An evolutionary tipping point in a changing environment

Preliminaries

For uniformity among figures

```
LabelSize = 16; (*size of axis label text*)
FigureSize = 400; (*size of figure*)
TickSize = 12; (*size of tick text*)
Pad = {{50, 10}, {40, 10}}; (*whitespace to leave around figures,
{{left,right},{bottom,top}}*)
letpos = {0.93, .93}; (*relative location of letter, eg A, in figure*)
ylabpos = {-0.125, 0.5}; (*relative location of y axis label position*)
LetterSize = 20; (*size of text in stability plots*)
```

Directories

```
SetDirectory[NotebookDirectory[]];
(*set current directory to be location of this file*)
imagedir = "../IMAGES/";(*directory to save figures in*)
simdir = "../../SIMULATIONS/"; (*directory with simulation results*)
```

Get package for plotting means with error bars

```
Needs["ErrorBarPlots`"]
```

Continuous time

Traditional fitness function (Lynch & Lande 1993)

Analytical treatment

Per capita growth rate (fitness) is a quadratic function of the difference between trait value, z, and the environmental optimum, θ, with stabilizing selection strength inversely related to σw

```
rTrad[z_] := rm - (z - θ)^2 / (2 σw^2)
```

Probability distribution of trait values in the population is normal with mean barg and variance σz^2

```
p[z_] := PDF[NormalDistribution[barg, σz], z]
```

Population mean fitness is then

```
barrTrad =
 Collect[Integrate[rTrad[z] p[z], {z, -∞, ∞}, Assumptions → {σz > 0, σw > 0}], rm]
```

$$rm - \frac{(barg - \theta)^2 + \sigma z^2}{2\ \sigma w^2}$$

The deterministic rate of change in the mean trait value (rate of evolution) is

```
dbargdtTrad = σg^2 D[barrTrad, barg]
```

$$-\frac{(barg - \theta)\ \sigma g^2}{\sigma w^2}$$

With uncertainty in the optimum (stochastic environment) and genetic drift, the rate of evolution is

```
dbargdtTrad + ϵg /. θ → k t + ϵθ
```

$$\epsilon g - \frac{(barg - k\ t - \epsilon\theta)\ \sigma g^2}{\sigma w^2}$$

The expected rate of change given barg and normally distributed genetic drift and noise in the optimum is

```
EdbargdtTrad = Simplify[Integrate[(dbargdtTrad + ϵg /. θ → k t + ϵθ)
     PDF[NormalDistribution[0, σθ], ϵθ] PDF[NormalDistribution[0, σdrift], ϵg],
    {ϵθ, -∞, ∞}, {ϵg, -∞, ∞}], {σθ > 0, σdrift > 0}]
```

$$-\frac{(barg - k\ t)\ \sigma g^2}{\sigma w^2}$$

The expected squared change is

```
Edbargdt2Trad = Simplify[Integrate[(dbargdtTrad + ϵg /. θ → k t + ϵθ)^2
     PDF[NormalDistribution[0, σθ], ϵθ] PDF[NormalDistribution[0, σdrift], ϵg],
    {ϵθ, -∞, ∞}, {ϵg, -∞, ∞}], {σθ > 0, σdrift > 0}]
```

$$\frac{barg^2\ \sigma g^4 - 2\ barg\ k\ t\ \sigma g^4 + k^2\ t^2\ \sigma g^4 + \sigma drift^2\ \sigma w^4 + \sigma g^4\ \sigma\theta^2}{\sigma w^4}$$

And thus the variance in the rate of change is

```
Edbargdt2Trad - EdbargdtTrad^2 // Simplify
```

$$\sigma drift^2 + \frac{\sigma g^4\ \sigma\theta^2}{\sigma w^4}$$

As described in Lande 1976 (in discrete time), with weak selection, the variance due to genetic drift (sampling of Ne parents with σg^2 variance after selection) is σg^2/Ne, so we can write

```
VdbargdtTrad = Simplify[Edbargdt2Trad - EdbargdtTrad^2] /. σdrift^2 → σg^2 / Ne
```

$$\frac{\sigma g^2}{Ne} + \frac{\sigma g^4\ \sigma\theta^2}{\sigma w^4}$$

Note that the expected change in the lag x = k t - barg can be written

$$\frac{\sigma g^2}{\sigma w^2}\left(\frac{\sigma w^2}{\sigma g^2}\ (\text{k - EdbargdtTrad})\ \text{/. barg - k t} \to \text{- x // Simplify}\right)$$

$$\frac{\sigma g^2\left(-x+\frac{k\,\sigma w^2}{\sigma g^2}\right)}{\sigma w^2}$$

while the variance remains constant ($\frac{\sigma g^2}{Ne}+\frac{\sigma g^4\,\sigma\theta^2}{\sigma w^4}$ is independent of t and x). We thus have an Orstein-Uhlenbeck process with mean $\mu = \frac{k\,\sigma w^2}{\sigma g^2}$, variance $\sigma^2 = \frac{\sigma g^2}{Ne}+\frac{\sigma g^4\,\sigma\theta^2}{\sigma w^4}$, and constant $\theta = \frac{\sigma g^2}{\sigma w^2}$). Thus the probability distribution of x at time t is normal with mean

$$\text{meanxt} = \mu + (\text{x0 - x})\ \text{Exp}[-\theta\ t]\ \text{/.}\ \mu \to \frac{k\,\sigma w^2}{\sigma g^2}\ \text{/. x} \to \text{k t - barg /. x0} \to \text{0 - barg0}$$

$$e^{-t\,\theta}\,(\text{barg} - \text{barg0} - k\,t) + \frac{k\,\sigma w^2}{\sigma g^2}$$

and variance

```
vbargt =
 VdbargdtTrad / (2 θ) (1 - Exp[-2 θ t]) /. θ → (EdbargdtTrad / (k t - barg)) // Simplify
```

$$-\frac{\left(-1+e^{-\frac{2\,t\,\sigma g^2}{\sigma w^2}}\right)\left(\sigma w^4 + Ne\,\sigma g^2\,\sigma\theta^2\right)}{2\,Ne\,\sigma w^2}$$

So at equilbrium the distribution of barg is normal with mean

$$\text{k t - meanxt /. } e^{-t\,\theta} \to 0$$

$$k\,t - \frac{k\,\sigma w^2}{\sigma g^2}$$

and variance

$$\text{Collect}\left[\text{vbargt /. } e^{-\frac{2\,t\,\sigma g^2}{\sigma w^2}} \to 0,\ \text{Ne}\right]$$

$$\frac{\sigma w^2}{2\,Ne}+\frac{\sigma g^2\,\sigma\theta^2}{2\,\sigma w^2}$$

The expected long-run population growth rate is then

```
Simplify[
  Integrate[barrTrad PDF[NormalDistribution[k t - k σw^2/σg^2, (σw^2/(2 Ne) + σg^2 σθ^2/(2 σw^2))^(1/2)], barg]
     PDF[NormalDistribution[k t, σθ], θ],
   {barg, -∞, ∞}, {θ, -∞, ∞}], {σθ > 0, σw > 0, Ne > 0, σg > 0}];
ErTrad = Collect[% // Expand, {σθ^2}]
```

$$-\frac{1}{4\,\mathrm{Ne}}+\mathrm{rm}-\frac{k^2\,\sigma w^2}{2\,\sigma g^4}-\frac{\sigma z^2}{2\,\sigma w^2}+\left(-\frac{\sigma g^2}{4\,\sigma w^4}-\frac{1}{2\,\sigma w^2}\right)\sigma\theta^2$$

and the critical rate of environmental change is

```
kcTrad = Solve[0 == ErTrad, k][[2]]
```

$$\left\{k\to\frac{\sigma g^2\sqrt{-\sigma w^4+4\,\mathrm{Ne}\,\mathrm{rm}\,\sigma w^4-2\,\mathrm{Ne}\,\sigma w^2\,\sigma z^2-\mathrm{Ne}\,\sigma g^2\,\sigma\theta^2-2\,\mathrm{Ne}\,\sigma w^2\,\sigma\theta^2}}{\sqrt{2}\,\sqrt{\mathrm{Ne}}\,\sigma w^3}\right\}$$

So with an infinitely large population in a deterministic environment the critical rate is

```
Simplify[Limit[k /. kcTrad, Ne → ∞] /. σθ^2 → 0, σw > 0]
```

$$\frac{\sigma g^2\sqrt{2\,\mathrm{rm}\,\sigma w^2-\sigma z^2}}{\sigma w^2}$$

Alternative fitness function

Analytical treatment

Per capita growth rate (fitness) as a Gaussian function

```
rAlt[z_] := rm - d (1 - Exp[- (z - θ)^2 / (2 σw^2)])
```

This alternative fitness function is equivalent to the traditional fitness function, to second order, when the lag is small and d=0

```
rTrad[z] == Normal[Series[rAlt[z], {z, θ, 2}]] /. d → 1
```

```
True
```

Probability distribution of trait values in the population is normal with mean barg and variance σz^2

```
p[z_] := PDF[NormalDistribution[barg, σz], z]
```

Population mean fitness is then

```
barrAlt =
 Collect[Integrate[rAlt[z] p[z], {z, -∞, ∞}, Assumptions → {σz > 0, σw > 0}], rm]
```

$$\mathrm{rm}+d\left(-1+\frac{e^{-\frac{(\mathrm{barg}-\theta)^2}{2\,(\sigma w^2+\sigma z^2)}}\,\sigma w}{\sqrt{\sigma w^2+\sigma z^2}}\right)$$

This has a maximum of (and approximation under weak selection)

```
barrAlt /. barg → θ
Simplify[Normal[Series[% /. σw → σw / ϵ^(1/2), {ϵ, 0, 0}]], σw > 0]
```

$$\mathrm{rm} + \mathrm{d}\left(-1 + \frac{\sigma w}{\sqrt{\sigma w^2 + \sigma z^2}}\right)$$

rm

and a minimum of

```
Limit[barrAlt /. barg → θ - L, L → ∞, Assumptions → {σw > 0, σz > 0}]
```

$$-\mathrm{d} + \mathrm{rm}$$

The deterministic rate of change in the trait value (rate of evolution) is

```
dbargdtAlt = σg^2 D[barrAlt, barg]
```

$$-\frac{\mathrm{d}\, e^{-\frac{(\mathrm{barg}-\theta)^2}{2(\sigma w^2+\sigma z^2)}} (\mathrm{barg}-\theta)\, \sigma g^2\, \sigma w}{\left(\sigma w^2 + \sigma z^2\right)^{3/2}}$$

With uncertainty in the optimum (stochastic environment) and genetic drift the rate of evolution is

```
dbargdtAlt + ϵg /. θ → k t + ϵθ
```

$$\epsilon g - \frac{\mathrm{d}\, e^{-\frac{(\mathrm{barg}-k\,t-\epsilon\theta)^2}{2(\sigma w^2+\sigma z^2)}} (\mathrm{barg}-k\,t-\epsilon\theta)\, \sigma g^2\, \sigma w}{\left(\sigma w^2 + \sigma z^2\right)^{3/2}}$$

The expected rate of change given barg and normally distributed genetic drift and noise in the optimum is

```
EdbargdtAlt = Simplify[Integrate[(dbargdtAlt + ϵg /. θ → k t + ϵθ)
    PDF[NormalDistribution[0, σθ], ϵθ] PDF[NormalDistribution[0, σdrift], ϵg],
   {ϵθ, -∞, ∞}, {ϵg, -∞, ∞}], {σθ > 0, σdrift > 0, σw > 0, σz > 0}]
```

$$-\frac{\mathrm{d}\, e^{-\frac{(\mathrm{barg}-k\,t)^2}{2(\sigma w^2+\sigma z^2+\sigma\theta^2)}} (\mathrm{barg}-k\,t)\, \sigma g^2\, \sigma w}{\left(\sigma w^2 + \sigma z^2 + \sigma\theta^2\right)^{3/2}}$$

The expected change is no longer linear in barg and the variance is no longer independent of barg or time, thus we cannot use the Orstein-Uhlenbeck results as we could for the traditional fitness function results. Instead we focus on the expected rate of evolution.

Note that there is a maximum in the expected rate of evolution at lag

```
Solve[0 == D[EdbargdtAlt /. barg - k t → -L, L], L][[2]]
```

$$\left\{L \to \sqrt{\sigma w^2 + \sigma z^2 + \sigma\theta^2}\right\}$$

The maximum rate of evolution is

```
ktip = EdbargdtAlt /. barg - k t → -L /. % /. σw^2 + σz^2 + σθ^2 → V
```

$$\frac{d\,\sigma g^2\,\sigma w}{\sqrt{e}\,V}$$

As long as the rate of environmental change is less than the maximum rate of evolution, the steady-state lag is

```
eqLAlt = Solve[EdbargdtAlt == k /. barg - k t → -L, L][[1]] /. σw^2 + σz^2 + σθ^2 → V
(*%/.σg→1/.σw→1/.rm→1.1/.σz→2/.σθ→1/.k→0.01*)
```

Solve::ifun : Inverse functions are being used by Solve, so
some solutions may not be found; use Reduce for complete solution information. ≫

$$\left\{L \to -i\sqrt{V}\,\sqrt{\text{ProductLog}\left[-\frac{k^2\,V^2}{d^2\,\sigma g^4\,\sigma w^2}\right]}\right\}$$

This is only biologically valid (real) when

```
Reduce[x > 0 && ProductLog[-x] < 0, x, Reals] /. x → k^2 V^2/(d^2 σg^4 σw^2)
```

$$0 < \frac{k^2\,V^2}{d^2\,\sigma g^4\,\sigma w^2} \leq \frac{1}{e}$$

i.e., when the rate of change in the environment is less than the maximum rate of evolution (as stated just above).

The long-run population growth rate, as long as the steady-state lag is valid, is then

```
barreqAlt = barrAlt /. barg - θ → L /. eqLAlt
```

$$rm + d\left(-1 + \frac{e^{\frac{V\,\text{ProductLog}\left[-\frac{k^2\,V^2}{d^2\,\sigma g^4\,\sigma w^2}\right]}{2\,(\sigma w^2+\sigma z^2)}}\,\sigma w}{\sqrt{\sigma w^2 + \sigma z^2}}\right)$$

Because this is a decreasing function of the rate of environmental change over its biologically valid range, the minimum value this can take on is

```
barreqAlt /. k → ktip
```

$$rm + d\left(-1 + \frac{e^{-\frac{V}{2\,(\sigma w^2+\sigma z^2)}}\,\sigma w}{\sqrt{\sigma w^2 + \sigma z^2}}\right)$$

When this minimum is less than zero we know that the population mean growth rate becomes zero before the maximum rate of evolution is reached, and thus there is a critical rate of environmental change. If, however, the population growth rate at the maximum rate of evolution is greater than zero then there is no critical rate of environmental change, as typically defined, and it is the maximum rate of evolution that determines persistence (as long as extinction is possible, rm-d<0). For this latter scenario of no critical rate we therefore need rm<d and

```
Reduce[σw > 0 && σz > 0 && V > 0 && 0 < rm && 0 < d && 0 < barreqAlt /. k → ktip, rm, Reals]
```

$$\sigma w \neq 0 \ \&\& \ d > 0 \ \&\& \ V > 0 \ \&\& \ \sigma w > 0 \ \&\& \ \sigma z > 0 \ \&\& \ rm > d - \sqrt{\frac{d^2\, e^{-\frac{V}{\sigma w^2+\sigma z^2}}\, \sigma w^2}{\sigma w^2 + \sigma z^2}}$$

Or, with weak selection,

```
Reduce[σw > 0 && σz > 0 && V > 0 && 0 < rm < d && 0 < d && 0 < Normal[Series[
      barreqAlt /. k → ktip /. V → σw^2 + σz^2 + σe^2 /. σw → σw / ϵ^(1/2), {ϵ, 0, 0}]], rm, Reals]
% //
 N
```

$$V > 0 \ \&\& \ \sigma z > 0 \ \&\& \ \sigma w > 0 \ \&\& \ d > 0 \ \&\& \ \frac{-d + d\sqrt{e}}{\sqrt{e}} < rm < d$$

$$V > 0. \ \&\& \ \sigma z > 0. \ \&\& \ \sigma w > 0. \ \&\& \ d > 0. \ \&\& \ 0.393469\, d < rm < d$$

When $d <$ rm the population never goes extinct, when $\frac{-d+d\sqrt{e}}{\sqrt{e}} < rm < d$ the maximum rate of evolution determines persistence, and when $rm < \frac{-d+d\sqrt{e}}{\sqrt{e}}$ the critical rate would be

```
Simplify[Solve[0 == barreqAlt, k][[2]], {σθ > 0, σw > 0, σg > 0, σz > 0, rm > 0, d > 0}]
(*%/.σg→1/.σw→1/.rm→0.9/.σz→2/.σθ→0*)
```

Solve::ifun : Inverse functions are being used by Solve, so
some solutions may not be found; use Reduce for complete solution information. ≫

$$\left\{k \to \sqrt{2}\, d\, \sigma g^2\, \sigma w \sqrt{-\frac{\left(\frac{(d-rm)\sqrt{\sigma w^2+\sigma z^2}}{d\,\sigma w}\right)^{\frac{2\left(\sigma w^2+\sigma z^2\right)}{V}} \left(\sigma w^2+\sigma z^2\right) \operatorname{Log}\left[\frac{(d-rm)\sqrt{\sigma w^2+\sigma z^2}}{d\,\sigma w}\right]}{V^3}}\right\}$$

