 2001) of the standardized quadratic selection
 gradient, γ , is wide and fairly symmetrical on the continuum of stabilizing ($\gamma < 0$) to disrup-
 704 tive selection ($\gamma > 0$), with median for the stabilizing selection $-\tilde{\gamma}_- = \frac{\tilde{V}_P}{2V_S} \doteq 0.1$, ranging
 from 1.5 to 0. This corresponds to $V_S/V_E = 5/(1 - h^2)$ rather than $V_S/V_E = 20$, which
 706 used to be the common consensus (see Johnson and Barton 2005). If we take heritability

$\tilde{h}^2 \doteq 1/2$ (which implies that $V_A = V_E + V_R$, where V_R are all non-additive components of genetic variance), the median of $A = \frac{V_E h^2}{r^* V_S}$ per a measured trait is $\tilde{A} \doteq 0.01$ for $r^* \doteq 1$ and, mostly, $A < 2$ (see below). The overall genetic load $A r^*/2$ scales with the number traits under selection, as the total effect on fitness would encompass independent components of the load for all traits.

712

Burt (1995, 2000) reviews evidence on the additive genetic variance for fitness, and makes an interesting argument concerning (in our notation) the scaled dispersal load, B^2 . He points out that the total dispersal load can be estimated from transplant experiments, in which individuals are moved from their native location, or are fertilized by pollen from elsewhere; this dispersal load must be balanced against the increase in relative mean fitness due to selection, which equals the standardized additive variance in fitness ($\frac{\Delta \bar{W}}{\bar{W}} = \frac{h^2 \text{Var}(W)}{\bar{W}^2} = V_W$). By dispersal of expected distance σ away from the optimal habitat, fitness decreases by $\Delta \bar{r}_{x \rightarrow x+\sigma} = B^2 r^{*2}$. The decrement of fitness due to dispersal and mutation ($\Delta \log(\bar{W}) \approx \Delta \bar{r}$) is at equilibrium balanced by its increase via additive variance in fitness, V_W : from Burt's reviews (above) we see that $V_W \leq 0.1$; if we ignore mutation, $\tilde{B} \doteq 0.15/r^*$ and $B \leq 0.3/r^*$.

How fast might optima change through time? In reality, change may occur over all timescales, rather than as a simple linear change as assumed here. However, fast changes will average out, and slow changes will have negligible effect: we are concerned with changes that occur over the joint evolutionary and ecological timescales. The load from a perfectly adapted population, due to changing optimum over characteristic time $1/r^*$, is $\frac{k^2}{2r^{*2}V_S} = \frac{k^{*2}r^*}{2}$. We can get an estimate of a load due to temporally changing environment from the speed of advance of the range due to temporal change in the environment. This speed (in terms of dispersal ranges, as $c^* = \frac{c}{\sigma} \sqrt{\frac{2}{r^*}}$), at which a point population density moves in space, is around $c^* \approx \frac{k^*}{B}$ when $\beta^* \rightarrow B$ or $A \ll 2B^2$. We give an example of one well studied, fast advancing, species. The butterfly *Hesperia comma* is advancing at a rate about $c \doteq 0.63\text{km}$ per generation due to rising temperature (Thomas et al. 2001), while its expected dispersal distance is about $\sigma \doteq 0.1\text{km}$ (as measured by Hill et al. (1996) for the first nine generations). Approximately, the load due to temporally changing optimum is around $\frac{k^{*2}r^*}{2} \approx (\frac{c}{\sigma})^2 B^{*2}$ at equilibrium; using the medians for B and r^* we get an upper estimate of k^* at about 2.7 (σ

738 is necessarily going to be an underestimate to some extent as migrants long distance away
will not be measured and because dispersal may increase during expansion).

740

Finally, the characteristic time is given by the inverse of the strength of density depen-
742 dence $1/r^*$, where r^* is the rate of return towards the equilibrium at carrying capacity, \hat{n}_m :
 $r^* = -\frac{d}{dn} \frac{dn}{dt} |_{n=\hat{n}_m} = -n \frac{d\bar{r}}{dn} |_{n=\hat{n}_m}$ Kirkpatrick and Barton (1997). Lande et al. (2002) and
744 Sæther et al. (2005) study this measure in detail, and give estimates both relative to a year,
 γ_d , and as change per generation, $D \equiv \Delta t \gamma_d$ (where Δt is generation time). Their growth
746 rate per generation is $\lambda^{\Delta t}$, therefore after t generations, population density is $n[t] = n_0 \lambda^{\Delta t t}$.
Throughout this paper, the time is thought in generations: with simple regulation (and ignor-
748 ing mutation) we have $n[t] = n_0 e^{\bar{r}t}$. Between the continuous and discrete time, $\bar{r} \sim \log(\lambda^{\Delta t})$,
and the measures of r^* and D are approximately equivalent. From Sæther et al. (2005), we
750 see that values of D lie mostly between 0 and 2.5: roughly, median for r^* is around 1. (We
included another estimate from Krüger et al. (2002), where continuous-time approximation
752 to their discrete-time autoregressive model directly gives the estimate for r^* for the logarith-
mic model, with mean strength of density-dependence $\bar{r}^* = -\overline{(1 + \beta_1)} \doteq 1$.) Also, for logistic
754 growth, the intrinsic growth rate \bar{r} gives the upper bound for r^* : Grosholz's (1996) study
provides \bar{r} for some invasive species: the range of $\bar{r} = 10^{-1}$ to 10, with median of $\bar{r} \leq r^*$ again
756 around 1 (see also Case and Taper 2000). The importance of strength of density dependence
for limits to species range, and behaviour at the margins is discussed in a recent paper by
758 Filin et al. (2008).

760 The above overview gives estimates for the standing genetic load per trait around $A\tilde{r}^*/2 \doteq$
0.005 (generally smaller than 0.7), the total dispersal load around $B^2\tilde{r}^{*2} \doteq 0.02$ (generally
762 smaller than 0.1) and the strength of density dependence $\tilde{r}^* \doteq 1$, mostly smaller than 2.5.
From the anecdotic butterfly example we see that some populations can adapt to a large
764 selection due to temporally changing optimum, obtaining the upper indirect estimate of the
load due to the temporal change $k^{*2}r^*/2 \doteq 3.6$. Ideally, we would like to get all three loads,
766 and the growth rate r^* estimated for one species, as they may well be correlated. We have
not find such data, and the above paragraphs are intended to give some idea about the range,
768 possible ways of estimating and illustrate the meaning of the load parameters.

770 **Predictions & nature**

772 There are many studies of and of adaptation to temporally changing environment (see
Etterson and Shaw 2001; Thomas et al. 2001; Warren et al. 2001; Parmesan and Yohe 2003),
774 and of increase of genetic differentiation in quantitative traits in a continuous population,
both due to sharply changing environments (Antonovics and Bradshaw 1970; Wilding et al.
776 2001) and variation on large scales (particularly Q_{ST} vs. F_{ST} studies: Prout and Barker
1989 and 1993; Spitze (1993); review by McKay and Latta 2002; Lynch et al. 1999; Whitlock
778 2008). Still, we did not find a study which would allow for a quantitative test of any of
your predictions on limits to a species' range as a function of our load parameters A, B^2 and
780 k^{*2} . However, a recent study by Bridle et al. (*in prep.*) of *Drosophila birchii* compared two
populations living on environmental gradients of different steepness in terms of distribution
782 of population density and adaptation in trait mean, assessing as well the genetic variance.
Consistent with predictions, population density was concave across space for the steeper gra-
784 dient, and uniform for the shallower one (see their Fig. 2); genetic variance did not differ
significantly. Currently, however, we still need more detailed studies to gain better under-
786 standing of robustness of the model predictions for experimental and natural populations.

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Appendix: Stability

Simple regulation

With simple regulation, we only need to follow the evolution of the trait mean, \bar{Z} (Eq. 10). We introduce a perturbation to the equilibrium solution for trait mean, obtaining $\bar{Z}_\epsilon = \beta^* X - q^* T + a^* + \epsilon[X, T]$. Equilibrium with uniform adaptation has $\beta^* = B$, $a^* = \frac{k^*}{A}$, $q^* = k^*$ and substituting \bar{Z}_ϵ into Eq. 10 leads:

$$\frac{\partial \epsilon}{\partial T} = \frac{\partial^2 \epsilon}{\partial X^2} - A\epsilon + O(\epsilon^2)$$

We can immediately see that perfect adaptation is locally stable, as perturbation always decreases over time - without migration, at a rate $\lambda = -A$.

Perturbation around "imperfect" adaptation, where $\beta^* = \frac{B}{2}(1 \pm \sqrt{1 - \frac{2A}{B^2}})$ and $q^* = 0$ (a^* is arbitrary, set to zero*) grows at a rate :

$$\frac{\partial \epsilon}{\partial T} = \frac{\partial^2 \epsilon}{\partial X^2} + 2X(B - \beta^*)(2\beta^* - B)\frac{\partial \epsilon}{\partial X} + O(\epsilon^2) = \frac{\partial^2 \epsilon}{\partial X^2} + 2X\frac{\partial \epsilon}{\partial X}(A - B\beta_c^*) + O(\epsilon^2)$$

where β_c^* is the complimentary solution for adaptation on limited range (β_+^* for β_-^* and vice versa). As the central position of such population is arbitrary, we can set the central location and the perturbation $\epsilon(0, T)$ to zero there without further loss of generality. For the gradient to change, the perturbation ϵ has to grow away from the origin, so $X\frac{\partial \epsilon}{\partial X}$ would be greater than zero. Such perturbation changes at a rate $2(A - B\beta_c^*)$ - which is always negative for the solution with shallower gradient, $\beta_-^* = \frac{B}{2}(1 - \sqrt{1 - \frac{2A}{B^2}})$, hence this solution is always locally stable. The converse holds for the locally unstable steeper solution. Global stability has been assessed numerically - the unstable solution $\beta_+^* = \frac{B}{2}(1 + \sqrt{1 - \frac{2A}{B^2}})$ acts

as a repeller, and gradient in trait mean evolves towards perfect adaptation if the initial
816 gradient β_0 in trait mean is greater than β_+^* and towards the solution with shallow gradient
if β_0 is smaller than β_+^* . The gradient in trait mean is independent on the rate the optimum
818 changes in time, k^* , and so is the stability.