Figure 1 (A-D): steady-state lag and long-run population mean growth rate as functions of the rate of environmental change

```
GrowthLag =
  Legended[
   Show[
    Plot[barrTrad /. rm → Log[B] /. σz^2 → σg^2 + σe^2 /. σg → (4 n μ α^2 Ne / (1 + α^2 Ne / Vs))^(1/2) /. Vs → σw^2 + 1 /.
            Ne → 2 B / (2 B - 1) KK /. KK → 128 /. n → 50 /. μ → 2 * 10^-4 /. α → 0.05^(1/2) /.
          B → 2 /. σe^2 → 1 /. θ → L + barg /. σw → ω /. ω → 3 /. θ → L + barg,
     {L, 0, 4.5}, AxesOrigin → {0, 0}, PlotStyle → {Gray, Thick}],
```

```
Plot[barrAlt /. rm → Log[B] /. σz^2 → σg^2 + σe^2 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → σw^2 + 1 /.
        Ne → (2 B)/(2 B - 1) KK /. KK → 128 /. n → 50 /. μ → 2 * 10^-4 /. α → 0.05^(1/2) /.
      B → 2 /. σe^2 → 1 /. θ → L + barg /. σw → ω /. ω → 3 /. θ → L + barg /.
   d → 1, {L, 0, 10}, Axes → False, PlotStyle → {Black, Thick}],
  (*Plot[0,{L,-10,10},PlotStyle→Black],*)
  PlotRange → {{0, 10}, {-0.5, 0.8}},
  Frame → False,
  PlotRangePadding → None,
  FrameLabel → {Style["", LabelSize], Style["", LabelSize]},
  ImageSize → FigureSize,
  ImagePadding → Pad,
  AxesStyle → Directive[FontSize → TickSize],
  TicksStyle → {{FontColor → White, Black}, {Black, Black}},
  Epilog → {
    Text[Style["A", LabelSize, Bold], Scaled@{0.05, 0.95}],
    Rotate[Text[Style["Population growth rate", LabelSize],
      Scaled@ylabpos], 90 Degree](*,
    Text[Style["Traditional",LabelSize],Scaled@{0.5,1}]*)
   },
  PlotRangeClipping → False
 ],
 Placed[
  LineLegend[{
    Directive[Gray, Thickness[0.2]],
    Directive[Black, Thickness[0.2]]
   },
   {
    Style["Traditional", LabelSize],
    Style["Alternative", LabelSize]
   },
   LegendFunction → "Frame",
   LegendLayout → "Column"(*,
   LegendLabel→"Fitness function"*)
  ],
  Scaled@{0.8, 0.9}
 ]
];

SelectionLag =
 Show[Plot[D[barrTrad, barg] /. σz^2 → σg^2 + σe^2 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → σw^2 + 1 /.
        Ne → (2 B)/(2 B - 1) KK /. KK → 128 /. n → 50 /. μ → 2 * 10^-4 /. α → 0.05^(1/2) /.
      B → 2 /. σe^2 → 1 /. θ → L + barg /. σw → ω /. ω → 3 /. θ → L + barg /. d → 1,
  {L, 0, 4.25}, AxesOrigin → {0, 0}, PlotStyle → {Gray, Thick}],
```

```
Plot[D[barrAlt, barg] /. σz^2 → σg^2 + σe^2 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → σw^2 + 1 /. Ne →
      (2 B)/(2 B - 1) KK /. KK → 128 /. n → 50 /. μ → 2 * 10^-4 /. α → 0.05^(1/2) /. B → 2 /.
    σe^2 → 1 /. θ → L + barg /. σw → ω /. ω → 3 /. θ → L + barg /. d → 1,
  {L, 0, 10}, Axes → False, PlotStyle → {Black, Thick}],
koverV = 0.15;
Plot[koverV, {L, 0, 10}, PlotStyle → {Black, Dashed}],
Graphics[{PointSize[0.03], Gray, Point[{
    L /. Solve[koverV == D[barrTrad, barg] /. σz^2 → σg^2 + σe^2 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /.
          Vs → σw^2 + 1 /. Ne → (2 B)/(2 B - 1) KK /. KK → 128 /. n → 50 /.
        μ → 2 * 10^-4 /. α → 0.05^(1/2) /. B → 2 /. σe^2 → 1 /. θ →
       L + barg /. σw → ω /. ω → 3 /. θ → L + barg /. d → 1, L][[1]],
    koverV
   }]}],
Graphics[{PointSize[0.03], Black, Point[{
    L /. Solve[koverV == D[barrAlt, barg] /. σz^2 → σg^2 + σe^2 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /.
          Vs → σw^2 + 1 /. Ne → (2 B)/(2 B - 1) KK /. KK → 128 /. n → 50 /.
        μ → 2 * 10^-4 /. α → 0.05^(1/2) /. B → 2 /. σe^2 → 1 /. θ →
       L + barg /. σw → ω /. ω → 3 /. θ → L + barg /. d → 1, L][[1]],
    koverV
   }]}],
ListPlot[{{
    L /. Solve[koverV == D[barrAlt, barg] /. σz^2 → σg^2 + σe^2 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /.
          Vs → σw^2 + 1 /. Ne → (2 B)/(2 B - 1) KK /. KK → 128 /. n → 50 /.
        μ → 2 * 10^-4 /. α → 0.05^(1/2) /. B → 2 /. σe^2 → 1 /. θ → L + barg /.
      σw → ω /. ω → 3 /. θ → L + barg /. d → 1, L][[2]],
    koverV
   }},
  PlotMarkers → Graphics[{Black, Thick, Circle[]}, ImageSize → 10]
 ],
```

```
    PlotRange → {{0, 10}, {0, 0.5}},
    Frame → {True, True, False, False},
    PlotRangePadding → None,
    FrameLabel → {Style["Mean phenotypic lag", LabelSize], Style["", LabelSize]},
    ImageSize → FigureSize,
    ImagePadding → Pad,
    FrameStyle → Directive[FontSize → TickSize],
    FrameTicksStyle → {{Black, Black}, {Black, Black}},
    Epilog → {
      Text[Style["B", LabelSize, Bold], Scaled@{0.05, 0.95}],
      Rotate[
       Text[Style["Selection gradient", LabelSize], Scaled@ylabpos], 90 Degree],
      Text[Style["k/σg^2", LabelSize], {9.8, 0.125}]
     },
    PlotRangeClipping → False
   ];
```

Solve::ifun : Inverse functions are being used by Solve, so
some solutions may not be found; use Reduce for complete solution information. ≫

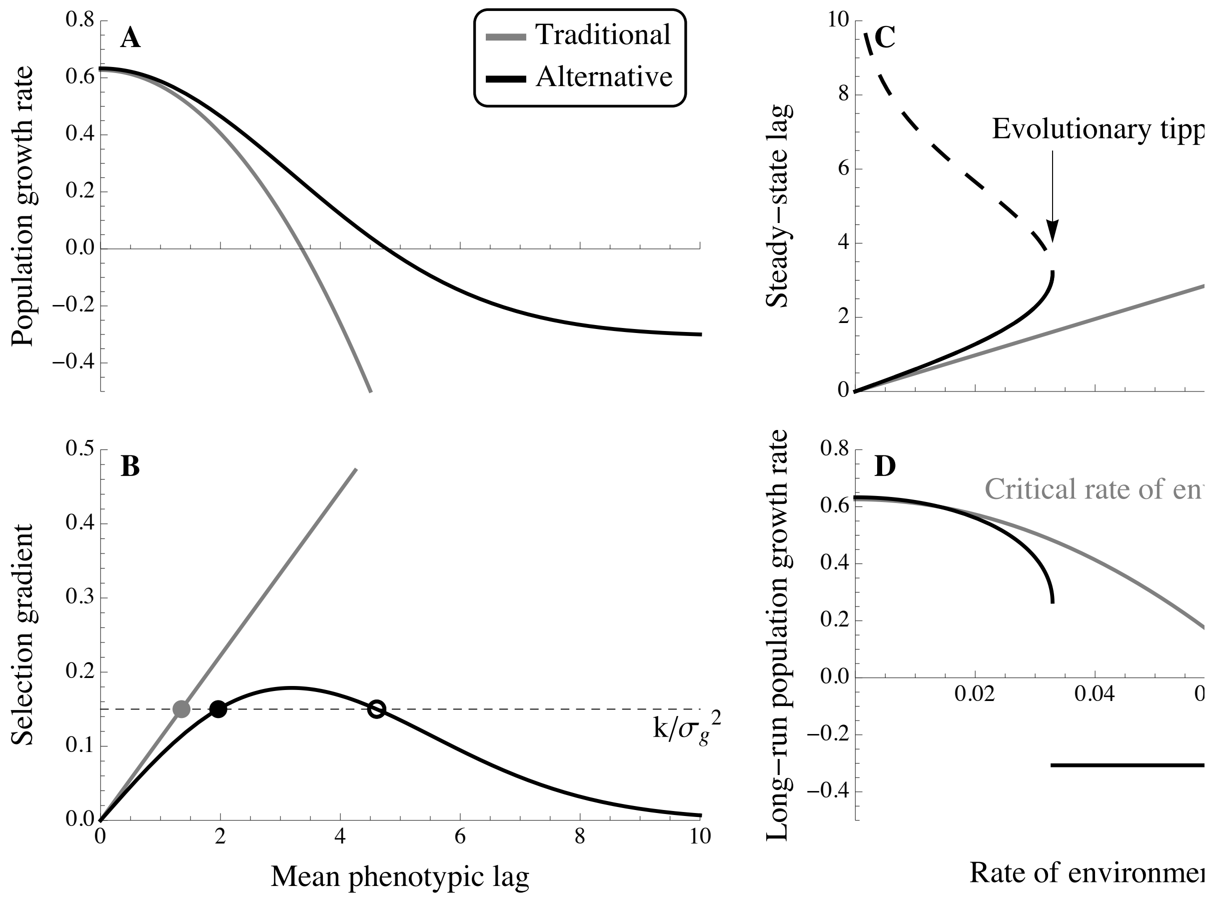
Solve::ifun : Inverse functions are being used by Solve, so
some solutions may not be found; use Reduce for complete solution information. ≫

```
SSLag = Show[
    Plot[(k σw^2)/(σg^2) /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → σw^2 + 1 /. Ne → (2 B)/(2 B - 1) KK /. B → 2 /. σw → 9^(1/2) /.
        KK → 128 /. n → 50 /. μ → 2 * 10^-4 /.
      α → 0.05^(1/2), {k, 0, 0.1}, PlotStyle → {Gray, Thick}],
    Plot[L /. eqLAlt /. V → σw^2 + σz^2 + σθ^2 /. σz^2 → σg^2 + 1 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /.
              Vs → σw^2 + 1 /. Ne → (2 B)/(2 B - 1) KK /. B → 2 /. σw → 9^(1/2) /. KK → 128 /.
         n → 50 /. μ → 2 * 10^-4 /. α → 0.05^(1/2) /. σθ → 0 /. d → 1,
     {k, 0, 0.1}, PlotStyle → {Black, Thick}],
    ParametricPlot[
     {σg^2 D[barrAlt, barg] /. V → σw^2 + σz^2 + σθ^2 /. σz^2 → σg^2 + 1 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /.
               Vs → σw^2 + 1 /. Ne → (2 B)/(2 B - 1) KK /. B → 2 /. σw → 9^(1/2) /. KK → 128 /. n → 50 /.
          μ → 2 * 10^-4 /. α → 0.05^(1/2) /. σθ → 0 /. d → 1 /. θ → barg + L, L},
     {L, 0, 10}, PlotStyle → {Black, Thick, Dashing[Large]}],
```

```
Graphics[Arrow[{{ktip /. V → σw^2 + σz^2 + σθ^2 /. σz^2 → σg^2 + σe^2 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /.
        Vs → σw^2 + 1 /. Ne → (2 B)/(2 B - 1) KK /. KK → 128 /. n → 50 /. μ → 2 * 10^-4 /.
      α → 0.05^(1/2) /. B → 2 /. σe^2 → 1 /. σθ → 0 /. σw → ω /. ω → 3 /. d → 1, 6.5},
   {ktip /. V → σw^2 + σz^2 + σθ^2 /. σz^2 → σg^2 + σe^2 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → σw^2 + 1 /.
        Ne → (2 B)/(2 B - 1) KK /. KK → 128 /. n → 50 /. μ → 2 * 10^-4 /. α → 0.05^(1/2) /.
      B → 2 /. σe^2 → 1 /. σθ → 0 /. σw → ω /. ω → 3 /. d → 1, 4}}]],
  PlotRange → {{0, 0.1}, {0, 10}},
  Frame → {True, True, False, False},
  PlotRangePadding → None,
  FrameLabel → {Style["", LabelSize], Style["", LabelSize]},
  ImageSize → FigureSize,
  ImagePadding → Pad,
  FrameStyle → Directive[FontSize → TickSize],
  FrameTicksStyle → {{Black, Black}, {Directive[FontColor → White], Black}},
  Epilog → {
    Text[Style["C", LabelSize, Bold], Scaled@{0.05, 0.95}],
    Rotate[
     Text[Style["Steady-state lag", LabelSize], Scaled@ylabpos], 90 Degree],
    Text[Style["Evolutionary tipping point", LabelSize], {0.05, 7}]
   },
  PlotRangeClipping → False
 ];

SSgrowth = Show[
  Plot[
   ErTrad /. σz^2 → σg^2 + 1 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → σw^2 + 1 /. Ne → (2 B)/(2 B - 1) KK /. rm →
        Log[B] /. B → 2 /. σθ → 0 /. σw → 9^(1/2) /. KK → 128 /. n → 50 /. μ → 2 * 10^-4 /.
    α → 0.05^(1/2), {k, 0, 0.0925}, PlotStyle → {Gray, Thick}, PlotRange → {-1, 1}],
  Plot[barreqAlt /. V → σw^2 + σz^2 + σθ^2 /. σz^2 → σg^2 + 1 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs →
        σw^2 + 1 /. Ne → (2 B)/(2 B - 1) KK /. rm → Log[B] /. B → 2 /. σθ → 0 /.
      σw → 9^(1/2) /. KK → 128 /. n → 50 /. μ → 2 * 10^-4 /. α → 0.05^(1/2) /. d → 1,
   {k, 0, 0.1}, PlotStyle → {Black, Thick}, PlotRange → {-1, 1}],
```

```
Plot[barrAlt /. rm → Log[B] /. σz^2 → σg^2 + σe^2 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → σw^2 + 1 /.
      Ne → (2 B)/(2 B - 1) KK /. KK → 128 /. n → 50 /. μ → 2 * 10^-4 /. α → 0.05^(1/2) /. B →
    2 /. σe^2 → 1 /. θ → L + barg /. σw → ω /. ω → 3 /. θ → L + barg /. d → 1 /. L → ∞,
  {k, ktip /. V → σw^2 + σz^2 + σθ^2 /. σz^2 → σg^2 + σe^2 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → σw^2 + 1 /.
      Ne → (2 B)/(2 B - 1) KK /. KK → 128 /. n → 50 /. μ → 2 * 10^-4 /. α → 0.05^(1/2) /.
    B → 2 /. σe^2 → 1 /. σθ → 0 /. σw → ω /. ω → 3 /. d → 1, 0.1},
  PlotStyle → {Black, Thick}, PlotRange → {-1, 1}],
Graphics[{Gray, Arrow[
   {{k /. kcTrad /. rm → Log[B] /. V → σw^2 + σz^2 + σθ^2 /. σz^2 → σg^2 + σe^2 /.
         σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → σw^2 + 1 /. Ne → (2 B)/(2 B - 1) KK /. KK →
        128 /. n → 50 /. μ → 2 * 10^-4 /. α → 0.05^(1/2) /. B → 2 /.
      σe^2 → 1 /. σθ → 0 /. σw → ω /. ω → 3 /. d → 1, 0.6},
    {k /. kcTrad /. rm → Log[B] /. V → σw^2 + σz^2 + σθ^2 /. σz^2 → σg^2 + σe^2 /.
         σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → σw^2 + 1 /. Ne → (2 B)/(2 B - 1) KK /.
       KK → 128 /. n → 50 /. μ → 2 * 10^-4 /. α → 0.05^(1/2) /. B → 2 /.
      σe^2 → 1 /. σθ → 0 /. σw → ω /. ω → 3 /. d → 1, 0.05}}]}],
PlotRange → {{0, 0.1}, {-0.5, 0.8}},
Frame → {False, False, False, False},
PlotRangePadding → None,
FrameLabel →
 {Style["Rate of environmental change", LabelSize], Style["", LabelSize]},
ImageSize → FigureSize,
ImagePadding → Pad,
AxesStyle → Directive[FontSize → TickSize],
TicksStyle → {{Black, Black}, {Black, Black}},
Epilog → {
  Text[Style["D", LabelSize, Bold], Scaled@{0.05, 0.95}],
  Rotate[Text[Style["Long-run population growth rate", LabelSize],
    Scaled@ylabpos], 90 Degree],
  Text[Style["Rate of environmental change", LabelSize], Scaled@{0.5, -0.15}],
  Text[Style[
    "Critical rate of environmental change", LabelSize, Gray], {0.06, 0.65}]
 },
PlotRangeClipping → False
].
```

```
GraphicsGrid[{{GrowthLag, SSLag}, {SelectionLag, SSgrowth}}, Spacings → {0, -20}]
Export[imagedir <> "Didactics.pdf", %];
```



Discrete time

Traditional fitness function (Burger & Lynch 1995)

Analytical treatment

Probability of survival (fitness) as a Gaussian function of trait value, z, around optimum θ with standard deviation ω

```
W[z_] := Exp[-(z - θ)^2 / (2 ω^2)]
```

we then have equivalence with the continuous time traditional fitness funciton used above, exp(r(z)) = B W(z), where B is an integer determining the number of offspring per suriviving parent

```
Exp[rm - (z - θ)^2 / (2 σw^2)] == B W[z] /. B → Exp[rm] /. σw → ω // Simplify
True
```

Probability distribution of trait values in the population is normal with mean barg and variance σz^2

```
p[z_] := PDF[NormalDistribution[barg, σz], z]
```

Population mean fitness is then

```
barW = Integrate[W[z] p[z], {z, -∞, ∞}, Assumptions → {σz > 0, ω > 0}]
```

$$\frac{e^{-\frac{(\text{barg}-\theta)^2}{2\,(\sigma z^2+\omega^2)}}\,\omega}{\sqrt{\sigma z^2+\omega^2}}$$

The deterministic rate of change in the mean trait value (rate of evolution) is

```
dbarg = σg^2 D[Log[barW], barg] /. σz^2 → σg^2 + σe^2 /. σe^2 → Vs - ω^2
```

$$-\frac{(\text{barg}-\theta)\,\sigma g^2}{\text{Vs}+\sigma g^2}$$

Let f[barg[t+1] | barg[t]] be the conditional distribution of the mean genetic value in the next generation given the mean genetic value in this generation. Following Lande 1976, given that selection is weak relative to the amount of additive genetic variance, $\omega^2 >> \sigma g^2$, the distribution of genetic values of survivors of viability selection remains normal with mean barg + dbarg and variance σg^2. Taking a random sample of N_e values from this normal distribution (the parents), the conditional distribution of the mean genetic value of offspring in the next generation, given the mean genetic value and optimum in the last generation, is normal with expectation barg + dbarg and variance $\sigma g^2/N_e$. The recursion for the unconditional distribution is then ϕ[barg[t+1]] = $\int$f[barg[t+1] | barg[t]] ϕ[barg[t]] d barg[t]. With weak selection f is normal, and because ϕ[barg[0]] is a dirac (the initial state is given), ϕ is normal and hence completely determined by its mean and variance. Because this is a linear Gaussian process, the dynamics of the mean and variance are easily found.