820 **Joint regulation: stability for $k = 0$, logarithmic model**

822 Under joint regulation, we follow both evolution of trait mean (Eq. 15) and dynamics of
the population density (Eq. 16). For uniform adaptation, around equilibrium at $k = 0$ we
824 have $\beta^* = B + \epsilon[X, T]$, $N = 1 + \nu[X, T]$. Linearizing gives

$$\frac{\partial \epsilon}{\partial T} = \frac{\partial^2 \epsilon}{\partial X^2} + 2B \frac{\partial \nu}{\partial X} - A\epsilon + O(\nu^2) + O(\epsilon\nu)$$

and

$$\frac{\partial \nu}{\partial T} = \frac{\partial^2 \nu}{\partial X^2} - \nu - \frac{1}{2}\epsilon^2 + O(\nu^2)$$

826 Hence without migration, the perturbation changes at a rate $\lambda_1 = -A$ and $\lambda_2 = -1$.
(The effect of the term $2B \frac{\partial \nu}{\partial X}$ on the rate of growth of the perturbation is of order $O(\epsilon^2)$
828 (from $\frac{\partial \nu}{\partial T}$) and hence can be omitted as for any $A \neq 1$, $|\lambda_1| \neq |\lambda_2| \neq 0$. The fixed point is
a stable node unless A is exactly 1 - the solution with perfect adaptation is always locally
830 stable on the infinite range.

832 For adaptation on limited range, around equilibrium we have (for $k^* = 0$) $\beta^* = B\phi +$
 $\epsilon[X, T]$, $N = e^{-\zeta^* - X^2 \frac{\zeta^*}{2}} + \nu[X, T]$. Linearizing gives

$$\frac{\partial \epsilon}{\partial T} = \frac{\partial^2 \epsilon}{\partial X^2} - \frac{\partial \epsilon}{\partial X} X \frac{\zeta^*}{2} + 2B\phi \left(\frac{\partial \nu}{\partial X} + \nu X \zeta^* e^{\zeta^* + X^2 \frac{\zeta^*}{2}} \right) - A\epsilon + O(\nu^2) + O(\epsilon\nu)$$

834 and

$$\frac{\partial \nu}{\partial T} = \frac{\partial^2 \nu}{\partial X^2} - \nu(1 - \zeta^* + X^2 \frac{\zeta^*}{2}) - \epsilon X B(1 - \phi) + O(\epsilon^2) + O(\nu^2)$$

836 Under joint regulation, obtaining eigenvalues for nonuniform solution appears intractable
even for $k^* = 0$, so we assess the stability using discrete lattice with stepping stone migra-
838 tion. Also, we know that the stability of the equilibrium is sensitive to behaviour on the

boundaries, which is easier to address in a stepping stone model.

840

Appendix: Scaling for the population genetic model

842

To scale the two-allele model, we define $A_m \equiv \frac{v_{max}}{r^*V_S}$, where $v_{max} = \frac{1}{2}\alpha^2n_l$. The equation
844 Eq. 20 then becomes:

$$\frac{\partial p_i}{\partial T} = \frac{\partial^2 p_i}{\partial X^2} + 2 \frac{\partial \log(n)}{\partial X} \frac{\partial p_i}{\partial X} + \frac{A_m}{n_l} p_i q_i (p_i - q_i - 2\delta^*) - \frac{\gamma_m}{2n_l} (p_i - q_i) \quad (22)$$

where $\delta^* = (\bar{Z} - BX) \sqrt{\frac{n_l}{2A_m}}$, $\bar{Z} = \frac{\bar{z}}{\sqrt{r^*V_S}} = \sqrt{\frac{2A_m}{n_l}} \sum_{i=1}^{n_l} p_i - q_i$ and scaled genetic vari-
846 ance is $V = \frac{V_A}{r^*V_S} = \frac{4A_m}{n_l} \sum_{i=1}^{n_l} p_i q_i$. Hence the scaled average effect of gene substitution is
 $\alpha_* = \sqrt{\frac{2A_m}{n_l}}$. The last term is mutation rate scaled by the intensity of density dependent
848 selection, r^* : $\gamma_m \equiv \frac{U}{r^*}$, where $U = 2n_l\mu$ is the genomic mutation rate. (The scaling is
the same as in Barton (2001) apart from that here V is not scaled directly relative to the
850 maximum variance possible and hence is consistent with \bar{Z} and maintains the same scale as
the parameter describing decrease of population density due to genetic variance, A .) When
852 solution is uniform, the second term vanishes - iterating the two-allele model, we drop the
term $2 \frac{\partial \log(n)}{\partial X} \frac{\partial p}{\partial X}$.

854

We follow the population density in the original units, attempting to match the continuous
856 equation $\frac{\partial n}{\partial T} = \frac{\partial^2 n}{\partial X^2} + \bar{R}n$ - with a stepping-stone model. After selection, the population
density is

$$n_w[X, T + \delta T] = n[X, T](1 + \delta T \bar{R}), \quad (23)$$

858 where the growth rate is either logarithmic,

$$\bar{R} = r_0 - (\log(n/K) - \frac{(\bar{Z} - BX + k^*T)^2}{2} - \frac{V}{2h^2}) \quad (24)$$

or logistic,

$$\bar{R} = \frac{r_m}{r^*} (1 - n/K) - (\frac{(\bar{Z} - BX + k^*T)^2}{2} - \frac{V}{2h^2}) \quad (25)$$

860 Migration is after selection (to keep the rate of change consistent with the continuous model,
 $T + \delta T \rightarrow T$),

$$n[X, T + \delta T] = n_w[X, T] + \frac{m}{2} (n_w[X + \delta X, T] + n_w[X - \delta X, T] - 2n_w[X, T]) \quad (26)$$

862 The carrying capacity is set to $K = 1$ and heritability $h^2 = 1$; for logarithmic model,
 $r_0 \equiv \frac{r_0}{r^*} = 0$, for logistic model $\frac{r_m}{r^*} = 1$.

864

After selection, the allele frequencies are

$$p_{i,w}[X, T + \delta T] = p_i[X, T] + \frac{\delta T}{n_l} (p_i[X, T] q_i[X, T] (p_i[X, T] - q_i[X, T] - 2\delta^*) - \frac{\gamma m}{2} (p_i[X, T] - q_i[X, T])) \quad (27)$$

866 and after migration,

$$p_i[X, T + \delta T] = p_{i,w}[X, T] + \frac{m}{2} (p_{i,w}[X + \delta X, T] + p_{i,w}[X - \delta X, T] - 2p_{i,w}[X, T]) \quad (28)$$

We use a stepping stone model on a spatial lattice with spacing δX and time step δT ,
 868 where the migration rate $m \leq 1/2$ is scaled according to the spacing, $m = \frac{2\delta T}{\delta X^2}$. (In relation
 to the continuous model, variance in dispersal is approximately $\sigma^2 \approx m\delta X^2$ and in the scaled
 870 continuous model, $\frac{\sigma^2}{2} = \delta T$.)

Throughout the MS, Mathematica (Wolfram Research) was used to manipulate some for-
 872 mulae and to obtain numerical solutions.

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Figures

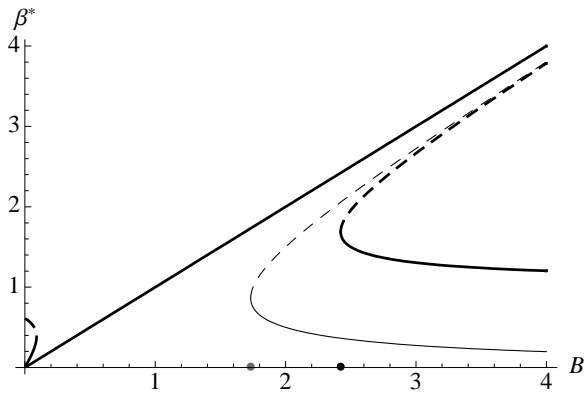


Figure 1: The chart illustrates the equilibrium values of scaled gradient in trait mean, β^* , for logarithmic growth rate (thick lines) and simple regulation (thin lines). The solution with $\beta^* = B$ always exists and the solution when the gradient in trait mean is shallower than B exists when the spatial gradient is steeper than the critical gradient B_c (dots, Fig 2). Thick line shows the solution for joint regulation with logarithmic density-dependence, $2B^2\phi^2(1 - \phi) = A^2(1 - \phi) + A\phi$, $\beta^* = B\phi$. The equilibrium value for imperfect adaptation under joint regulation tends to the one with simple regulation as $A \rightarrow 0$. When population density is just given by mean fitness, as under simple regulation, the gradient in trait mean for limited adaptation is $\beta^* = \frac{B}{2}(1 \pm \sqrt{1 - \frac{2A}{B^2}})$. Equilibrium gradients in trait mean which are always unstable are shown in a dashed line. The dots illustrate the critical gradient B_c (see Fig 2).