The conditional distribution of the mean genetic value in the next generation given the current mean genetic value and current optimum is

```
f[bargnext_, barg_] := PDF[NormalDistribution[barg + dbarg, (σg^2 / Ne)^(1/2)], bargnext]
```

The unconditional distribution for the mean genetic value in the current generation (this remains normal) is

```
ϕ[barg_] := PDF[NormalDistribution[μ, σ], barg]
```

Then the unconditional distribution for the mean genetic value in the next generation is

```
phinext = Simplify[
  Integrate[f[bargnext, barg] ϕ[barg], {barg, -∞, ∞}], {σg > 0, Vs > 0, Ne > 0, σ > 0}]
```

$$\frac{e^{-\frac{\text{Ne}\,(\text{Vs}\,\mu+\theta\,\sigma g^2-\text{bargnext}\,(\text{Vs}+\sigma g^2))^2}{2\,(\text{Ne}\,\text{Vs}^2\,\sigma^2+\sigma g^2\,(\text{Vs}+\sigma g^2)^2)}}\,(\text{Vs}+\sigma g^2)\,\sqrt{\frac{\text{Ne}}{\text{Ne}\,\text{Vs}^2\,\sigma^2+\sigma g^2\,(\text{Vs}+\sigma g^2)^2}}}{\sqrt{2\,\pi}}$$

From this one can see that the expected mean genetic value changes from μ to $\mu+\frac{\sigma g^2}{\text{Vs}+\sigma g^2}\,(\theta-\mu)$ and the variance in the mean genetic value changes from σ^2 to $\left(\frac{\text{Vs}}{\text{Vs}+\sigma g^2}\right)^2\sigma^2+\frac{\sigma g^2}{\text{Ne}}$

Check:

$$\texttt{Simplify}\left[\texttt{PDF}\left[\texttt{NormalDistribution}\left[\mu + \frac{\sigma g^2}{\texttt{Vs} + \sigma g^2}\,(\theta - \mu),\ \left(\left(\frac{\texttt{Vs}}{\texttt{Vs} + \sigma g^2}\right)^2 \sigma^2 + \frac{\sigma g^2}{\texttt{Ne}}\right)^{1/2}\right],\ \texttt{bargnext}\right] \Big/ \texttt{phinext},\ \{\texttt{Vs} > 0,\ \sigma g > 0,\ \texttt{Ne} > 0,\ \sigma > 0\}\right]$$

1

We can then solve these recursions to get the mean and variance of the unconditional distribution for the mean genetic value (and thus the whole distribution) at any time t

$$\texttt{meanrec = Collect}\left[\texttt{RSolve}\left[\left\{\mu[\texttt{t}+1] == \mu[\texttt{t}] + \frac{\sigma g^2}{\texttt{Vs} + \sigma g^2}\,(\texttt{k t} - \mu[\texttt{t}]),\ \mu[0] == \mu 0\right\},\ \mu[\texttt{t}],\ \texttt{t}\right],\ \{\mu 0,\ \texttt{t},\ \texttt{k}\},\ \texttt{Simplify}\right] \texttt{ /. } \frac{\texttt{Vs}}{\texttt{Vs} + \sigma g^2} \to 1 - \texttt{s} \texttt{ /. } \texttt{Vs} + \sigma g^2 \to \sigma g^2 \big/ \texttt{s}$$

$$\left\{\left\{\mu[\texttt{t}] \to \frac{\texttt{k}\,(-1 + (1 - \texttt{s})^{\texttt{t}})}{\texttt{s}} + \texttt{k t} + (1 - \texttt{s})^{\texttt{t}}\,\mu 0\right\}\right\}$$

$$\texttt{Collect}\left[\texttt{RSolve}\left[\left\{\texttt{V}[\texttt{t}+1] == \left(\frac{\texttt{Vs}}{\texttt{Vs} + \sigma g^2}\right)^2 \texttt{V}[\texttt{t}] + \frac{\sigma g^2}{\texttt{Ne}},\ \texttt{V}[0] == \texttt{V0}\right\},\ \texttt{V}[\texttt{t}],\ \texttt{t}\right],\ \{\texttt{V0}\},\ \texttt{Simplify}\right] \texttt{ /. } \frac{\texttt{Vs}^2}{(\texttt{Vs} + \sigma g^2)^2} \to (1 - \texttt{s})^2$$

$$\left\{\left\{\texttt{V}[\texttt{t}] \to \left((1 - \texttt{s})^2\right)^{\texttt{t}}\,\texttt{V0} - \frac{\left(-1 + \left((1 - \texttt{s})^2\right)^{\texttt{t}}\right)\left(\texttt{Vs} + \sigma g^2\right)^2}{\texttt{Ne}\left(2\,\texttt{Vs} + \sigma g^2\right)}\right\}\right\}$$

If the optimum is also stochastic (an independent random normal variable with mean k t and variance $\sigma\theta^2$ in each generation) we have

```
phinext2 =
 Simplify[Integrate[phinext PDF[NormalDistribution[k t, σθ], θ], {θ, -∞, ∞}],
  {σg > 0, Vs > 0, Ne > 0, σ > 0, σθ > 0}]
```

$$\frac{e^{-\frac{\texttt{Ne}\left(\texttt{Vs}\,\mu + \texttt{k t}\,\sigma g^2 - \texttt{bargnext}\left(\texttt{Vs} + \sigma g^2\right)\right)^2}{2\left(\sigma g^2\left(\texttt{Vs} + \sigma g^2\right)^2 + \texttt{Ne}\left(\texttt{Vs}^2\,\sigma^2 + \sigma g^4\,\sigma\theta^2\right)\right)}}\left(\texttt{Vs} + \sigma g^2\right)\sqrt{\frac{\texttt{Ne}}{\sigma g^2\left(\texttt{Vs} + \sigma g^2\right)^2 + \texttt{Ne}\left(\texttt{Vs}^2\,\sigma^2 + \sigma g^4\,\sigma\theta^2\right)}}}{\sqrt{2\,\pi}}$$

The change in the mean remains the same while the change in the variance alters a little, now σ^2 becomes $\left(\frac{\text{Vs}}{\text{Vs}+\sigma g^2}\right)^2 \sigma^2 + \frac{\sigma g^2}{\text{Ne}} + \left(\frac{\sigma g^2}{\text{Vs}+\sigma g^2}\right)^2 \sigma\theta^2$. Check:

$$\texttt{Simplify}\Big[\texttt{PDF}\Big[\texttt{NormalDistribution}\Big[\mu + \frac{\sigma g^2}{Vs + \sigma g^2}(\theta - \mu), \left(\left(\frac{Vs}{Vs + \sigma g^2}\right)^2 \sigma^2 + \frac{\sigma g^2}{Ne} + \left(\frac{\sigma g^2}{Vs + \sigma g^2}\right)^2 \sigma\theta^2\right)^{1/2}\Big], \texttt{bargnext}\Big] \Big/ \texttt{phinext2} \text{ /. } \theta \to k\,t, \{Vs > 0, \sigma g > 0, Ne > 0, \sigma > 0, \sigma\theta > 0\}\Big]$$

1

The solution to the variance recursion is then

$$\texttt{varrec} = \texttt{Collect}\Big[\texttt{RSolve}\Big[\Big\{V[t+1] == \left(\frac{Vs}{Vs + \sigma g^2}\right)^2 V[t] + \frac{\sigma g^2}{Ne} + \left(\frac{\sigma g^2}{Vs + \sigma g^2}\right)^2 \sigma\theta^2, V[0] == V0\Big\}, V[t], t\Big], \{V0, \sigma\theta^2\}, \texttt{Simplify}\Big] \text{ /. } \frac{Vs^2}{(Vs + \sigma g^2)^2} \to (1-s)^2$$

$$\left\{\left\{V[t] \to \left((1-s)^2\right)^t V0 - \frac{\left(-1 + \left((1-s)^2\right)^t\right)\left(Vs + \sigma g^2\right)^2}{Ne\left(2\,Vs + \sigma g^2\right)} - \frac{\left(-1 + \left((1-s)^2\right)^t\right)\sigma g^2\,\sigma\theta^2}{2\,Vs + \sigma g^2}\right\}\right\}$$

as t becomes large the expected mean becomes

$$\mu[t] \text{ /. meanrec /. } (1-s)^t \to 0$$

$$\left\{-\frac{k}{s} + k\,t\right\}$$

and the variance in the mean becomes (and approximately given weak selection relative to genetic variance, Vs >> σg^2)

$$V[t] \text{ /. varrec /. } \left((1-s)^2\right)^t \to 0$$

$$\% \text{ /. } Vs + \sigma g^2 \to Vs \text{ /. } 2\,Vs + \sigma g^2 \to 2\,Vs$$

$$\left\{\frac{\left(Vs + \sigma g^2\right)^2}{Ne\left(2\,Vs + \sigma g^2\right)} + \frac{\sigma g^2\,\sigma\theta^2}{2\,Vs + \sigma g^2}\right\}$$

$$\left\{\frac{Vs}{2\,Ne} + \frac{\sigma g^2\,\sigma\theta^2}{2\,Vs}\right\}$$

The expected population growth rate in generation t is then

$$E\lambda t = \texttt{Simplify}\Big[B\,\texttt{Integrate}\Big[\left(\texttt{barW} \text{ /. } \sigma z^2 \to \sigma g^2 + \sigma e^2 \text{ /. } \sigma e^2 \to Vs - \omega^2\right) \texttt{PDF}[\texttt{NormalDistribution}[k\,t, \sigma\theta], \theta]\,\texttt{PDF}\Big[\texttt{NormalDistribution}\Big[\mu[t], V[t]^{1/2}\Big], \texttt{barg}\Big], \{\theta, -\infty, \infty\}, \{\texttt{barg}, -\infty, \infty\}\Big], \{\sigma\theta > 0, Vs > 0, \sigma g > 0, V[t] > 0\}\Big]$$

$$\frac{B\,e^{-\frac{(-k\,t + \mu[t])^2}{2\left(Vs + \sigma g^2 + \sigma\theta^2 + V[t]\right)}}\,\omega}{\sqrt{Vs + \sigma g^2 + \sigma\theta^2 + V[t]}}$$

which can be rewritten as in Burger & Lynch 1995 (equation 9). Check:

$$\texttt{Simplify}\left[\texttt{E}\lambda\texttt{t} \Big/ \left(\texttt{B0}\left(\texttt{PDF}\left[\texttt{NormalDistribution}\left[\texttt{k t, V}\lambda^{1/2}\right], \mu[\texttt{t}]\right]\sqrt{2\,\pi\,\texttt{V}\lambda}\right) \text{/. } \texttt{B0} \to \frac{\texttt{B}\ \omega}{\sqrt{\texttt{V}\lambda}} \text{/. } \texttt{V}\lambda \to \texttt{Vs} + \sigma g^2 + \sigma\theta^2 + \texttt{V[t]}\right), \{\sigma\theta > 0, \texttt{Vs} > 0, \sigma g > 0, \texttt{V[t]} > 0, \texttt{Ne} > 0, \omega > 0, \texttt{s} > 0\}\right]$$

1

As time gets large the expected growth rate becomes

$$\texttt{E}\lambda = \texttt{Simplify}\left[\texttt{E}\lambda\texttt{t} \text{ /. } \texttt{V[t]} \to \frac{(\texttt{Vs} + \sigma g^2)^2}{\texttt{Ne}\,(2\,\texttt{Vs} + \sigma g^2)} + \frac{\sigma g^2\,\sigma\theta^2}{2\,\texttt{Vs} + \sigma g^2} \text{ /. } \mu[\texttt{t}] \to -\frac{\texttt{k}}{\texttt{s}} + \texttt{k t}, \{\sigma\theta > 0, \texttt{Vs} > 0, \sigma g > 0, \texttt{V[t]} > 0, \texttt{Ne} > 0, \omega > 0\}\right]$$

$$\mathrm{B}\, e^{-\frac{k^2\,\mathrm{Ne}\,(2\,\mathrm{Vs}+\sigma g^2)}{2\,s^2\,(\mathrm{Vs}+\sigma g^2)\,(\mathrm{Vs}+2\,\mathrm{Ne}\,\mathrm{Vs}+(1+\mathrm{Ne})\,\sigma g^2+2\,\mathrm{Ne}\,\sigma\theta^2)}}\sqrt{\frac{\mathrm{Ne}\,(2\,\mathrm{Vs}+\sigma g^2)}{(\mathrm{Vs}+\sigma g^2)\,(\mathrm{Vs}+2\,\mathrm{Ne}\,\mathrm{Vs}+(1+\mathrm{Ne})\,\sigma g^2+2\,\mathrm{Ne}\,\sigma\theta^2)}}\ \omega$$

The critical rate occurs where the expected growth rate as time gets large becomes 1

```
kc = Simplify[Solve[1 == Eλ, k] /. C[1] → 0,
    {σθ > 0, Vs > 0, σg > 0, V[t] > 0, Ne > 0, ω > 0}][[2]]
```

$$\left\{k \to \frac{\sqrt{2}\sqrt{\mathrm{Log}\left[\mathrm{B}\sqrt{\frac{\mathrm{Ne}\,(2\,\mathrm{Vs}+\sigma g^2)}{(\mathrm{Vs}+\sigma g^2)\,(\mathrm{Vs}+2\,\mathrm{Ne}\,\mathrm{Vs}+(1+\mathrm{Ne})\,\sigma g^2+2\,\mathrm{Ne}\,\sigma\theta^2)}}\ \omega\right]}}{\sqrt{\frac{\mathrm{Ne}\,(2\,\mathrm{Vs}+\sigma g^2)}{s^2\,(\mathrm{Vs}+\sigma g^2)\,(\mathrm{Vs}+2\,\mathrm{Ne}\,\mathrm{Vs}+(1+\mathrm{Ne})\,\sigma g^2+2\,\mathrm{Ne}\,\sigma\theta^2)}}}\right\}$$

This can be rewritten as in Burger & Lynch 1995 (equation 10). Check:

$$\texttt{Simplify}\left[(\texttt{k /. kc}) \Big/ \left(\texttt{s}\sqrt{2\,\texttt{V}\lambda\,\texttt{Log[B0]}} \text{ /. } \texttt{B0} \to \frac{\texttt{B}\ \omega}{\sqrt{\texttt{V}\lambda}} \text{ /. } \texttt{V}\lambda \to \texttt{Vs} + \sigma g^2 + \sigma\theta^2 + \texttt{V[t]} \text{ /. } \texttt{V[t]} \to \frac{(\texttt{Vs} + \sigma g^2)^2}{\texttt{Ne}\,(2\,\texttt{Vs} + \sigma g^2)} + \frac{\sigma g^2\,\sigma\theta^2}{2\,\texttt{Vs} + \sigma g^2}\right), \{\sigma\theta > 0, \texttt{Vs} > 0, \sigma g > 0, \texttt{V[t]} > 0, \texttt{Ne} > 0, \omega > 0, \texttt{s} > 0\}\right]$$

1

Alternative fitness function

Analytical treatment

An alternate function for the probability of survival (fitness)

$$\texttt{W[z\_] := (1 - dp) Exp}\left[-\texttt{d}\left(1 - \texttt{Exp}\left[-(\theta - \texttt{z})^2 / (2\,\omega^2)\right]\right)\right]$$

we then have equivalence with the continuous time alternative fitness funciton used above, exp(r(z)) = B W(z), when the probability of death of optimally adapted individuals is dp=0

```
Exp[rm - d (1 - Exp[- (z - θ)^2 / (2 σw^2)])] == B W[z] /. B → Exp[rm] /. σw → ω /. dp → 0 //
 Simplify
```

```
True
```

In discrete time the alternative fitness function (red) asymptotes at a higher value (when d<∞) than the traditionally used Gaussian fitness function (i.e., the probability of survival has some minimum greater than 0)

```
Limit[W[z] /. θ → L + z, L → ∞, Assumptions → ω > 0]
Limit[Exp[- (θ - z)^2 / (2 ω^2)] /. θ → L + z, L → ∞, Assumptions → ω > 0]
```

$-(-1+\mathrm{dp})\, e^{-d}$

0

but is identical to second order when there is little lag, θ-z near 0, and d=1 and dp=0

```
Series[Exp[- (θ - z)^2 / (2 ω^2)], {z, θ, 2}] == Series[W[z], {z, θ, 2}] /. d → 1 /. dp → 0
```

```
True
```

In continuous time a bigger difference emerges: the alternative fitness function does not allow infinitely negative growth rates and its slope is bounded while the traditional Gaussian becomes ever more negative and ever more steep as trait values depart from the optimum

```
D[Log[B Exp[- (θ - z)^2 / (2 ω^2)]] /. θ → L + z, L]
Limit[D[Log[B Exp[- (θ - z)^2 / (2 ω^2)]] /. θ → L + z, L], L → ∞, Assumptions → {ω > 0}]
D[Log[B W[z]] /. θ → L + z, L]
Limit[D[Log[B W[z]] /. θ → L + z, L], L → ∞, Assumptions → {ω > 0}]
```

$-\frac{L}{\omega^2}$

$-\infty$

$-\frac{d\, e^{-\frac{L^2}{2\omega^2}}\, L}{\omega^2}$

0

The minimum expected number of offspring is

```
Limit[B W[z] /. θ → L + z, L → ∞, Assumptions → ω > 0]
```

$-B\,(-1+\mathrm{dp})\, e^{-d}$

which is below replacement as long as

```
Reduce[% < 1 && 1 < B && 0 < d && 0 < dp < 1, B, Reals]
```

$d > 0\ \&\&\ 0 < \mathrm{dp} < 1\ \&\&\ 1 < B < -\frac{e^{d}}{-1+\mathrm{dp}}$

With this more complicated function we are unable to integrate to get mean viability, but when phenotypic variation is small we can approximate mean viability by replacing z with the mean value of z in the fitness function, and the deterministic rate of evolution is then approximately

```
dbarg = σg² D[Log[W[barg]], barg]
```

$$\frac{d\, e^{-\frac{(-barg+\theta)^2}{2\omega^2}} (-barg+\theta)\ \sigma g^2}{\omega^2}$$

Note that this has one maximum at over all positive lags

```
Solve[0 == D[dbarg /. barg → θ - L, L], L]
```

$\{\{L \to -\omega\}, \{L \to \omega\}\}$

The maximum rate of evolution is thus

```
dbarg /. barg → θ - L /. L → ω
```

$$\frac{d\ \sigma g^2}{\sqrt{e}\ \omega}$$

If this maximum rate of evolution is smaller than the critical rate then it is the one that determines persistence.

The steady-state lag is

```
leq = Solve[dbarg == k /. barg → θ - L, L][[1]]
```

Solve::ifun : Inverse functions are being used by Solve, so some solutions may not be found; use Reduce for complete solution information. ≫

$$\left\{L \to -i\ \omega \sqrt{\text{ProductLog}\left[-\frac{k^2\ \omega^2}{d^2\ \sigma g^4}\right]}\right\}$$

This becomes an imaginary number at the maximum rate of evolution

$$\textbf{Solve}\left[-1 == \textbf{ProductLog}\left[-\frac{k^2\ \omega^2}{d^2\ \sigma g^4}\right], k\right]$$

$$\left\{\left\{k \to -\frac{d\ \sigma g^2}{\sqrt{e}\ \omega}\right\}, \left\{k \to \frac{d\ \sigma g^2}{\sqrt{e}\ \omega}\right\}\right\}$$

Given the lag is real (i.e., the rate of environmental change is less than the maximum rate of evolution), the expected number of offspring per surviving offspring is

```
B W[z] /. θ → L + z /. leq
```

$$B\ (1 - dp)\ e^{-d\left(1 - e^{\frac{1}{2}\text{ProductLog}\left[-\frac{k^2\ \omega^2}{d^2\ \sigma g^4}\right]}\right)}$$

The minimum value this can take on (while the lag is real) is

```
% /. %%[[2]]
```

$$B\ (1 - dp)\ e^{-d\left(1 - \frac{1}{\sqrt{e}}\right)}$$

If this value is always above 1 then there is no critical rate of environmental change. i.e., there is no critical rate of environmental change when

```
Reduce[% > 1 && 1 < B && 0 < d && 0 < dp < 1, B, Reals] // Simplify
```

$$d > 0 \,\&\&\, 0 < dp < 1 \,\&\&\, B > \frac{e^{d-\frac{d}{\sqrt{e}}}}{1 - dp}$$

Recalling from above that we need B to be small enough such that the minimum expected number of offspring is below 1 (so that the population can go extinct), our condition for the maximum rate of evolution determining persistence (and thus the existence of a tipping point) is

$$\text{Reduce}\left[\%\% > 1 \,\&\&\, 1 < B < -\frac{e^{d}}{-1 + dp} \,\&\&\, 0 < d \,\&\&\, 0 < dp < 1,\ B,\ \text{Reals}\right] \text{ // Simplify}$$

$$d > 0 \,\&\&\, 0 < dp < 1 \,\&\&\, \frac{e^{d-\frac{d}{\sqrt{e}}}}{1 - dp} < B < -\frac{e^{d}}{-1 + dp}$$