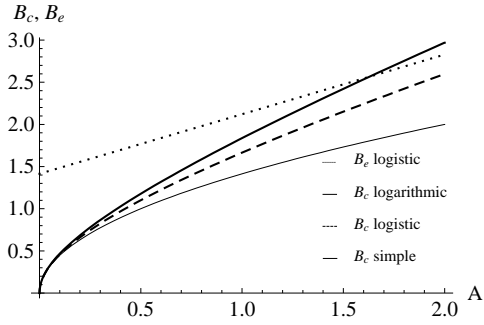


Figure 2: A solution on a limited range only exists for steep gradients: thick, dashed and thin lines show the critical gradient, B_c , for logarithmic, logistic and simple regulation. A critical gradient for simple regulation, $B_c = \sqrt{2A}$ (solid line), is also the approximation for the joint regulation for A small. The exact formula for logarithmic model is $B_c = \frac{1}{4}\sqrt{20A + (1 + 8A)^{3/2} - 1 + 8A^2}$ and the approximation (using a Gaussian density and $k^* = 0$) for the logistic model gives $B_c \approx \frac{1}{4}\sqrt{20A + 2(1 + 4A)^{3/2} - 2 + 4A^2}$. In the simple and logarithmic models, the critical gradient does not depend on the rate at which optimum changes in time, and the dependence is weak for the logistic model. The dotted line is the estimated extinction gradient for logistic growth rate and imperfect adaptation, $B_e = \frac{2+A}{\sqrt{2}}$; hence the area between the dotted and dashed line delimitates the region where solution with limited range exists for the logistic model. In the logarithmic model, density $N \rightarrow 0$ as $B \rightarrow \infty$, so extinction gradient depends on the (arbitrary) choice of density, N_{tr} , which would be deemed as subcritical. Extinction gradients are discussed in the text and Fig. 6. (Note that the solid lines for B_c in the figure are the same as in Barton (2001), but the dashed line for the logistic model differs, because here we do not assume that B is large when estimating B_c .)

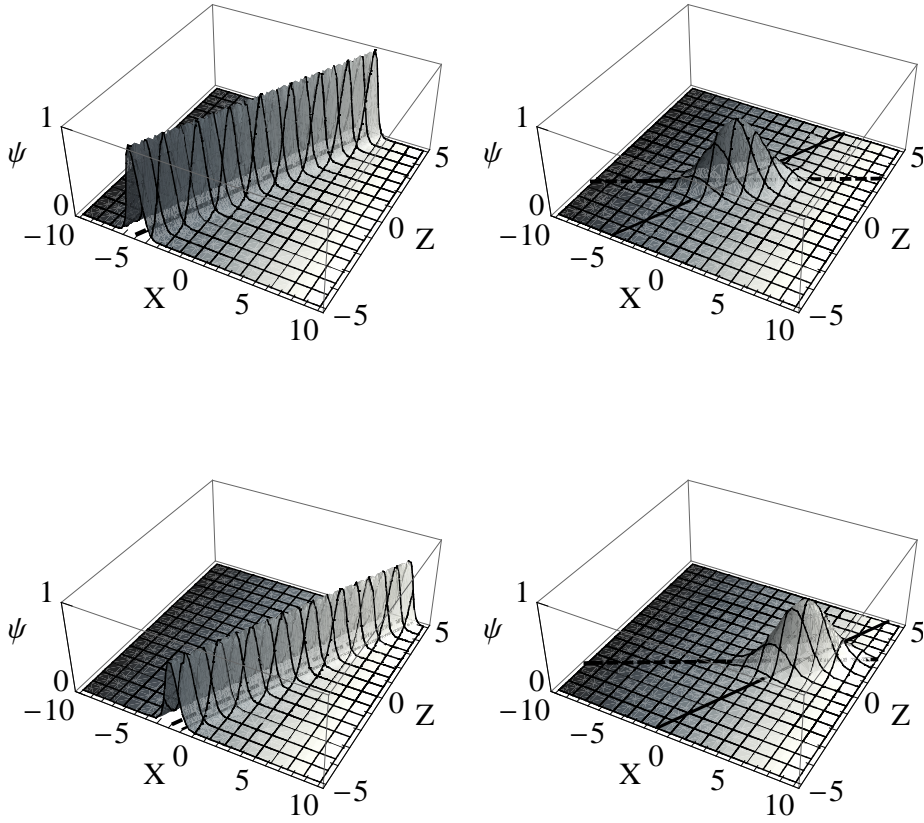


Figure 3: The graphical representation of numerical solutions for distribution of phenotypic density for logarithmic model with spatially and temporally varying environment: left: uniform adaptation, right: limited range. Upper row shows the equilibrium density when optimum is stable in time ($k^* = 0$), lower row the density when optimum is changing at speed $k^* = 0.2$ at time $T = 20$. Environmental optimum is shown by the solid line; dashed line depicts the trait mean. Notice the decrease of density for uniform adaptation, where the lag behind the optimum is about $a^* = 1$. Other parameters in the illustration are kept the same: $A = 1/4, B = 1$.