For example, with d=1 and dp=0 the only value of B that creates an evolutionary tipping point is B=2

$$\frac{e^{d-\frac{d}{\sqrt{e}}}}{1 - dp} < B < -\frac{e^{d}}{-1 + dp} \text{ /. } d \to 1. \text{ /. } dp \to 0$$

$$1.48211 < B < 2.71828$$

Simulation results

Figure 2 (A-E): summary (traditional)

```
(*parameter values*)
KK = 512;
B = 2;
ω = 3;
μ = 0.0002;
α = 0.05^(1/2);
n = 50;
σθ = 0;

(*crtical rate of change*)
```

$$kc = \frac{\sqrt{2}\sqrt{\mathrm{Log}\left[B\sqrt{\frac{Ne\,(2\,Vs+\sigma g^2)}{(Vs+\sigma g^2)\,(Vs+2\,Ne\,Vs+(1+Ne)\,\sigma g^2+2\,Ne\,\sigma\theta^2)}}\,\omega\right]}}{\sqrt{\frac{Ne\,(2\,Vs+\sigma g^2)}{s^2\,(Vs+\sigma g^2)\,(Vs+2\,Ne\,Vs+(1+Ne)\,\sigma g^2+2\,Ne\,\sigma\theta^2)}}};$$

$$kc1 = kc\ /.\ s \to \frac{\sigma g^2}{\sigma g^2+Vs}\ /.\ Vs \to \omega^2+1\ /.\ \sigma g \to \left(4\,n\,\mu\,\alpha^2\,Ne\right)^{1/2}\ /.\ Ne \to \frac{2\,B}{2\,B-1}\,KK;$$

```
(*crit rate with neutral gen var*)
```

$$kc2 = kc\ /.\ s \to \frac{\sigma g^2}{\sigma g^2+Vs}\ /.\ \sigma g \to \left(\frac{4\,n\,\mu\,\alpha^2\,Ne}{1+\frac{\alpha^2\,Ne}{Vs}}\right)^{1/2}\ /.\ Vs \to \omega^2+1\ /.\ Ne \to \frac{2\,B}{2\,B-1}\,KK;$$

```
(*crit rate with SHC gen var*)
(*x limits*)
kmin = -0.005;
kmax = Max[kc1, kc2];(*max critical rate*)

klist = Table[i * 0.01, {i, 0, 25}]; (*all rates of change simulated*)

repmax = 9; (*number of reps minus 1*)
burngens = 1000;
genmax = 10 000 + burngens; (*last gen recorded for surviving reps*)

maxtpoints = 10; (*max number of recorded timepoints to average over*)

(*directory with data*)
datadir = simdir <> "data6/";

(*simulation identifier*)
simname[k_, rep_] := "K" <> ToString[KK] <> "_B" <> ToString[B] <> "_w" <> ToString[ω] <>
   "_u" <> ToString[μ] <> "_alphasqrd" <> ToString[α^2] <> "_n" <> ToString[n] <>
   "_k" <> ToString[NumberForm[k, {2, 2}]] <> "_rep" <> ToString[rep] <> ".csv";

(*expected growth rate*)
```

$$E\lambda = B\,e^{-\frac{k^2\,Ne\,(2\,Vs+\sigma g^2)}{2\,s^2\,(Vs+\sigma g^2)\,(Vs+2\,Ne\,Vs+(1+Ne)\,\sigma g^2+2\,Ne\,\sigma\theta^2)}}\sqrt{\frac{Ne\,(2\,Vs+\sigma g^2)}{(Vs+\sigma g^2)\,(Vs+2\,Ne\,Vs+(1+Ne)\,\sigma g^2+2\,Ne\,\sigma\theta^2)}}\,\omega;$$

```
(*mean mean lag, over last 10 time steps*)
meanlagpersist =
```

```
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
    gens = Select[gens[[1]], # > burngens &];
    x = gens[[-1]];
    phenos = Import[datadir <> "phenos_" <> simname[k, rep]];
    tpoints = Min[maxtpoints, Length[gens]];
    If[x < genmax, Null,
     Mean[Table[k (gens[[-t]] - burngens) - Mean[phenos[[-t]]], {t, 1, tpoints}]]]
   },
   {k, klist},
   {rep, 0, repmax}
  ];

meanlagextinct =
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
    gens = Select[gens[[1]], # > burngens &];
    x = gens[[-1]];
    phenos = Import[datadir <> "phenos_" <> simname[k, rep]];
    tpoints = Min[maxtpoints, Length[gens]];
    If[x == genmax, Null,
     Mean[Table[k (gens[[-t]] - burngens) - Mean[phenos[[-t]]], {t, 1, tpoints}]]]
   },
   {k, klist},
   {rep, 0, repmax}
  ];

(*genetic variance at last time step*)
genvarpersist =
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
    gens = Select[gens[[1]], # > burngens &];
    x = gens[[-1]];
    genos = Import[datadir <> "genos_" <> simname[k, rep]];
    tpoints = Min[maxtpoints, Length[gens]];
    If[x < genmax, Null, Mean[Table[Variance[genos[[-t]]], {t, 1, tpoints}]]]
   },
   {k, klist},
   {rep, 0, repmax}
  ];

genvarextinct =
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
    gens = Select[gens[[1]], # > burngens &];
    x = gens[[-1]];
    genos = Import[datadir <> "genos_" <> simname[k, rep]];
    tpoints = Min[maxtpoints, Length[gens]];
    If[x == genmax, Null, Mean[Table[Variance[genos[[-t]]], {t, 1, tpoints}]]]
   },
```

```
    {k, klist},
    {rep, 0, repmax}
   ];

(*popn growth rate before carrying capacity at last time step*)
rpersist =
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
    gens = Select[gens[[1]], # > burngens &];
    x = gens[[-1]];
    ns = Import[datadir <> "n_" <> simname[k, rep]];
    numparents = Import[datadir <> "numparents_" <> simname[k, rep]];
    tpoints = Min[maxtpoints, Length[gens]];
    If[x < genmax, Null,
     Mean[Table[ns[[1, -t]] / numparents[[1, -t]] - 1 // N, {t, 1, tpoints}]]]
   },
   {k, klist},
   {rep, 0, repmax}
  ];

rextinct =
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
    gens = Select[gens[[1]], # > burngens &];
    x = gens[[-1]];
    ns = Import[datadir <> "n_" <> simname[k, rep]];
    numparents = Import[datadir <> "numparents_" <> simname[k, rep]];
    tpoints = Min[maxtpoints, Length[gens]];
    If[x == genmax, Null,
     Mean[Table[ns[[1, -t]] / numparents[[1, -t]] - 1 // N, {t, 1, tpoints}]]]
   },
   {k, klist},
   {rep, 0, repmax}
  ];

(*percent reps extinct before end of simulation*)
percentextinct = Table[
   {k, Mean[Table[
        {
         ns = Import[datadir <> "n_" <> simname[k, rep]];
         If[ns[[1, Length[ns[[1]]]]] < 2, 1, 0]
        },
        {rep, 0, repmax}
       ]][[1]]},
   {k, klist}
  ];

(*time to extinction given extinct*)
extincttime =
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
```

```
    gens = Select[gens[[1]], # > burngens &];
    x = gens[[-1]];
    If[x == genmax, Null, x - burngens]
   },
   {k, klist},
   {rep, 0, repmax}
  ];

(*mean lag*)
lagtradplot = Show[
```

$$\text{Plot}\left[\frac{k}{s} \text{ /. } s \to \frac{\sigma g^2}{\sigma g^2 + Vs} \text{ /. } \sigma g \to \left(\frac{4\, n\, \mu\, \alpha^2\, Ne}{1 + \frac{\alpha^2\, Ne}{Vs}}\right)^{1/2} \text{ /. } Vs \to \omega^2 + 1 \text{ /. } Ne \to \frac{2\,B}{2\,B - 1}\, KK,\right.$$

```
    {k, 0, kc2}, PlotRange → {0, All},
    PlotStyle → {Black, Thick, Dashing[Large]}, Axes → False],
```

$$\text{Plot}\left[\frac{k}{s} \text{ /. } s \to \frac{\sigma g^2}{\sigma g^2 + Vs} \text{ /. } \sigma g \to \left(4\, n\, \mu\, \alpha^2\, Ne\right)^{1/2} \text{ /. } Vs \to \omega^2 + 1 \text{ /. } Ne \to \frac{2\,B}{2\,B - 1}\, KK, \{k, 0,\right.$$

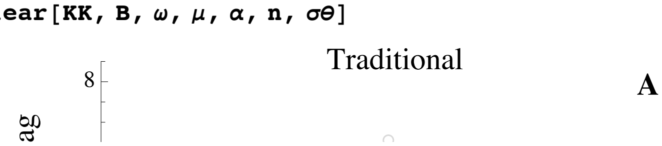
```
     kc1}, PlotRange → {0, All}, PlotStyle → {Black, Thick, Dotted}, Axes → False],
   ListPlot[
    meanlagpersist, PlotMarkers → Style["∘", 20, Black]
   ],
   ListPlot[
    meanlagextinct, PlotMarkers → Style["∘", 20, LightGray]
   ],
   PlotRange → {{kmin, kmax}, {-0.5, 8.5}},
   Frame → {True, True, False, False},
   PlotRangePadding → None,
   FrameLabel → {"", Style["", LabelSize]},
   FrameStyle → Directive[FontSize → TickSize],
   Epilog → {
     Text[Style["A", LabelSize, Bold], Scaled@letpos],
     Rotate[
      Text[Style["Mean phenotypic lag", LabelSize], Scaled@ylabpos], 90 Degree],
     Text[Style["Traditional", LabelSize], Scaled@{0.5, 1}]
    },
   ImagePadding → Pad,
   FrameTicksStyle → {{Black, Black}, {Directive[FontColor → White], Black}},
   PlotRangeClipping → False
  ];

(*genetic variance*)
vartradplot = Show[
```

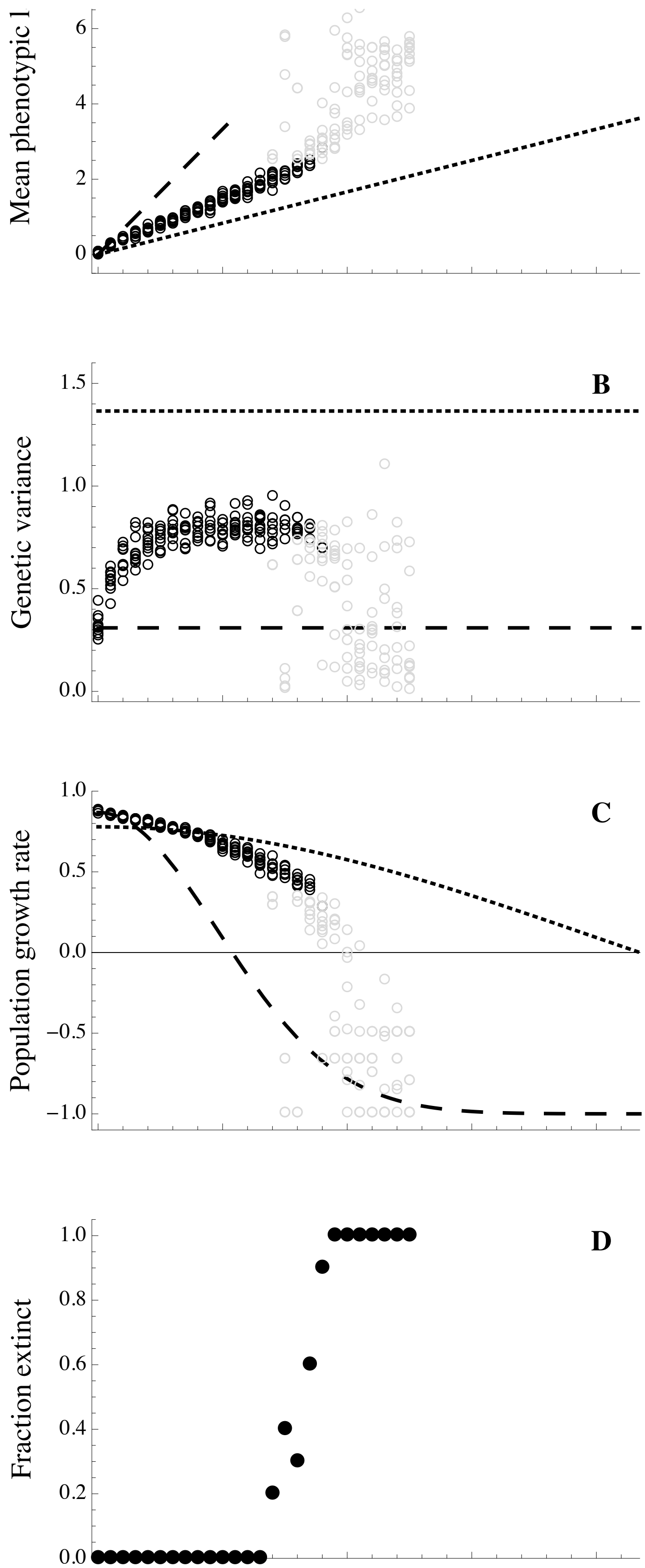
$$\text{Plot}\left[\sigma g^2 \text{ /. } \sigma g \to \left(\frac{4\, n\, \mu\, \alpha^2\, Ne}{1 + \frac{\alpha^2\, Ne}{Vs}}\right)^{1/2} \text{ /. } Vs \to \omega^2 + 1 \text{ /. } Ne \to \frac{2\,B}{2\,B - 1}\, KK,\right.$$

```
    {k, 0, kmax}, PlotRange → {0, All},
    PlotStyle → {Black, Thick, Dashing[Large]}, Axes → False],
```

```
  Plot[σg^2 /. σg^2 → 4 n μ α^2 Ne /. Ne → (2 B)/(2 B - 1) KK, {k, 0, kmax},
   PlotRange → {0, All}, PlotStyle → {Black, Thick, Dotted}],
  ListPlot[
   genvarpersist, PlotMarkers → Style["∘", 20, Black]
  ],
  ListPlot[
   genvarextinct, PlotMarkers → Style["∘", 20, LightGray]
  ],
  PlotRange → {{kmin, kmax}, {-0.05, 1.6}},
  Frame → {True, True, False, False},
  PlotRangePadding → None,
  FrameLabel → {"", Style["", LabelSize]},
  FrameStyle → Directive[FontSize → TickSize],
  Epilog → {
    Text[Style["B", LabelSize, Bold], Scaled@letpos],
    Rotate[
     Text[Style["Genetic variance", LabelSize], Scaled@ylabpos], 90 Degree]
   },
  ImagePadding → Pad,
  FrameTicksStyle → {{Black, Black}, {Directive[FontColor → White], Black}},
  PlotRangeClipping → False
 ];

(*popn growth rate*)
rtradplot = Show[

  Plot[Eλ - 1 /. s → σg^2/(σg^2 + Vs) /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → ω^2 + 1 /. Ne → (2 B)/(2 B - 1) KK,
   {k, 0, kmax}, PlotRange → All,
   PlotStyle → {Black, Thick, Dashing[Large]}, Axes → False],
  Plot[Eλ - 1 /. s → σg^2/(σg^2 + Vs) /. σg → (4 n μ α^2 Ne)^(1/2) /. Vs → ω^2 + 1 /. Ne → (2 B)/(2 B - 1) KK,
   {k, 0, kmax}, PlotRange → All, PlotStyle → {Black, Thick, Dotted}],
  Plot[0, {k, kmin, kmax}, PlotStyle → Black],
  ListPlot[
   rpersist, PlotMarkers → Style["∘", 20, Black]
  ],
  ListPlot[
   rextinct, PlotMarkers → Style["∘", 20, LightGray]
  ],
  PlotRange → {{kmin, kmax}, {-1.1, 1}},
  Frame → {True, True, False, False},
  PlotRangePadding → None,
  FrameLabel → {"", Style["", LabelSize]},
  FrameStyle → Directive[FontSize → TickSize],
  Epilog → {
    Text[Style["C", LabelSize, Bold], Scaled@letpos],
    Rotate[
```

```
      Text[Style["Population growth rate", LabelSize], Scaled@ylabpos], 90 Degree]
     },
    ImagePadding → Pad,
    FrameTicksStyle → {{Black, Black}, {Directive[FontColor → White], Black}},
    PlotRangeClipping → False
   ];

(*percent extinct*)
percenttradplot = Show[
    ListPlot[percentextinct, PlotMarkers → Style["•", 20, Black], Axes → False],
    PlotRange → {{kmin, kmax}, {0, 1.05}},
    Frame → {True, True, False, False},
    PlotRangePadding → None,
    FrameLabel → {"", Style["", LabelSize]},
    FrameStyle → Directive[FontSize → TickSize],
    Epilog → {
      Text[Style["D", LabelSize, Bold], Scaled@letpos],
      Rotate[
       Text[Style["Fraction extinct", LabelSize], Scaled@ylabpos], 90 Degree]
     },
    ImagePadding → Pad,
    FrameTicksStyle → {{Black, Black}, {Directive[FontColor → White], Black}},
    PlotRangeClipping → False
   ];

(*mean time to extinction*)
timetradplot = Show[
    ListPlot[extincttime,
     PlotMarkers → Style["∘", 20, Black], PlotRange → {{0, kmax}, {0, 10 200}}],
    PlotRange → {{kmin, kmax}, {-200, 10 200}},
    Frame → {True, True, False, False},
    PlotRangePadding → None,
    FrameLabel →
     {Style["Rate of environmental change", LabelSize], Style["", LabelSize]},
    FrameStyle → Directive[FontSize → TickSize],
    Epilog → {
      Text[Style["E", LabelSize, Bold], Scaled@letpos],
      Rotate[Text[Style["Generation extinct | extinct", LabelSize],
        Scaled@ylabpos], 90 Degree]
     },
    ImagePadding → Pad,
    FrameTicksStyle → {{Black, Black}, {Black, Black}},
    PlotRangeClipping → False
   ];

GraphicsGrid[{{lagtradplot}, {vartradplot}, {rtradplot},
  {percenttradplot}, {timetradplot}}, ImageSize → FigureSize, Spacings → 0]

Export[imagedir <> "TradSummaryMeanLargeBurn.pdf", %];

Clear[KK, B, ω, μ, α, n, σθ]
```




Mean phenotypic l
6
4
2
0
B
Genetic variance
1.5
1.0
0.5
0.0
C
Population growth rate
1.0
0.5
0.0
−0.5
−1.0
D
Fraction extinct
1.0
0.8
0.6
0.4
0.2
0.0

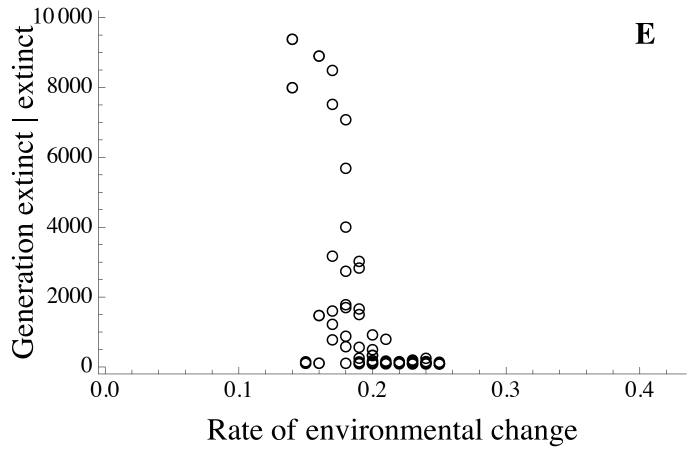


Figure 2 (F-J): summary (alternative)

```
(*parameter values*)
KK = 512;
B = 2;
ω = 3;
μ = 0.0002;
α = 0.05^(1/2);
n = 50;
σθ = 0;
```

$$\text{kc} = \frac{\sqrt{2}\sqrt{\text{Log}\left[\text{B}\sqrt{\frac{\text{Ne}\,(2\,\text{Vs}+\sigma\text{g}^2)}{(\text{Vs}+\sigma\text{g}^2)\,(\text{Vs}+2\,\text{Ne}\,\text{Vs}+(1+\text{Ne})\,\sigma\text{g}^2+2\,\text{Ne}\,\sigma\theta^2)}}\;\omega\right]}}{\sqrt{\frac{\text{Ne}\,(2\,\text{Vs}+\sigma\text{g}^2)}{\text{s}^2\,(\text{Vs}+\sigma\text{g}^2)\,(\text{Vs}+2\,\text{Ne}\,\text{Vs}+(1+\text{Ne})\,\sigma\text{g}^2+2\,\text{Ne}\,\sigma\theta^2)}}};\text{(*critical rate*)}$$

$$\text{kc1} = \frac{\sigma\text{g}^2}{\sqrt{e}\;\omega}\;/.\;\text{s}\to\frac{\sigma\text{g}^2}{\sigma\text{g}^2+\text{Vs}}\;/.\;\text{Vs}\to\omega^2+1\;/.\;\sigma\text{g}\to\left(4\,\text{n}\,\mu\,\alpha^2\,\text{Ne}\right)^{1/2}\;/.\;\text{Ne}\to\frac{2\,\text{B}}{2\,\text{B}-1}\,\text{KK};$$

```
(*tip pt with neutral gen var*)
```

$$\text{kc2} = \frac{\sigma\text{g}^2}{\sqrt{e}\;\omega}\;/.\;\text{s}\to\frac{\sigma\text{g}^2}{\sigma\text{g}^2+\text{Vs}}\;/.\;\sigma\text{g}\to\left(\frac{4\,\text{n}\,\mu\,\alpha^2\,\text{Ne}}{1+\frac{\alpha^2\,\text{Ne}}{\text{Vs}}}\right)^{1/2}\;/.\;\text{Vs}\to\omega^2+1\;/.\;\text{Ne}\to\frac{2\,\text{B}}{2\,\text{B}-1}\,\text{KK};$$

```
(*tip pt with SHC gen var*)
```

$$\text{kc3} = \text{kc}\;/.\;\text{s}\to\frac{\sigma\text{g}^2}{\sigma\text{g}^2+\text{Vs}}\;/.\;\text{Vs}\to\omega^2+1\;/.\;\sigma\text{g}\to\left(4\,\text{n}\,\mu\,\alpha^2\,\text{Ne}\right)^{1/2}\;/.\;\text{Ne}\to\frac{2\,\text{B}}{2\,\text{B}-1}\,\text{KK};$$

```
(*crit rate with neutral gen var*)
```

$$\text{kc4} = \text{kc}\;/.\;\text{s}\to\frac{\sigma\text{g}^2}{\sigma\text{g}^2+\text{Vs}}\;/.\;\sigma\text{g}\to\left(\frac{4\,\text{n}\,\mu\,\alpha^2\,\text{Ne}}{1+\frac{\alpha^2\,\text{Ne}}{\text{Vs}}}\right)^{1/2}\;/.\;\text{Vs}\to\omega^2+1\;/.\;\text{Ne}\to\frac{2\,\text{B}}{2\,\text{B}-1}\,\text{KK};$$

```
(*crit rate with SHC gen var*)
(*x limits*)
```

```
kmin = -0.005;
kmax = Max[kc3, kc4];(*max critical rate*)

klist = Table[i * 0.01, {i, 0, 25}]; (*all rates of change simulated*)

repmax = 9; (*number of reps minus 1*)
burngens = 1000;
genmax = 10 000 + burngens; (*last gen recorded for surviving reps*)

maxtpoints = 10; (*max number of recorded timepoints to average over*)

(*directory with data*)
datadir = simdir <> "altdata5/";

(*simulation identifier*)
simname[k_, rep_] := "K" <> ToString[KK] <> "_B" <> ToString[B] <> "_w" <> ToString[ω] <>
   "_u" <> ToString[μ] <> "_alphasqrd" <> ToString[α^2] <> "_n" <> ToString[n] <>
   "_k" <> ToString[NumberForm[k, {2, 3}]] <> "_rep" <> ToString[rep] <> ".csv";

(*expected growth rate*)
Eλ = B Exp[- (1 - Exp[- (θ - z)^2 / (2 ω^2)])] /. θ → L + z /.
    L → - i ω Sqrt[ProductLog[- k^2 ω^2 / (d^2 σg^4)]] /. d → 1;

(*mean mean lag, over last 10 time steps*)
meanlagpersist =
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
    gens = Select[gens[[1]], # > burngens &];
    x = gens[[-1]];
    phenos = Import[datadir <> "phenos_" <> simname[k, rep]];
    tpoints = Min[maxtpoints, Length[gens]];
    If[x < genmax, Null,
     Mean[Table[k ( gens[[-t]] - burngens) - Mean[phenos[[-t]]], {t, 1, tpoints}]]]
   },
   {k, klist},
   {rep, 0, repmax}
  ];

meanlagextinct =
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
    gens = Select[gens[[1]], # > burngens &];
    x = gens[[-1]];
    phenos = Import[datadir <> "phenos_" <> simname[k, rep]];
    tpoints = Min[maxtpoints, Length[gens]];
    If[x == genmax, Null,
     Mean[Table[k ( gens[[-t]] - burngens) - Mean[phenos[[-t]]], {t, 1, tpoints}]]]
   },
   {k, klist},
```

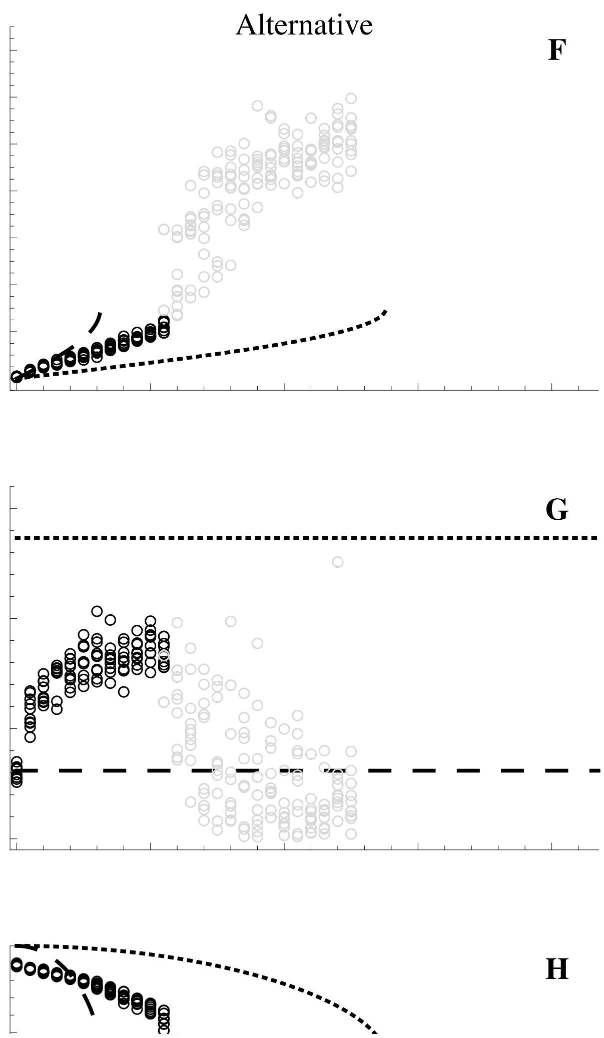
```
    {rep, 0, repmax}
   ];

(*genetic variance at last time step*)
genvarpersist =
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
    gens = Select[gens[[1]], # > burngens &];
    x = gens[[-1]];
    genos = Import[datadir <> "genos_" <> simname[k, rep]];
    tpoints = Min[maxtpoints, Length[gens]];
    If[x < genmax, Null, Mean[Table[Variance[genos[[-t]]], {t, 1, tpoints}]]]
   },
   {k, klist},
   {rep, 0, repmax}
  ];

genvarextinct =
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
    gens = Select[gens[[1]], # > burngens &];
    x = gens[[-1]];
    genos = Import[datadir <> "genos_" <> simname[k, rep]];
    tpoints = Min[maxtpoints, Length[gens]];
    If[x == genmax, Null, Mean[Table[Variance[genos[[-t]]], {t, 1, tpoints}]]]
   },
   {k, klist},
   {rep, 0, repmax}
  ];

(*popn growth rate before carrying capacity at last time step*)
rpersist =
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
    gens = Select[gens[[1]], # > burngens &];
    x = gens[[-1]];
    ns = Import[datadir <> "n_" <> simname[k, rep]];
    numparents = Import[datadir <> "numparents_" <> simname[k, rep]];
    tpoints = Min[maxtpoints, Length[gens]];
    If[x < genmax, Null,
     Mean[Table[ns[[1, -t]] / numparents[[1, -t]] - 1 // N, {t, 1, tpoints}]]]
   },
   {k, klist},
   {rep, 0, repmax}
  ];

rextinct =
  Table[{
    k,
    gens = Import[datadir <> "gens_" <> simname[k, rep]];
    gens = Select[gens[[1]], # > burngens &];
```

```
      x = gens[[-1]];
      ns = Import[datadir <> "n_" <> simname[k, rep]];
      numparents = Import[datadir <> "numparents_" <> simname[k, rep]];
      tpoints = Min[maxtpoints, Length[gens]];
      If[x == genmax, Null,
       Mean[Table[ns[[1, -t]] / numparents[[1, -t]] - 1 // N, {t, 1, tpoints}]]]
     },
     {k, klist},
     {rep, 0, repmax}
    ];

  (*percent reps extinct before end of simulation*)
  percentextinct = Table[
     {k, Mean[Table[
          {
           ns = Import[datadir <> "n_" <> simname[k, rep]];
           If[ns[[1, Length[ns[[1]]]]] < 2, 1, 0]
          },
          {rep, 0, repmax}
         ]][[1]]},
     {k, klist}
    ];

  (*time to extinction given extinct*)
  extincttime =
    Table[{
      k,
      gens = Import[datadir <> "gens_" <> simname[k, rep]];
      gens = Select[gens[[1]], # > burngens &];
      x = gens[[-1]];
      If[x == genmax, Null, x - burngens]
     },
     {k, klist},
     {rep, 0, repmax}
    ];

  (*mean lag*)
  lagaltplot = Show[
     Plot[ω Sqrt[-ProductLog[-k^2 ω^2/σg^4]] /. σg → ((4 n μ α^2 Ne)/(1 + α^2 Ne/Vs))^(1/2) /. Vs → ω^2 + 1 /. Ne → 2 B/(2 B - 1) KK,
      {k, 0, kc2}, PlotRange → {0, All}, PlotStyle → {Black, Thick, Dashing[Large]}],
     Plot[ω Sqrt[-ProductLog[-k^2 ω^2/σg^4]] /. σg → (4 n μ α^2 Ne)^(1/2) /. Vs → ω^2 + 1 /. Ne → 2 B/(2 B - 1) KK,
      {k, 0, kc1}, PlotRange → {0, All}, PlotStyle → {Black, Thick, Dotted}],
     ListPlot[
      meanlagpersist, PlotMarkers → Style["∘", 20, Black]
     ],
     ListPlot[
      meanlagextinct, PlotMarkers → Style["∘", 20, LightGray]
```

```
 ],
 PlotRange → {{kmin, kmax}, {-0.5, 15}},
 Frame → {True, True, False, False},
 PlotRangePadding → None,
 FrameLabel → {"", Style["", LabelSize]},
 FrameStyle → Directive[FontSize → TickSize],
 Epilog → {
   Text[Style["F", LabelSize, Bold], Scaled@letpos],
   Rotate[Text[Style["", LabelSize], Scaled@ylabpos], 90 Degree],
   Text[Style["Alternative", LabelSize], Scaled@{0.5, 1}]
  },
 ImagePadding → Pad,
 FrameTicksStyle →
  {{Directive[FontColor → White], Black}, {Directive[FontColor → White], Black}},
 PlotRangeClipping → False
];

(*genetic variance*)
varaltplot = Show[
 Plot[σg^2 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → ω^2 + 1 /. Ne → (2 B)/(2 B - 1) KK,
  {k, 0, kmax}, PlotRange → {0, All},
  PlotStyle → {Black, Thick, Dashing[Large]}, Axes → False],
 Plot[σg^2 /. σg → (4 n μ α^2 Ne)^(1/2) /. Ne → (2 B)/(2 B - 1) KK, {k, 0, kmax},
  PlotRange → {0, All}, PlotStyle → {Black, Thick, Dotted}],
 ListPlot[
  genvarpersist, PlotMarkers → Style["∘", 20, Black]
 ],
 ListPlot[
  genvarextinct, PlotMarkers → Style["∘", 20, LightGray]
 ],
 PlotRange → {{kmin, kmax}, {-0.05, 1.6}},
 Frame → {True, True, False, False},
 PlotRangePadding → None,
 FrameLabel → {"", Style["", LabelSize]},
 FrameStyle → Directive[FontSize → TickSize],
 Epilog → {
   Text[Style["G", LabelSize, Bold], Scaled@letpos],
   Rotate[Text[Style["", LabelSize], Scaled@ylabpos], 90 Degree]
  },
 ImagePadding → Pad,
 FrameTicksStyle →
  {{Directive[FontColor → White], Black}, {Directive[FontColor → White], Black}},
 PlotRangeClipping → False
];

(*popn growth rate*)
```

```
raltplot = Show[
   Plot[Eλ - 1 /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → ω^2 + 1 /. Ne → (2 B)/(2 B - 1) KK, {k, 0, kmax},
    PlotRange → All, PlotStyle → {Black, Thick, Dashing[Large]}, Axes → False],
   Plot[Eλ - 1 /. σg → (4 n μ α^2 Ne)^(1/2) /. Vs → ω^2 + 1 /. Ne → (2 B)/(2 B - 1) KK,
    {k, 0, kmax}, PlotRange → All, PlotStyle → {Black, Thick, Dotted}],
   Plot[0, {k, kmin, kmax}, PlotStyle → Black],
   ListPlot[
    rpersist, PlotMarkers → Style["∘", 20, Black]
   ],
   ListPlot[
    rextinct, PlotMarkers → Style["∘", 20, LightGray]
   ],
   PlotRange → {{kmin, kmax}, {-1.1, 1}},
   Frame → {True, True, False, False},
   PlotRangePadding → None,
   FrameLabel → {"", Style["", LabelSize]},
   FrameStyle → Directive[FontSize → TickSize],
   Epilog → {
     Text[Style["H", LabelSize, Bold], Scaled@letpos],
     Rotate[Text[Style["", LabelSize], Scaled@ylabpos], 90 Degree]
    },
   ImagePadding → Pad,
   FrameTicksStyle →
    {{Directive[FontColor → White], Black}, {Directive[FontColor → White], Black}},
   PlotRangeClipping → False
  ];

(*percent extinct*)
percentaltplot = Show[
   ListPlot[percentextinct, PlotMarkers → Style["•", 20, Black]],
   PlotRange → {{kmin, kmax}, {0, 1.05}},
   Frame → {True, True, False, False},
   PlotRangePadding → None,
   FrameLabel → {"", Style["", LabelSize]},
   FrameStyle → Directive[FontSize → TickSize],
   Epilog → {
     Text[Style["I", LabelSize, Bold], Scaled@letpos],
     Rotate[Text[Style["", LabelSize], Scaled@ylabpos], 90 Degree]
    },
   ImagePadding → Pad,
   FrameTicksStyle →
    {{Directive[FontColor → White], Black}, {Directive[FontColor → White], Black}},
   PlotRangeClipping → False
  ];

(*mean time to extinction*)
timealtplot = Show[
   ListPlot[extincttime,
```

```
    PlotMarkers → Style["∘", 20, Black], PlotRange → {{0, kmax}, {0, 10 200}}],
   PlotRange → {{kmin, kmax}, {-200, 10 200}},
   Frame → {True, True, False, False},
   PlotRangePadding → None,
   FrameLabel →
    {Style["Rate of environmental change", LabelSize], Style["", LabelSize]},
   FrameStyle → Directive[FontSize → TickSize],
   Epilog → {
     Text[Style["J", LabelSize, Bold], Scaled@letpos],
     Rotate[Text[Style["", LabelSize], Scaled@ylabpos], 90 Degree]
    },
   ImagePadding → Pad,
   FrameTicksStyle → {{Directive[FontColor → White], Black}, {Black, Black}},
   PlotRangeClipping → False
  ];

GraphicsGrid[{{lagaltplot}, {varaltplot}, {raltplot},
  {percentaltplot}, {timealtplot}}, ImageSize → FigureSize, Spacings → 0]

Export[imagedir <> "AltSummaryMeanLargeBurn.pdf", %];

Clear[KK, B, ω, μ, α, n, rep, σθ, kmax]
```