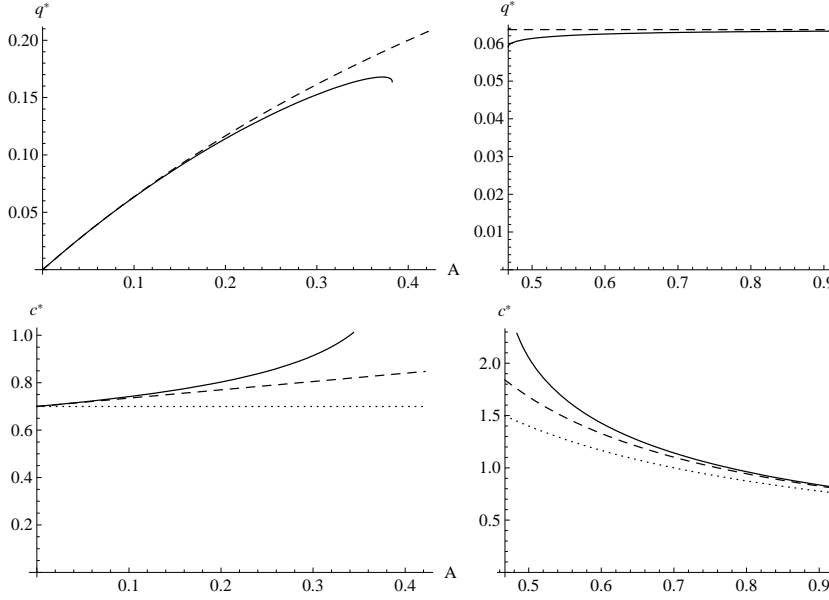


Figure 4: The charts show the scaled rate of adaptation, q^* , and the speed of traveling wave, c^* , for the solution with limited range, $\beta^* < B$ - solid line is the exact solution for logarithmic growth rate, dashed line an approximation. The scaled rate of adaptation is approximately $q^* \approx \frac{k^*A}{1+A}$. The scaled lag of trait mean behind the optimum at equilibrium is $a^* = \frac{q^*}{A}$; hence $a^* \approx \frac{k^*}{1+A}$ (not shown). With uniform adaptation, trait mean tracks the optimum matching its rates of change both space $\beta^* = B$ and time $q^* = k^* = 0.7$, and the scaled lag is $a^* = \frac{k^*}{A}$ (not shown). The scaled rate at which the point (e.g., center of) population density moves in space is $c^* \approx \frac{k^*}{B}(1 + \frac{A}{2B^2})$. Dotted line depicts the solution for uniform adaptation, where any point moves at speed $c^* = \frac{k^*}{B}$. For the first column, $B = 1$; for the second, $A = 0.1$.

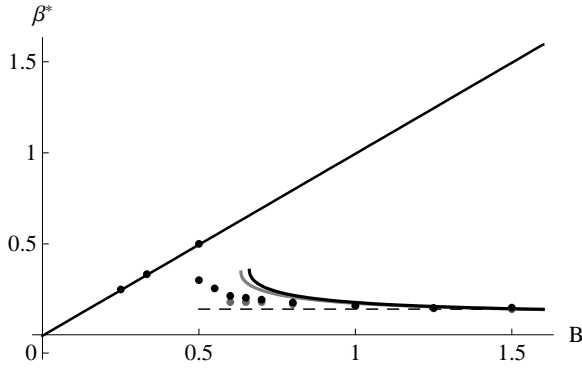


Figure 5: As optimum moves in time, equilibrium gradients in trait mean, β^* , stays close to the static value - if population can persist. In a static environment (black), the solution with $\beta^* = B$ always exists and the solution when the gradient in trait mean, β^* is shallower than B exists when the spatial gradient B is steeper than the critical gradient B_c (see Figs. 1 and 2). Numerical solutions for scaled rate of temporal change $k^* = 0.5$ are shown with grey dots - we have $A = 1/5$, hence uniformly adapted population cannot persist ($k^* > k_e^* \approx \sqrt{2}A$). When gradient is too steep, $B > \frac{A+2}{\sqrt{2}}$, the density drops to zero. Dashed line depicts the prediction for steep gradients: $\beta^* = \frac{A}{\sqrt{2}}$. Parameters: $A = 1/5$, $k^* = 0$ (black), $k^* = 0.5$ (grey). The numerical solutions run on spatial lattice with spacing $\delta X = 1/16$ and time step is $\delta T = \frac{\delta X^2}{4}$ (so that consistently with the scaled model, migration is $m = \frac{2\delta T}{\delta X^2} = 1/2$), and there is no migration over the margins (reflective boundary conditions).