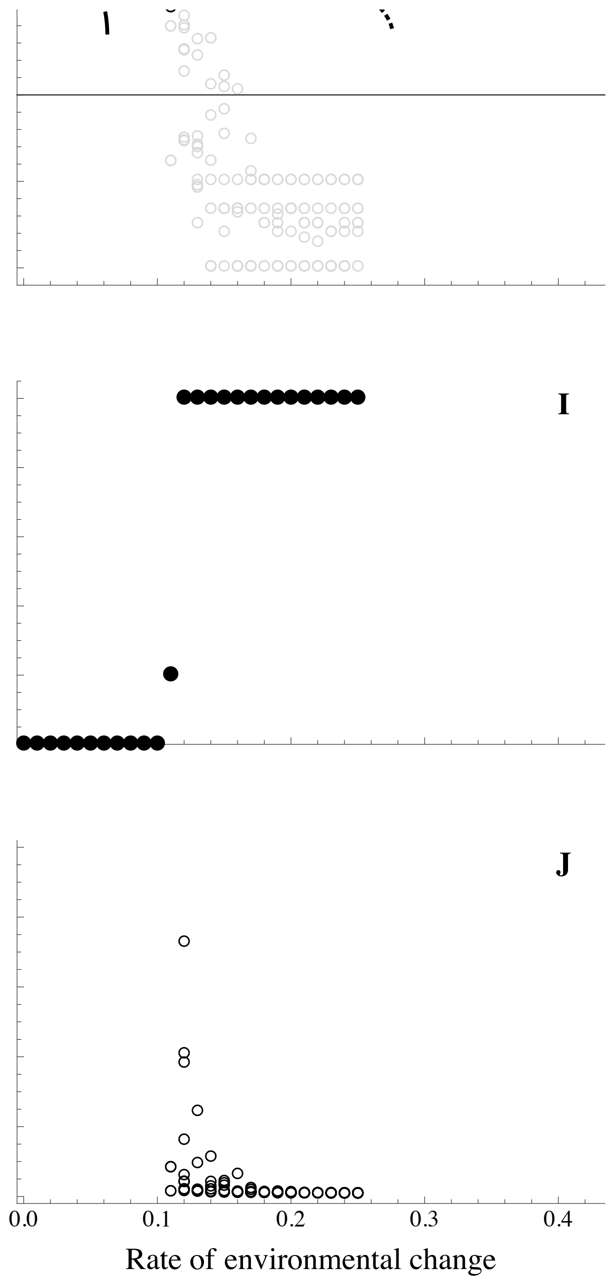


Figure 3 (A-C): early warning signs over time series with increasing k (traditional)

```
Pad2 = {{50, 50}, {40, 15}}; (*whitespace to leave around figures,
{{left,right},{bottom,top}}*)

(*parameter values*)
KK = 512;
B = 2;
ω = 3;
μ = 0.0002;
α = 0.05^(1/2);
n = 50;
```

```
dk = 0.000001;
σθ = 0;
repmax = 9;
burngens = 1000;
totaltime = 200 000 + burngens;

(*size of moving window;
number of gens to calculate autocorr and var in mean lag over*)
window = 30;

(*directory and sim name*)
Clear[sim]
datadir = simdir <> "datatimeseries3/";
sim[rep_] := "K" <> ToString[KK] <> "_B" <> ToString[B] <> "_w" <>
   ToString[ω] <> "_u" <> ToString[μ] <> "_alphasqrd" <> ToString[α^2] <> "_n" <>
   ToString[n] <> "_dk" <> "0.000001" <> "_rep" <> ToString[rep] <> ".csv";

(*simulation results*)
Clear[gens, genos, phenos, ns, numparents]
gens[rep_] := gens[rep] = Import[datadir <> "gens_" <> sim[rep]];
genos[rep_] := genos[rep] = Import[datadir <> "genos_" <> sim[rep]];
phenos[rep_] := phenos[rep] = Import[datadir <> "phenos_" <> sim[rep]];
ns[rep_] := ns[rep] = Import[datadir <> "n_" <> sim[rep]];
numparents[rep_] :=
  numparents[rep] = Import[datadir <> "numparents_" <> sim[rep]];

(*number of recordings and max time*)
Clear[imax, tmax]
imax[rep_] := imax[rep] = Length[gens[rep][[1]]];
tmax[rep_] := tmax[rep] = gens[[1, imax[rep]]];
(*survivors of viability selection*)
(*Show[
 Table[ListPlot[Table[{gens[rep][[1,i]],ns[rep][[1,i]]},{i,0,imax[rep],di}],
   Joined→True,PlotRange→{0,All},PlotStyle→Black],{rep,0,repmax}],
 Plot[KK,{t,0,totaltime}(*,PlotStyle→{Thin}*),PlotStyle→Black],
 Plot[2B/(2B-1) KK,{t,0,totaltime},PlotStyle→{Black,Thick}],
 PlotRange→{{0,totaltime},All},
 Frame→{True,True,False,False},
 PlotRangePadding→None,
 FrameLabel→{"","# survivors"}
]*)

(*mean lag and population growth rate*)
(*Show[
 Table[ListPlot[
   Table[{gens[rep][[1,i]],dk gens[rep][[1,i]]^2/2-Mean[phenos[rep][[i]]]},
    {i,1,imax[rep],di}],Joined→True,Axes→False,PlotStyle→Black],{rep,0,repmax}],
 Table[ListPlot[
   Table[{gens[rep][[1,i]],ns[rep][[1,i]]/numparents[rep][[1,i]]-1},
    {i,1,imax[rep],di}],Joined→True,Axes→False,PlotStyle→Gray],{rep,0,repmax}],
 PlotRange→{{0,totaltime},All},
```

```
 Frame→{True,True,False,False},
 PlotRangePadding→None,
 FrameLabel→{"",""}
]*)

fig3A = Overlay[{
    Show[
     Table[ListPlot[Table[{gens[rep][[1, i]], dk (gens[rep][[1, i]] - burngens)^2/2 -
          Mean[phenos[rep][[i]]]}, {i, window + 1, imax[rep], window}],
       Joined → True, Axes → False, PlotStyle → Black], {rep, 0, repmax}],
     PlotRange → {{0, totaltime}, {-1, 8}},
     Frame → {True, True, False, False},
     ImagePadding → Pad2,
     PlotRangePadding → None,
     FrameLabel → {"", ""},
     ImageSize → FigureSize,
     FrameStyle → Directive[FontSize → TickSize],
     FrameTicksStyle → {{Black, Black}, {Directive[FontColor → White], Black}},
     Epilog → {
       Text[Style["A", LabelSize, Bold], Scaled@letpos],
       Rotate[Text[
         Style["Mean phenotypic lag", LabelSize], Scaled@ylabpos], 90 Degree],
       Text[Style["Traditional", LabelSize], Scaled@{0.5, 1}]
      },
     PlotRangeClipping → False
    ],
    Show[
     Table[ListPlot[
       Table[{gens[rep][[1, i]], ns[rep][[1, i]] / numparents[rep][[1, i]] - 1},
        {i, window + 1, imax[rep], window}], Joined → True,
       Axes → False, PlotStyle → Gray], {rep, 0, repmax}],
     PlotRange → {{0, totaltime}, {-1.2, 1.2}},
     Frame → {False, False, False, True},
     FrameTicks → {None, None, None, All},
     FrameStyle → {Automatic, Automatic,
       Automatic, Directive[FontSize → TickSize, FontColor → Gray]},
     ImagePadding → Pad2,
     PlotRangePadding → None,
     ImageSize → FigureSize,
     Epilog → {
       Rotate[Text[Style["Population growth rate", LabelSize, Gray],
         Scaled@(ylabpos * {-1, 1} + {1, 0})], 270 Degree]
      },
     PlotRangeClipping → False
    ]
   }];

(*Export[imagedir<>"TradLagGrowthTimeSeries.pdf",%];*)

(*variance in mean lag and population growth rate over previous window*)
fig3B = Overlay[{
    Show[
```

```
      Table[ListPlot[Table[{gens[rep][[1, i]], Variance[
            Table[dk (gens[rep][[1, j]] - burngens)^2 / 2 - Mean[phenos[rep][[j]]],
             {j, i - window, i}]]}, {i, window + 1, imax[rep], window}],
        Joined -> True, Axes -> False, PlotStyle -> Black], {rep, 0, repmax}],
      PlotRange -> {{0, totaltime}, {0, 1}},
      Frame -> {True, True, False, False},
      ImagePadding -> Pad2,
      PlotRangePadding -> None,
      FrameLabel -> {"", ""},
      ImageSize -> FigureSize,
      FrameStyle -> Directive[FontSize -> TickSize],
      FrameTicksStyle -> {{Black, Black}, {Directive[FontColor -> White], Black}},
      Epilog -> {
        Text[Style["B", LabelSize, Bold], Scaled@letpos],
        Rotate[Text[Style["Temporal variance in mean lag", LabelSize],
          Scaled@ylabpos], 90 Degree],
        Text[Style["", LabelSize], Scaled@{0.5, 1}]
       },
      PlotRangeClipping -> False
     ],
     Show[
      Table[ListPlot[Table[{gens[rep][[1, i]], Variance[
            Table[ns[rep][[1, j]] / numparents[rep][[1, j]] - 1, {j, i - window, i}]]},
          {i, window + 1, imax[rep], window}], Joined -> True,
        Axes -> False, PlotStyle -> Gray], {rep, 0, repmax}],
      PlotRange -> {{0, totaltime}, {0, 0.1}},
      Frame -> {False, False, False, True},
      FrameTicks -> {None, None, None, All},
      FrameStyle -> {Automatic, Automatic,
        Automatic, Directive[FontSize -> TickSize, FontColor -> Gray]},
      ImagePadding -> Pad2,
      PlotRangePadding -> None,
      ImageSize -> FigureSize,
      Epilog -> {
        Rotate[Text[Style["Temporal variance in growth rate", LabelSize, Gray],
          Scaled@(ylabpos * {-1, 1} + {1, 0})], 270 Degree]
       },
      PlotRangeClipping -> False
     ]
    }];

(*Export[imagedir<>"TradVarianceTimeSeries.pdf",%];*)

(*Overlay[{
  Show[
   Table[
    ListPlot[Table[{gens[rep][[1,i]],Variance[Table[dk gens[rep][[1,j]]^2/2-Mean[
             phenos[rep][[j]]],{j,i-window,i}]]^1/2/Mean[
         Table[dk gens[rep][[1,j]]^2/2-Mean[phenos[rep][[j]]],{j,i-window,i}]]},
```

```
        {i,window,imax[rep],di}],Joined→True,Axes→False,
       PlotStyle→Black],{rep,0,repmax}],
     PlotRange→{{0,totaltime},{0,All}},
     Frame→{True,True,False,False},
     ImagePadding→Pad2,
     PlotRangePadding→None,
     FrameLabel→{"",""},
     ImageSize→FigureSize,
     FrameStyle→Directive[FontSize→TickSize],
     FrameTicksStyle→{{Black,Black},{Directive[FontColor→White],Black}},
     Epilog→{
       Text[Style["B",LabelSize,Bold],Scaled@letpos],
       Rotate[Text[Style["CV in mean lag",LabelSize],Scaled@ylabpos],90 Degree],
       Text[Style["",LabelSize],Scaled@{0.5,1}]
      },
     PlotRangeClipping→False
    ],
    Show[
     Table[ListPlot[Table[{gens[rep][[1,i]],
          Variance[Table[ns[rep][[1,j]]/numparents[rep][[1,j]]-1,{j,i-window,i}]]^(1/2)/
           Mean[Table[ns[rep][[1,j]]/numparents[rep][[1,j]]-1,{j,i-window,i}]]},
        {i,window,imax[rep],di}],Joined→True,Axes→False,PlotStyle→Gray],
      {rep,0,repmax}],
     PlotRange→{{0,totaltime},{0,All}},
     Frame→{False,False,False,True},
     FrameTicks→{None,None,None,All},
     FrameStyle→
      {Automatic,Automatic,Automatic,Directive[FontSize→TickSize,FontColor→Gray]},
     ImagePadding→Pad2,
     PlotRangePadding→None,
     ImageSize→FigureSize,
     Epilog→{
       Rotate[Text[Style["CV in mean growth rate",LabelSize,Gray],
         Scaled@(ylabpos*{-1,1}+{1,0})],90 Degree]
      },
     PlotRangeClipping→False
    ]
   }]*)

  (*lag-1 autocorrelation in mean lag
    and population growth rate over previous window*)
  fig3C = Show[
     Table[ListPlot[
       Table[{gens[rep][[1, i]], CorrelationFunction[
          Table[dk (gens[rep][[1, j]] - burngens)^2 / 2 - Mean[phenos[rep][[j]]],
           {j, i - window, i}], 1]}, {i, window + 1, imax[rep], window}],
       Joined → True, Axes → False, PlotStyle → Black], {rep, 0, repmax}],
     Table[ListPlot[
```

```
      Table[{gens[rep][[1, i]], CorrelationFunction[
          Table[ns[rep][[1, j]] / numparents[rep][[1, j]] - 1, {j, i - window, i}], 1]},
        {i, window + 1, imax[rep], window}], Joined → True, Axes → False,
      PlotStyle → Gray], {rep, 0, repmax}],
    PlotRange → {{0, totaltime}, {-1, 1}},
    Frame → {True, True, False, False},
    PlotRangePadding → None,
    FrameLabel → {Style["Generation", LabelSize], ""},
    ImagePadding → Pad2,
    ImageSize → FigureSize,
    FrameStyle → Directive[FontSize → TickSize],
    FrameTicksStyle → {{Black, Black}, {Black, Black}},
    Epilog → {
      Text[Style["C", LabelSize, Bold], Scaled@letpos],
      Rotate[
       Text[Style["Lag-1 autocorrelation", LabelSize], Scaled@ylabpos], 90 Degree],
      Text[Style["", LabelSize], Scaled@{0.5, 1}]
     },
    PlotRangeClipping → False
   ];

(*Export[imagedir<>"TradAutoCorrTimeSeries.pdf",%];*)

Clear[KK, B, ω, μ, α, n, dk, rep, σθ, repmax, window, totaltime]
```

Figure 3 (D-F): early warning signs over time series with increasing k (alternative)

```
Pad2 = {{50, 50}, {40, 15}}; (*whitespace to leave around figures,
{{left,right},{bottom,top}}*)

(*parameter values*)
KK = 512;
B = 2;
ω = 3;
μ = 0.0002;
α = 0.05^(1/2);
n = 50;
dk = 0.000001;
σθ = 0;
repmax = 9;
burngens = 1000;
totaltime = 200 000 + burngens;

(*size of moving window;
number of recorded time points to calculate autocorr and var in mean lag over*)
window = 30;

(*directory and sim name*)
Clear[sim]
datadir = simdir <> "altdatatimeseries3/";
sim[rep_] := "K" <> ToString[KK] <> "_B" <> ToString[B] <> "_w" <>
    ToString[ω] <> "_u" <> ToString[μ] <> "_alphasqrd" <> ToString[α^2] <> "_n" <>
    ToString[n] <> "_dk" <> "0.000001" <> "_rep" <> ToString[rep] <> ".csv";
```

```
(*simulation results*)
Clear[gens, genos, phenos, ns, numparents]
gens[rep_] := gens[rep] = Import[datadir <> "gens_" <> sim[rep]];
genos[rep_] := genos[rep] = Import[datadir <> "genos_" <> sim[rep]];
phenos[rep_] := phenos[rep] = Import[datadir <> "phenos_" <> sim[rep]];
ns[rep_] := ns[rep] = Import[datadir <> "n_" <> sim[rep]];
numparents[rep_] :=
  numparents[rep] = Import[datadir <> "numparents_" <> sim[rep]];

(*number of recordings and max time*)
Clear[imax, tmax]
imax[rep_] := imax[rep] = Length[gens[rep][[1]]];
tmax[rep_] := tmax[rep] = gens[[1, imax[rep]]];

(*survivors of viability selection*)
(*Show[
 Table[ListPlot[Table[{gens[rep][[1,i]],ns[rep][[1,i]]},{i,0,imax[rep],di}],
   Joined→True,PlotRange→{0,All},PlotStyle→Black],{rep,0,repmax}],
 Plot[KK,{t,0,totaltime}(*,PlotStyle→{Thin}*),PlotStyle→Black],
 Plot[2B/(2B-1) KK,{t,0,totaltime},PlotStyle→{Black,Thick}],
 PlotRange→{{0,totaltime},All},
 Frame→{True,True,False,False},
 PlotRangePadding→None,
 FrameLabel→{"","# survivors"}
]*)

(*mean lag and population growth rate*)
(*Show[
 Table[ListPlot[
   Table[{gens[rep][[1,i]],dk gens[rep][[1,i]]^2/2-Mean[phenos[rep][[i]]]},
    {i,1,imax[rep],di}],Joined→True,Axes→False,PlotStyle→Black],{rep,0,repmax}],
 Table[ListPlot[
   Table[{gens[rep][[1,i]],ns[rep][[1,i]]/numparents[rep][[1,i]]-1},
    {i,1,imax[rep],di}],Joined→True,Axes→False,PlotStyle→Gray],{rep,0,repmax}],
 PlotRange→{{0,totaltime},All},
 Frame→{True,True,False,False},
 PlotRangePadding→None,
 FrameLabel→{"",""}
]*)

fig3D = Overlay[{
    Show[
     Table[ListPlot[Table[{gens[rep][[1, i]], dk (gens[rep][[1, i]] - burngens)^2 / 2 -
          Mean[phenos[rep][[i]]]}, {i, window + 1, imax[rep], window}],
       Joined → True, Axes → False, PlotStyle → Black], {rep, 0, repmax}],
     PlotRange → {{0, totaltime}, {-1, 8}},
     Frame → {True, True, False, False},
     ImagePadding → Pad2,
     PlotRangePadding → None,
```

```
      FrameLabel → {"", ""},
      ImageSize → FigureSize,
      FrameStyle → Directive[FontSize → TickSize],
      FrameTicksStyle → {{Black, Black}, {Directive[FontColor → White], Black}},
      Epilog → {
        Text[Style["D", LabelSize, Bold], Scaled@letpos],
        Rotate[Text[
          Style["Mean phenotypic lag", LabelSize], Scaled@ylabpos], 90 Degree],
        Text[Style["Alternative", LabelSize], Scaled@{0.5, 1}]
       },
      PlotRangeClipping → False
     ],
     Show[
      Table[ListPlot[
        Table[{gens[rep][[1, i]], ns[rep][[1, i]] / numparents[rep][[1, i]] - 1},
         {i, window + 1, imax[rep], window}], Joined → True,
        Axes → False, PlotStyle → Gray], {rep, 0, repmax}],
      PlotRange → {{0, totaltime}, {-1.2, 1.2}},
      Frame → {False, False, False, True},
      FrameTicks → {None, None, None, All},
      FrameStyle → {Automatic, Automatic,
        Automatic, Directive[FontSize → TickSize, FontColor → Gray]},
      ImagePadding → Pad2,
      PlotRangePadding → None,
      ImageSize → FigureSize,
      Epilog → {
        Rotate[Text[Style["Population growth rate", LabelSize, Gray],
          Scaled@(ylabpos * {-1, 1} + {1, 0})], 270 Degree]
       },
      PlotRangeClipping → False
     ]
    }];

(*Export[imagedir<>"AltLagGrowthTimeSeries.pdf",%];*)

(*variance in mean lag and population growth rate over previous window*)
fig3E = Overlay[{
     Show[
      Table[ListPlot[Table[{gens[rep][[1, i]], Variance[
            Table[dk (gens[rep][[1, j]] - burngens)^2 / 2 - Mean[phenos[rep][[j]]],
             {j, i - window, i}]]}, {i, window + 1, imax[rep], window}],
        Joined → True, Axes → False, PlotStyle → Black], {rep, 0, repmax}],
      PlotRange → {{0, totaltime}, {0, 1}},
      Frame → {True, True, False, False},
      ImagePadding → Pad2,
      PlotRangePadding → None,
      FrameLabel → {"", ""},
      ImageSize → FigureSize,
      FrameStyle → Directive[FontSize → TickSize],
      FrameTicksStyle → {{Black, Black}, {Directive[FontColor → White], Black}},
      Epilog → {
        Text[Style["E", LabelSize, Bold], Scaled@letpos],
        Rotate[Text[Style["Temporal variance in mean lag", LabelSize],
```

```
          Scaled@ylabpos], 90 Degree],
        Text[Style["", LabelSize], Scaled@{0.5, 1}]
       },
      PlotRangeClipping → False
     ],
     Show[
      Table[ListPlot[Table[{gens[rep][[1, i]], Variance[
            Table[ns[rep][[1, j]] / numparents[rep][[1, j]] - 1, {j, i - window, i}]]},
         {i, window + 1, imax[rep], window}], Joined → True,
        Axes → False, PlotStyle → Gray], {rep, 0, repmax}],
      PlotRange → {{0, totaltime}, {0, 0.1}},
      Frame → {False, False, False, True},
      FrameTicks → {None, None, None, All},
      FrameStyle → {Automatic, Automatic,
        Automatic, Directive[FontSize → TickSize, FontColor → Gray]},
      ImagePadding → Pad2,
      PlotRangePadding → None,
      ImageSize → FigureSize,
      Epilog → {
        Rotate[Text[Style["Temporal variance in growth rate", LabelSize, Gray],
          Scaled@(ylabpos * {-1, 1} + {1, 0})], 270 Degree]
       },
      PlotRangeClipping → False
     ]
    }];

(*Export[imagedir<>"AltVarianceTimeSeries.pdf",%];*)

(*Overlay[{
  Show[
   Table[
    ListPlot[Table[{gens[rep][[1,i]],Variance[Table[dk gens[rep][[1,j]]^2/2-Mean[
            phenos[rep][[j]]],{j,i-window,i}]]^(1/2)/Mean[
          Table[dk gens[rep][[1,j]]^2/2-Mean[phenos[rep][[j]]],{j,i-window,i}]]},
      {i,window,imax[rep],di}],Joined→True,Axes→False,
     PlotStyle→Black],{rep,0,repmax}],
   PlotRange→{{0,totaltime},{0,All}},
   Frame→{True,True,False,False},
   ImagePadding→Pad2,
   PlotRangePadding→None,
   FrameLabel→{"",""},
   ImageSize→FigureSize,
   FrameStyle→Directive[FontSize→TickSize],
   FrameTicksStyle→{{Black,Black},{Directive[FontColor→White],Black}},
   Epilog→{
     Text[Style["B",LabelSize,Bold],Scaled@letpos],
     Rotate[Text[Style["CV in mean lag",LabelSize],Scaled@ylabpos],90 Degree],
     Text[Style["",LabelSize],Scaled@{0.5,1}]
    },
```

```
    PlotRangeClipping→False
   ],
   Show[
    Table[ListPlot[Table[{gens[rep][[1,i]],
        Variance[Table[ns[rep][[1,j]]/numparents[rep][[1,j]]-1,{j,i-window,i}]]^(1/2)/
         Mean[Table[ns[rep][[1,j]]/numparents[rep][[1,j]]-1,{j,i-window,i}]]},
       {i,window,imax[rep],di}],Joined→True,Axes→False,PlotStyle→Gray],
     {rep,0,repmax}],
    PlotRange→{{0,totaltime},{0,All}},
    Frame→{False,False,False,True},
    FrameTicks→{None,None,None,All},
    FrameStyle→
     {Automatic,Automatic,Automatic,Directive[FontSize→TickSize,FontColor→Gray]},
    ImagePadding→Pad2,
    PlotRangePadding→None,
    ImageSize→FigureSize,
    Epilog→{
      Rotate[Text[Style["CV in mean growth rate",LabelSize,Gray],
        Scaled@(ylabpos*{-1,1}+{1,0})],90 Degree]
     },
    PlotRangeClipping→False
   ]
  }]*)

(*lag-1 autocorrelation in mean lag
  and population growth rate over previous window*)
fig3F = Show[
    Table[ListPlot[
      Table[{gens[rep][[1, i]], CorrelationFunction[
         Table[dk (gens[rep][[1, j]] - burngens)^2 / 2 - Mean[phenos[rep][[j]]],
          {j, i - window, i}], 1]}, {i, window + 1, imax[rep], window}],
      Joined → True, Axes → False, PlotStyle → Black], {rep, 0, repmax}],
    Table[ListPlot[
      Table[{gens[rep][[1, i]], CorrelationFunction[
         Table[ns[rep][[1, j]] / numparents[rep][[1, j]] - 1, {j, i - window, i}], 1]},
       {i, window + 1, imax[rep], window}], Joined → True, Axes → False,
      PlotStyle → Gray], {rep, 0, repmax}],
    PlotRange → {{0, totaltime}, {-1, 1}},
    Frame → {True, True, False, False},
    PlotRangePadding → None,
    FrameLabel → {Style["Generation", LabelSize], ""},
    ImagePadding → Pad2,
    ImageSize → FigureSize,
    FrameStyle → Directive[FontSize → TickSize],
    FrameTicksStyle → {{Black, Black}, {Black, Black}},
    Epilog → {
      Text[Style["F", LabelSize, Bold], Scaled@letpos],
      Rotate[
       Text[Style["Lag-1 autocorrelation", LabelSize], Scaled@ylabpos], 90 Degree],
      Text[Style["", LabelSize], Scaled@{0.5, 1}]
```

```
    },
   PlotRangeClipping → False
  ];

(*Export[imagedir<>"AltAutoCorrTimeSeries.pdf",%];*)

Clear[KK, B, ω, μ, α, n, dk, rep, σθ, repmax, window, totaltime]
```

Figure 3 (G-H): Kendall rank correlation coefficients and related statistics

```
(*parameter values*)
KK = 512;
B = 2;
ω = 3;
μ = 0.0002;
α = 0.05^(1/2);
n = 50;
dk = 0.000001;
σθ = 0;
repmax = 9;
burngens = 1000;
totaltime = 200 000 + burngens;

(*size of moving window;
number of recorded time points to calculate autocorr and var in mean lag over*)
window = 30;

(*directory and sim name*)
Clear[sim]
datadir = simdir <> "altdatatimeseries3/";
sim[rep_] := "K" <> ToString[KK] <> "_B" <> ToString[B] <> "_w" <>
   ToString[ω] <> "_u" <> ToString[μ] <> "_alphasqrd" <> ToString[α^2] <> "_n" <>
   ToString[n] <> "_dk" <> "0.000001" <> "_rep" <> ToString[rep] <> ".csv";

(*simulation results*)
Clear[gens, genos, phenos, ns, numparents]
gens[rep_] := gens[rep] = Import[datadir <> "gens_" <> sim[rep]];
genos[rep_] := genos[rep] = Import[datadir <> "genos_" <> sim[rep]];
phenos[rep_] := phenos[rep] = Import[datadir <> "phenos_" <> sim[rep]];
ns[rep_] := ns[rep] = Import[datadir <> "n_" <> sim[rep]];
numparents[rep_] :=
  numparents[rep] = Import[datadir <> "numparents_" <> sim[rep]];

(*number of recordings and max time*)
Clear[imax, tmax]
imax[rep_] := imax[rep] = Length[gens[rep][[1]]];
tmax[rep_] := tmax[rep] = gens[[1, imax[rep]]];


(*variance in mean lag and population growth rate over previous window*)
Clear[lagvar, growthvar]
lagvar[rep_] := lagvar[rep] = Table[{gens[rep][[1, i]],
```

```
    Variance[Table[dk (gens[rep][[1, j]] - burngens)^2 / 2 - Mean[phenos[rep][[j]]],
      {j, i - window, i}]]}, {i, window + 1, imax[rep], window}];
growthvar[rep_] := growthvar[rep] = Table[{gens[rep][[1, i]], Variance[
     Table[ns[rep][[1, j]] / numparents[rep][[1, j]] - 1, {j, i - window, i}]]},
   {i, window + 1, imax[rep], window}];

alttaulagvar = Table[KendallTau[lagvar[rep]][[1, 2]], {rep, 0, repmax}] // N;
alttaugrowthvar = Table[KendallTau[growthvar[rep]][[1, 2]], {rep, 0, repmax}] // N;

(*lag-1 autocorrelation in mean lag
  and population growth rate over previous window*)
Clear[lagac, growthac]
lagac[rep_] := lagac[rep] = Table[{gens[rep][[1, i]], CorrelationFunction[
     Table[dk (gens[rep][[1, j]] - burngens)^2 / 2 - Mean[phenos[rep][[j]]],
      {j, i - window, i}], 1]}, {i, window + 1, imax[rep], window}];
growthac[rep_] := growthac[rep] = Table[{gens[rep][[1, i]], CorrelationFunction[
     Table[ns[rep][[1, j]] / numparents[rep][[1, j]] - 1, {j, i - window, i}], 1]},
   {i, window + 1, imax[rep], window}];

alttaulagac = Table[KendallTau[lagac[rep]][[1, 2]], {rep, 0, repmax}] // N;
alttaugrowthac = Table[KendallTau[growthac[rep]][[1, 2]], {rep, 0, repmax}] // N;

(*directory and sim name*)
Clear[sim]
datadir = simdir <> "datatimeseries3/";
sim[rep_] := "K" <> ToString[KK] <> "_B" <> ToString[B] <> "_w" <>
   ToString[ω] <> "_u" <> ToString[μ] <> "_alphasqrd" <> ToString[α^2] <> "_n" <>
   ToString[n] <> "_dk" <> "0.000001" <> "_rep" <> ToString[rep] <> ".csv";

(*simulation results*)
Clear[gens, genos, phenos, ns, numparents]
gens[rep_] := gens[rep] = Import[datadir <> "gens_" <> sim[rep]];
genos[rep_] := genos[rep] = Import[datadir <> "genos_" <> sim[rep]];
phenos[rep_] := phenos[rep] = Import[datadir <> "phenos_" <> sim[rep]];
ns[rep_] := ns[rep] = Import[datadir <> "n_" <> sim[rep]];
numparents[rep_] :=
  numparents[rep] = Import[datadir <> "numparents_" <> sim[rep]];

(*number of recordings and max time*)
Clear[imax, tmax]
imax[rep_] := imax[rep] = Length[gens[rep][[1]]];
tmax[rep_] := tmax[rep] = gens[[1, imax[rep]]];


(*variance in mean lag and population growth rate over previous window*)
Clear[lagvar, growthvar]
lagvar[rep_] := lagvar[rep] = Table[{gens[rep][[1, i]],
    Variance[Table[dk ( gens[rep][[1, j]] - burngens)^2 / 2 - Mean[phenos[rep][[j]]],
      {j, i - window, i}]]}, {i, window + 1, imax[rep], window}];
growthvar[rep_] := growthvar[rep] = Table[{gens[rep][[1, i]], Variance[
     Table[ns[rep][[1, j]] / numparents[rep][[1, j]] - 1, {j, i - window, i}]]},
```

```
    {i, window + 1, imax[rep], window}];

tradtaulagvar = Table[KendallTau[lagvar[rep]][[1, 2]], {rep, 0, repmax}] // N;
tradtaugrowthvar = Table[KendallTau[growthvar[rep]][[1, 2]], {rep, 0, repmax}] // N;

(*lag-1 autocorrelation in mean lag
  and population growth rate over previous window*)
Clear[lagac, growthac]
lagac[rep_] := lagac[rep] = Table[{gens[rep][[1, i]], CorrelationFunction[
      Table[dk (gens[rep][[1, j]] - burngens)^2 / 2 - Mean[phenos[rep][[j]]],
       {j, i - window, i}], 1]}, {i, window + 1, imax[rep], window}];
growthac[rep_] := growthac[rep] = Table[{gens[rep][[1, i]], CorrelationFunction[
      Table[ns[rep][[1, j]] / numparents[rep][[1, j]] - 1, {j, i - window, i}], 1]},
    {i, window + 1, imax[rep], window}];

tradtaulagac = Table[KendallTau[lagac[rep]][[1, 2]], {rep, 0, repmax}] // N;
tradtaugrowthac = Table[KendallTau[growthac[rep]][[1, 2]], {rep, 0, repmax}] // N;

Clear[KK, B, ω, μ, α, n, dk, rep, σθ, repmax, totaltime, window]

fig3G =
  BoxWhiskerChart[
   {{tradtaulagvar, alttaulagvar}, {tradtaugrowthvar, alttaugrowthvar}},
   {{"Outliers"}, {"MedianMarker", White}},
   ChartStyle → {{Black, Gray}, None},
   ChartLabels → {{Style["Mean lag", 16], Style["Population growth rate", 16]},
     {Style["Traditional", 11], Style["Alternative", 11]}},
   FrameStyle → Directive[FontSize → TickSize],
   Epilog → {
     Text[Style["G", LabelSize, Bold], Scaled@letpos],
     Rotate[Text[Style["Kendall's τ", LabelSize], Scaled@ylabpos], 90 Degree],
     Text[Style["Temporal variance", LabelSize], Scaled@{0.25, 0.9}]
    },
   PlotRangeClipping → False,
   ImagePadding → Pad2
  ];
(*Export[imagedir<>"TauVariance.pdf",%];*)

TTest[{tradtaulagvar, alttaulagvar},
 Automatic, {"TestDataTable", "DegreesOfFreedom"}]
(*MannWhitneyTest[{tradtaulagvar,alttaulagvar},Automatic,"TestDataTable"]*)
```

{

	Statistic	P-Value
T	-0.478989	0.640273

, 12.4155}

```
TTest[{tradtaugrowthvar, alttaugrowthvar},
 Automatic, {"TestDataTable", "DegreesOfFreedom"}]
(*MannWhitneyTest[{tradtaugrowthvar,alttaugrowthvar},Automatic,"TestDataTable"]*)
```

{

	Statistic	P-Value
T	1.74619	0.109008

, 10.8419}

```
fig3H =
  BoxWhiskerChart[
   {{tradtaulagac, alttaulagac}, {tradtaugrowthac, alttaugrowthac}},
   {{"Outliers"}, {"MedianMarker", White}},
   ChartStyle → {{Black, Gray}, None},
   ChartLabels → {{Style["Mean lag", 16], Style["Population growth rate", 16]},
     {Style["Traditional", 11], Style["Alternative", 11]}},
   FrameStyle → Directive[FontSize → TickSize],
   Epilog → {
     Text[Style["H", LabelSize, Bold], Scaled@letpos],
     Rotate[Text[Style["Kendall's τ", LabelSize], Scaled@ylabpos], 90 Degree],
     Text[Style["Lag-1 autocorrelation", LabelSize], Scaled@{0.3, 0.9}]
    },
   PlotRangeClipping → False,
   ImagePadding → Pad2
  ];
(*Export[imagedir<>"TauAutocorrelation.pdf",%];*)
```

```
TTest[{tradtaulagac, alttaulagac},
 Automatic, {"TestDataTable", "DegreesOfFreedom"}]
(*MannWhitneyTest[{tradtaulagac,alttaulagac},Automatic,"TestDataTable"]*)
```

{

	Statistic	P-Value
T	-3.18157	0.0051676

, 18}

```
TTest[{tradtaugrowthac, alttaugrowthac},
 Automatic, {"TestDataTable", "DegreesOfFreedom"}]
(*MannWhitneyTest[{tradtaugrowthac,alttaugrowthac},Automatic,"TestDataTable"]*)
```

{

	Statistic	P-Value
T	-2.89168	0.0125653

, 13.0505}

Does the most positive distribution have a mean different from zero?

```
TTest[alttaugrowthac, Automatic, {"TestDataTable", "DegreesOfFreedom"}]
```

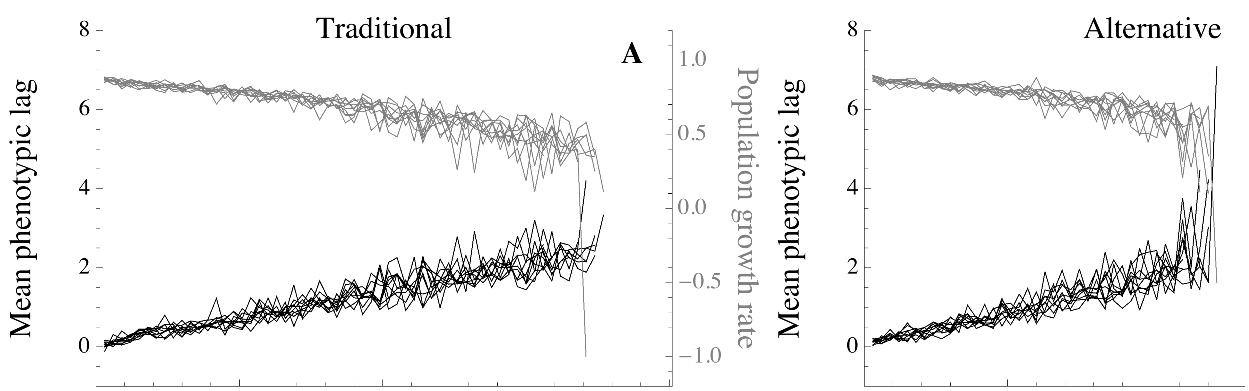
{

	Statistic	P-Value
T	1.31252	0.221829

, 9}

Figure 3 (A-H)

```
GraphicsGrid[{{fig3A, fig3D}, {fig3B, fig3E}, {fig3C, fig3F}, {fig3G, fig3H}},
 ImageSize → 800, Spacings → {0, 0}]
Export[imagedir <> "EarlyWarningSignsLarge.eps", %];
```