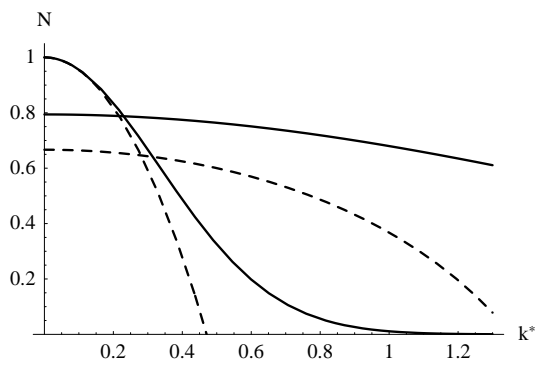


Figure 6: Population density for the uniform population (where $\beta^* = B$) decreases fast as the optimum moves: $N = e^{-\frac{k^{*2}}{A^2}}$ for the logarithmic model (solid) and $(N = 1 - \frac{k^{*2}}{A^2})$ for the logistic model (dashed). Local population density becomes higher for population adapted on a limited range (where $\beta^* < B$) as the population density can slide along the environmental gradient - upper (for $k^* > 0.4$) solid line shows the density for logarithmic model, upper dashed line for logistic model. The rate of change of the optimum when local population density is higher for the population living on a limited range increases with A (not shown). Parameters $A = 1/3$, $B = 1$.

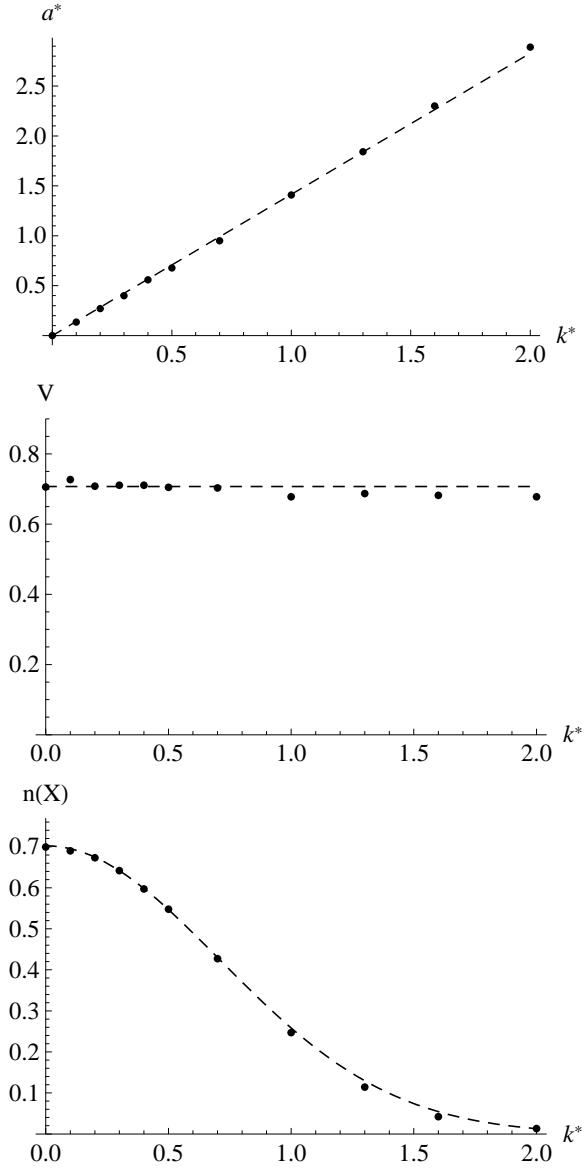


Figure 7: The simulations (dots) and predictions (lines) for the 2-allele model with logarithmic regulation match well. Top: The lag of the trait mean behind the optimum matches the analytical solution shown by the dashed line $a^* = \frac{k^*}{V}$, where $V = B\sqrt{2}$ - in the original units, $a = \frac{kV_S}{V_A}$. Middle: Genetic variance stays close to prediction for a fixed gradient, $V = B\sqrt{2}$ (rescaling back to the original units, $V_A = \sigma b\sqrt{V_S}$). Bottom: Population density at equilibrium is $n = Ke^{r_0 - \frac{1}{2}(\frac{A}{h^2} + \frac{k^{*2}}{A^2})}$. The dots show results of a stepping stone model on a spatial lattice with range $\langle -X_m, X_m \rangle$ and spacing δX . In the scaled model, the time step must be $\delta T = \sigma^2/2 = m\delta X^2/2$, where $m \leq 1/2$ is the migration rate. Parameters: $B = 1/2$, number of loci $n_l = 20$, $\delta X = 1/2$, $m = 1/2$, $X_m = 50$. The maximum scaled variance is taken at $A_m = \frac{B^2 X_m^2}{n_l}$; and as we display the density $n(x)$ in the original units, further parameters are $K = 1$, $r_0 = 0$, $h^2 = 1$. Cline shapes and more details of the equilibrium solution are shown in the appendix (Fig. 9 and 8).

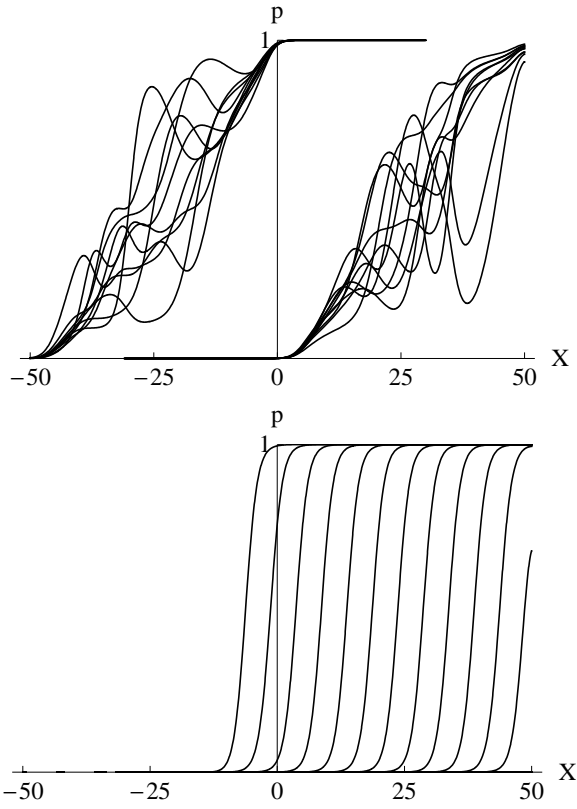


Figure 8: Illustration of the shape of allele frequencies at time $T = 5$ (top) and $T = 70$ (bottom). At equilibrium, the cline shape is $\hat{p}[X] = 1/(1 + e^{-\frac{4}{W}(X+c^*T)})$, where the scaled cline width is $W = 4\sqrt{\frac{n_l}{A_m}}$, and the clines move across the space X at a speed $c^* = k^*/B$. The allelic effect is scaled as $\alpha = \alpha^* = \frac{BX_m}{n_l}$ and the maximum scaled variance is $A_m = \frac{1}{2} \frac{\alpha^2 n_l}{r^* V_S}$. Fixing α^* and A_m , and taking higher number of loci than can fix in the static case, $n_l > BX_m/\alpha^*$, does not lead to a higher number of diversified loci (and hence higher variance). Parameters as in Fig. 7, $k^* = 0.3$.

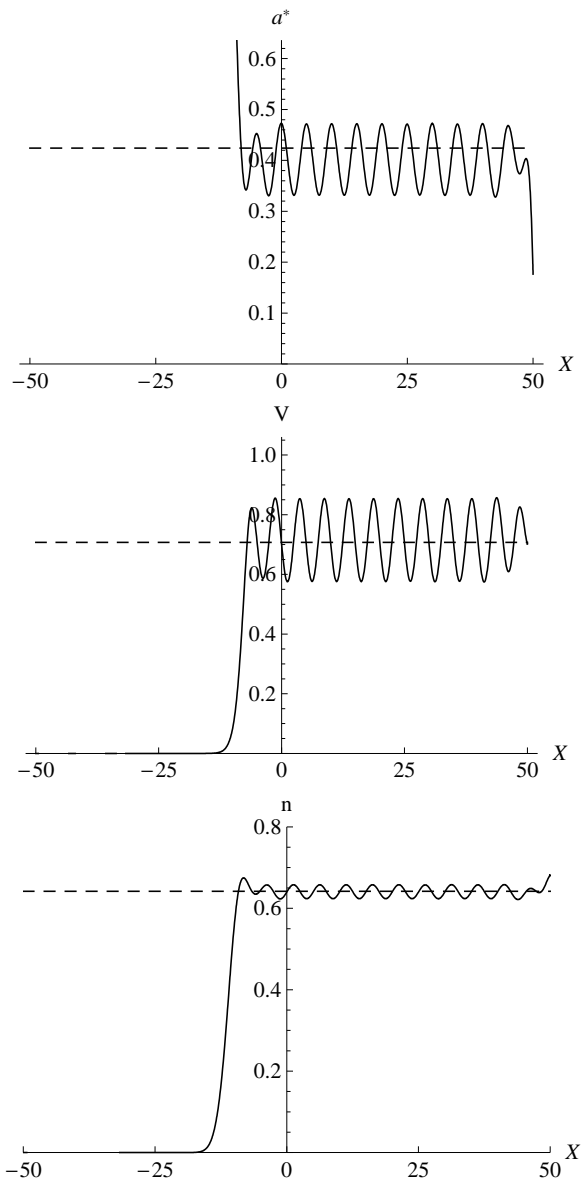


Figure 9: Scaled lag of the trait mean behind the optimum, a^* , scaled variance V and the population density $n(X)$ vary periodically as the optimum is matched by a finite number of alleles. Parameters as in Fig. 7, $k^* = 0.3$, $T = 70$.