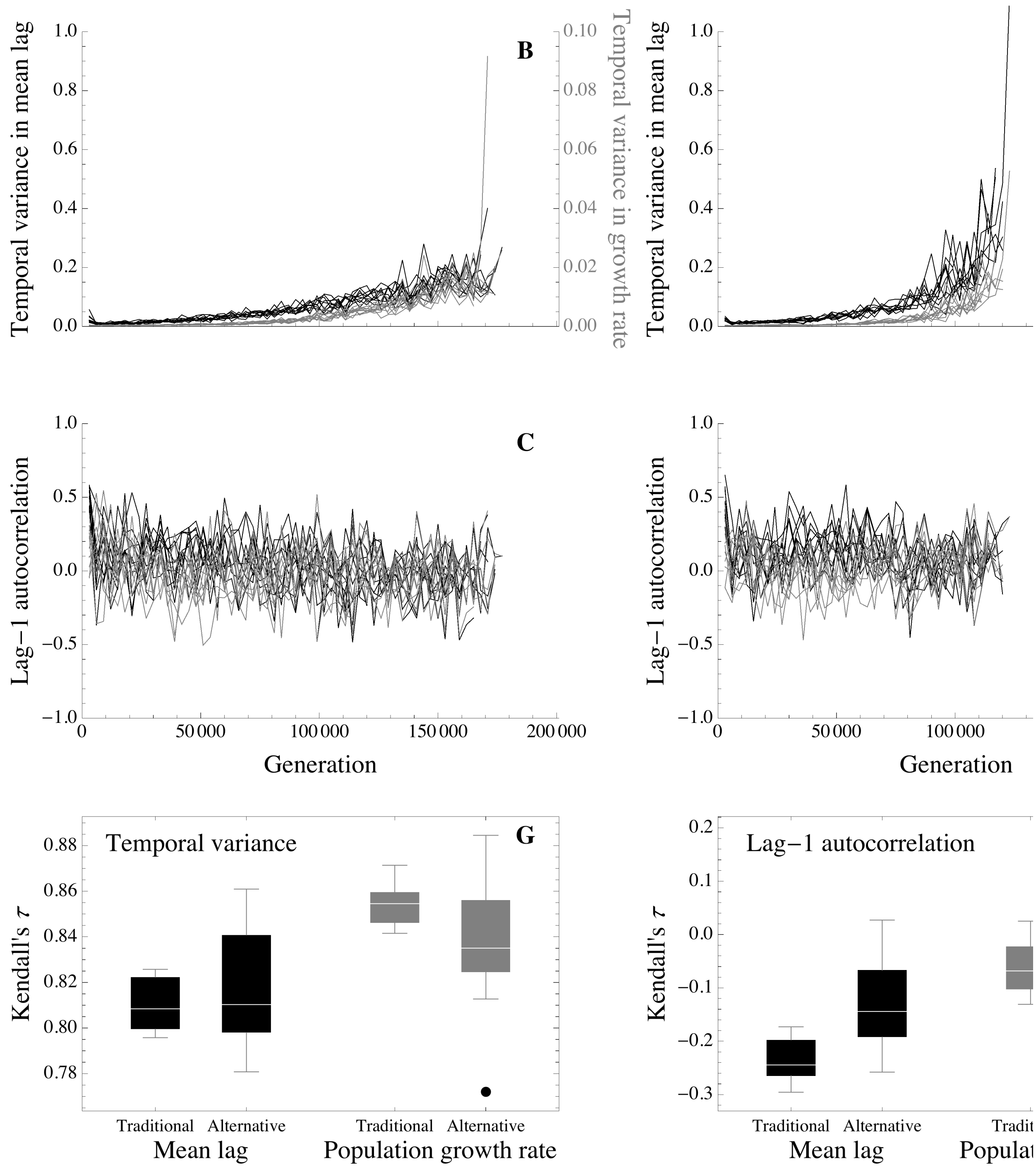


Figure 4 (A-D): hysteresis snapshot (traditional)

```
(*parameter values*)
KK = 512;
```

```
B = 3;
ω = 3;
μ = 0.0002;
α = 0.05^(1/2);
n = 50;
k = 0.1;
σθ = 0;

burngens = 1000;
genjump = 5000; (*time when optimum jumps*)
jumpsize = 5; (*amt by which optimum jumps*)
maxrep = 9;(*number of replicates minus 1*)
mintime = genjump - 500;
maxtime = genjump + 500;

(*directory and sim name*)
datadir = simdir <> "tradhysteresis/";
Clear[sim]
sim[i_] := "K" <> ToString[KK] <> "_B" <> ToString[B] <> "_w" <> ToString[ω] <>
    "_u" <> ToString[μ] <> "_alphasqrd" <> ToString[α^2] <> "_n" <> ToString[n] <>
    "_k" <> ToString[NumberForm[k, {2, 2}]] <> "_rep" <> ToString[i] <> ".csv";

(*simulation results*)
Clear[gens, genos, phenos, ns, numparents]
gens[i_] := gens[i] = Import[datadir <> "gens_" <> sim[i]];
genos[i_] := genos[i] = Import[datadir <> "genos_" <> sim[i]];
phenos[i_] := phenos[i] = Import[datadir <> "phenos_" <> sim[i]];
ns[i_] := ns[i] = Import[datadir <> "n_" <> sim[i]];
numparents[i_] := numparents[i] = Import[datadir <> "numparents_" <> sim[i]];

(*indices to plot*)
Clear[imin, imax]
imin[i_] := imin[i] = Position[gens[i][[1]], mintime][[1]][[1]]
imax[i_] :=
 imax[i] = Max[Position[gens[i][[1]], maxtime][[1]][[1]], Length[gens[i][[1]]]]

(*mean phenotypic lag*)
plot1 = Show[
   (*Plot[Max[L/.NSolve[(E^(-(-barg+θ)^2/(2 ω^2)) (-barg+θ) σg^2)/ω^2==k/.θ->L+barg/.σg->((4n μ α^2Ne)/(1+(α^2Ne)/Vs))^(1/2)/.Vs->ω^2+1/.
        Ne->(2B)/(2B-1)KK,L]],{t,mintime,maxtime},
    PlotRange->{0,All},PlotStyle->{Gray,Thick,Dashing[Large]},Axes->False],
   Plot[Min[L/.NSolve[(E^(-(-barg+θ)^2/(2 ω^2)) (-barg+θ) σg^2)/ω^2==k/.θ->L+barg/.σg->((4n μ α^2Ne)/(1+(α^2Ne)/Vs))^(1/2)/.Vs->ω^2+1/.
        Ne->(2B)/(2B-1)KK,L]],{t,mintime,maxtime},PlotRange->{0,All},
    PlotStyle->{Black,Thick,Dashing[Large]},Axes->False],
```

```
Plot[Max[L/.NSolve[(e^(-((-barg+θ)^2/(2 ω^2))) (-barg+θ) σg^2)/ω^2==k/.θ→L+barg/.σg→(4n μ α^2Ne)^(1/2)/.Vs→ω^2+1/.
      Ne→(2B)/(2B-1) KK,L]] ,{t,mintime,maxtime},
  PlotRange→{0,All},PlotStyle→{Gray,Thick,Dotted}],

Plot[Min[L/.NSolve[(e^(-((-barg+θ)^2/(2 ω^2))) (-barg+θ) σg^2)/ω^2==k/.θ→L+barg/.σg→(4n μ α^2Ne)^(1/2)/.Vs→ω^2+1/.
      Ne→(2B)/(2B-1) KK,L] ],{t,mintime,maxtime},
  PlotRange→{0,All},PlotStyle→{Black,Thick,Dotted}],*)
Table[ListPlot[Table[{gens[i][[1, j]], If[gens[i][[1, j]] < genjump,
      k (gens[i][[1, j]] - burngens) - Mean[phenos[i][[j]]],
      k (gens[i][[1, j]] - burngens) + jumpsize - Mean[phenos[i][[j]]]]},
    {j, imin[i], imax[i]}], Joined → True, PlotStyle → Black,
   Axes → False], {i, 0, maxrep}],
PlotRange → {{mintime, maxtime}, {0, 50}},
Frame → {True, True, False, False},
PlotRangePadding → None,
FrameLabel → {"", Style["", LabelSize]},
FrameStyle → Directive[FontSize → TickSize],
Epilog → {
   Text[Style["A", LabelSize, Bold], Scaled@letpos],
   Rotate[Text[Style["Mean lag", LabelSize], Scaled@ylabpos], 90 Degree],
   Text[Style["Traditional", LabelSize], Scaled@{0.5, 1}]
  },
ImagePadding → Pad,
FrameTicksStyle → {{Black, Black}, {Directive[FontColor → White], Black}},
PlotRangeClipping → False
];


(*(*genetic variance*)
plot2=Show[

Plot[σg^2/.σg→((4n μ α^2Ne)/(1+(α^2Ne)/Vs))^(1/2) /.Vs→ω^2+1/.Ne→(2B)/(2B-1) KK,
  {t,mintime,maxtime},PlotRange→{0,1},
  PlotStyle→{Black,Thick,Dashing[Large]},Axes→False],
Plot[σg^2/.σg^2→4n μ α^2Ne/.Ne→(2B)/(2B-1) KK,{t,mintime,maxtime},
  PlotRange→{0,0.5},PlotStyle→{Black,Thick,Dotted}],
Table[ListPlot[Table[{gens[i][[1,j]],Variance[genos[i][[j]]]},
    {j,imin[i],imax[i]}],Joined→True,PlotStyle→Black],{i,0,maxrep}],
Frame→{True,True,False,False},
PlotRangePadding→None,
FrameLabel→{"",Style["",LabelSize]},
FrameStyle→Directive[FontSize→TickSize],
Epilog→{
   Text[Style["B",LabelSize,Bold],Scaled@letpos],
   Rotate[Text[Style["Genetic variance",LabelSize],Scaled@ylabpos],90 Degree]
```

```
    },
   ImagePadding→Pad,
   FrameTicksStyle→{{Black,Black},{Directive[FontColor→White],Black}},
   PlotRangeClipping→False
  ];*)

(*rate of evo*)
plot2 = Show[
   Table[
    ListPlot[Table[{gens[i][[1, j]], (Mean[genos[i][[j]]] - Mean[genos[i][[j - 1]]])/(gens[i][[1, j]] - gens[i][[1, j - 1]])},
      {j, imin[i], imax[i]}], Joined → True, PlotRange → {{mintime, maxtime}, All},
     Axes → False, PlotStyle → Black], {i, 0, maxrep}],
   (*Plot[σg^2/(Sqrt[ⅇ] ω)/.σg→((4n μ α^2Ne)/(1+α^2Ne/Vs))^(1/2)/.Vs→ω^2+1/.Ne→2B/(2B-1)KK,{t,mintime,maxtime},
    PlotStyle→{Black,Thick,Dashing[Large]}],
   Plot[σg^2/(Sqrt[ⅇ] ω)/.σg→(4n μ α^2Ne)^(1/2)/.Ne→2B/(2B-1)KK,{t,mintime,maxtime},
    PlotStyle→{Black,Thick,Dotted}],*)
   PlotRange → {{mintime, maxtime}, {-0.05, 0.30}},
   Frame → {True, True, False, False},
   PlotRangePadding → None,
   FrameLabel → {Style["", LabelSize], Style["", LabelSize]},
   FrameStyle → Directive[FontSize → TickSize],
   Epilog → {
     Text[Style["B", LabelSize, Bold], Scaled@letpos],
     Rotate[
      Text[Style["Rate of evolution", LabelSize], Scaled@ylabpos], 90 Degree]
    },
   ImagePadding → Pad,
   FrameTicksStyle → {{Black, Black}, {Directive[FontColor → White], Black}},
   PlotRangeClipping → False
  ];

(*popn growth rate*)
plot3 = Show[
   Table[ListPlot[Table[{gens[i][[1, j]], ns[i][[1, j]] / numparents[i][[1, j]] - 1},
      {j, imin[i], imax[i]}], Joined → True,
     PlotRange → {{mintime, maxtime}, {-1, 2}}, Axes → False,
     PlotStyle → Black], {i, 0, maxrep}],
   Plot[0, {t, mintime, maxtime}, PlotStyle → {Black, Thick}],
   Frame → {True, True, False, False},
   PlotRangePadding → None,
   FrameLabel → {"", Style["", LabelSize]},
   FrameStyle → Directive[FontSize → TickSize],
   Epilog → {
     Text[Style["C", LabelSize, Bold], Scaled@letpos],
```

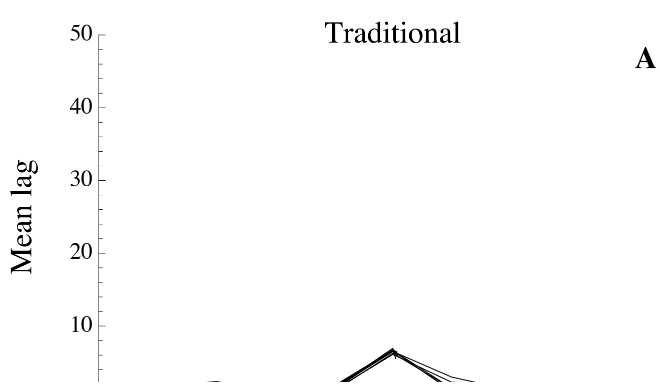
```
      Rotate[
        Text[Style["Population growth rate", LabelSize], Scaled@ylabpos], 90 Degree]
      },
    ImagePadding → Pad,
    FrameTicksStyle → {{Black, Black}, {Directive[FontColor → White], Black}},
    PlotRangeClipping → False
   ];

(*survivors of viability selection*)
plot4 = Show[
    Table[ListPlot[Table[{gens[i][[1, j]], ns[i][[1, j]]}, {j, imin[i], imax[i]}],
      Joined → True, PlotRange → {{mintime, maxtime}, {0, 1300}}, Axes → False,
      PlotStyle → Black, PlotRangeClipping → True], {i, 0, maxrep}],
    Plot[KK, {t, mintime, maxtime}, PlotStyle → {Black, Thick}],
    (*Plot[2B/(2B-1) KK,{t,mintime,maxtime},PlotStyle→{Thick,Black}],*)
    Frame → {True, True, False, False},
    PlotRangePadding → None,
    FrameLabel → {Style["Generation", LabelSize], Style["", LabelSize]},
    FrameStyle → Directive[FontSize → TickSize],
    Epilog → {
      Text[Style["D", LabelSize, Bold], Scaled@letpos],
      Rotate[Text[Style["Number of surviving offspring", LabelSize],
        Scaled@ylabpos], 90 Degree]
      },
    ImagePadding → Pad,
    FrameTicksStyle → {{Black, Black}, {Black, Black}},
    PlotRangeClipping → False
   ];

GraphicsGrid[{{plot1}, {plot2}, {plot3}, {plot4}(*,{plot5}*)},
  ImageSize → FigureSize, Spacings → 0]

Export[imagedir <> "TradHysteresisSnapshotLarge.pdf", %];

Clear[KK, B, ω, μ, α, n, k, rep, σθ]
```

Part::partw : Part 1 of {} does not exist. ≫

Part::partw : Part 1 of {} does not exist. ≫

Part::partw : Part 1 of {} does not exist. ≫

General::stop : Further output of Part::partw will be suppressed during this calculation. ≫



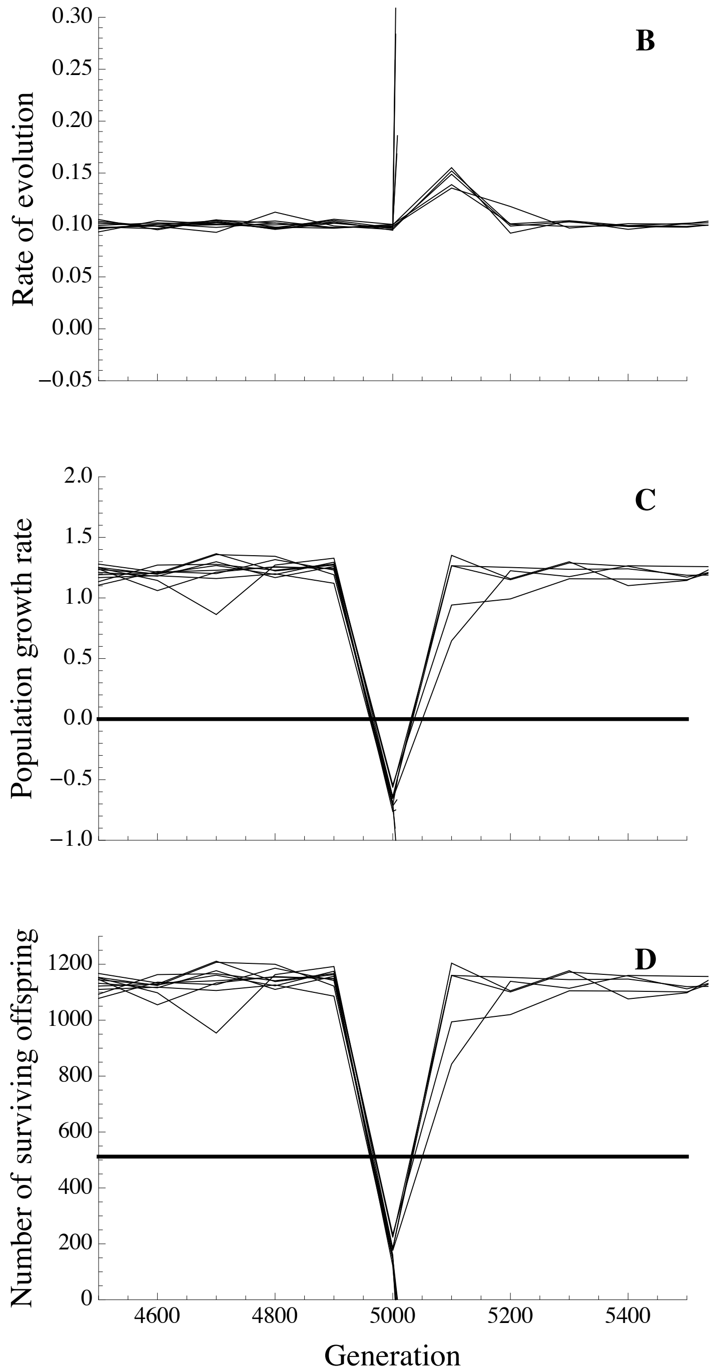


Figure 4 (E-F): hysteresis snapshot (alternative)

```
(*parameter values*)
KK = 512;
B = 3;
ω = 3;
```

```
μ = 0.0002;
α = 0.05^(1/2);
n = 50;
k = 0.1;
σθ = 0;

burngens = 1000;
genjump = 5000; (*time when optimum jumps*)
jumpsize = 5; (*amt by which optimum jumps*)
maxrep = 9;(*number of replicates minus 1*)
mintime = genjump - 500;
maxtime = genjump + 500;

(*directory and sim name*)
datadir = simdir <> "althysteresis/";
Clear[sim]
sim[i_] := "K" <> ToString[KK] <> "_B" <> ToString[B] <> "_w" <> ToString[ω] <>
   "_u" <> ToString[μ] <> "_alphasqrd" <> ToString[α^2] <> "_n" <> ToString[n] <>
   "_k" <> ToString[NumberForm[k, {2, 2}]] <> "_rep" <> ToString[i] <> ".csv";

(*simulation results*)
Clear[gens, genos, phenos, ns, numparents]
gens[i_] := gens[i] = Import[datadir <> "gens_" <> sim[i]];
genos[i_] := genos[i] = Import[datadir <> "genos_" <> sim[i]];
phenos[i_] := phenos[i] = Import[datadir <> "phenos_" <> sim[i]];
ns[i_] := ns[i] = Import[datadir <> "n_" <> sim[i]];
numparents[i_] := numparents[i] = Import[datadir <> "numparents_" <> sim[i]];

(*indices to plot*)
Clear[imin, imax]
imin[i_] := imin[i] = Position[gens[i][[1]], mintime][[1]][[1]]
imax[i_] :=
 imax[i] = Max[Position[gens[i][[1]], maxtime][[1]][[1]], Length[gens[i][[1]]]]

(*mean phenotypic lag*)
plot1 = Show[
   (*Plot[Max[L/.NSolve[ (e^(-(-barg+θ)^2/(2 ω^2)) (-barg+θ) σg^2)/ω^2 ==k/.θ->L+barg/.σg->((4n μ α^2Ne)/(1+(α^2Ne)/Vs))^(1/2) /.Vs->ω^2+1/.
        Ne->(2B)/(2B-1) KK,L]  ],{t,mintime,maxtime},
    PlotRange->{0,All},PlotStyle->{Gray,Thick,Dashing[Large]},Axes->False],
   Plot[Min[L/.NSolve[ (e^(-(-barg+θ)^2/(2 ω^2)) (-barg+θ) σg^2)/ω^2 ==k/.θ->L+barg/.σg->((4n μ α^2Ne)/(1+(α^2Ne)/Vs))^(1/2) /.Vs->ω^2+1/.
        Ne->(2B)/(2B-1) KK,L]],{t,mintime,maxtime},PlotRange->{0,All},
    PlotStyle->{Black,Thick,Dashing[Large]},Axes->False],*)

   Plot[Max[L /. NSolve[ (e^(-(-barg+θ)^2/(2 ω^2)) (-barg + θ) σg^2)/ω^2 == k /. θ -> L + barg /.
```

```
            σg → (4 n μ α^2 Ne)^(1/2) /. Vs → ω^2 + 1 /. Ne → (2 B)/(2 B - 1) KK, L]] ,
      {t, mintime, maxtime}, PlotRange → {0, All}, PlotStyle → {Black, Thick, Dotted},
      Axes → False],
    (*Plot[Min[L/.NSolve[(e^(-(-barg+θ)^2/(2 ω^2)) (-barg+θ) σg^2)/ω^2==k/.θ→L+barg/.σg→(4n μ α^2Ne)^(1/2)/.Vs→ω^2+1/.
          Ne→2B/(2B-1)KK,L] ],{t,mintime,maxtime},
      PlotRange→{0,All},PlotStyle→{Black,Thick,Dotted}],*)
    Table[ListPlot[Table[{gens[i][[1, j]], If[gens[i][[1, j]] < genjump,
          k (gens[i][[1, j]] - burngens) - Mean[phenos[i][[j]]],
          k (gens[i][[1, j]] - burngens) + jumpsize - Mean[phenos[i][[j]]]]},
        {j, imin[i], imax[i]}], Joined → True, PlotStyle → Black,
      Axes → False], {i, 0, maxrep}],
    PlotRange → {{mintime, maxtime}, {0, 50}},
    Frame → {True, True, False, False},
    PlotRangePadding → None,
    FrameLabel → {"", Style["", LabelSize]},
    FrameStyle → Directive[FontSize → TickSize],
    Epilog → {
      Text[Style["E", LabelSize, Bold], Scaled@letpos],
      Rotate[Text[Style["", LabelSize], Scaled@ylabpos], 90 Degree],
      Text[Style["Alternative", LabelSize], Scaled@{0.5, 1}]
     },
    ImagePadding → Pad,
    FrameTicksStyle →
     {{Directive[FontColor → White], Black}, {Directive[FontColor → White], Black}},
    PlotRangeClipping → False
   ];

 (*(*genetic variance*)
plot2=Show[
    Plot[σg^2/.σg→((4n μ α^2Ne)/(1+(α^2Ne)/Vs))^(1/2) /.Vs→ω^2+1/.Ne→2B/(2B-1)KK,
      {t,mintime,maxtime},PlotRange→{0,1},
      PlotStyle→{Black,Thick,Dashing[Large]},Axes→False],
    Plot[σg^2/.σg^2→4n μ α^2Ne/.Ne→2B/(2B-1)KK,{t,mintime,maxtime},
      PlotRange→{0,0.5},PlotStyle→{Black,Thick,Dotted}],
    Table[ListPlot[Table[{gens[i][[1,j]],Variance[genos[i][[j]]]},
       {j,imin[i],imax[i]}],Joined→True,PlotStyle→Black],{i,0,maxrep}],
    Frame→{True,True,False,False},
    PlotRangePadding→None,
    FrameLabel→{"",Style["",LabelSize]},
    FrameStyle→Directive[FontSize→TickSize],
    Epilog→{
      Text[Style["B",LabelSize,Bold],Scaled@letpos],
      Rotate[Text[Style["Genetic variance",LabelSize],Scaled@ylabpos],90 Degree]
     },
```

```
    ImagePadding→Pad,
    FrameTicksStyle→{{Black,Black},{Directive[FontColor→White],Black}},
    PlotRangeClipping→False
   ];*)

 (*rate of evo*)
 plot2 = Show[
    Table[
     ListPlot[Table[{gens[i][[1, j]], (Mean[genos[i][[j]]] - Mean[genos[i][[j - 1]]]) / (gens[i][[1, j]] - gens[i][[1, j - 1]])},
       {j, imin[i], imax[i]}], Joined → True, PlotRange → {{mintime, maxtime}, All},
      Axes → False, PlotStyle → Black], {i, 0, maxrep}],
    Plot[σg^2/(Sqrt[ⅇ] ω) /. σg → ((4 n μ α^2 Ne)/(1 + (α^2 Ne)/Vs))^(1/2) /. Vs → ω^2 + 1 /. Ne → (2 B)/(2 B - 1) KK,
     {t, mintime, maxtime}, PlotStyle → {Black, Thick, Dashing[Large]}],
    Plot[σg^2/(Sqrt[ⅇ] ω) /. σg → (4 n μ α^2 Ne)^(1/2) /. Ne → (2 B)/(2 B - 1) KK,
     {t, mintime, maxtime}, PlotStyle → {Black, Thick, Dotted}],
    PlotRange → {{mintime, maxtime}, {-0.05, 0.30}},
    Frame → {True, True, False, False},
    PlotRangePadding → None,
    FrameLabel → {Style["", LabelSize], Style["", LabelSize]},
    FrameStyle → Directive[FontSize → TickSize],
    Epilog → {
      Text[Style["F", LabelSize, Bold], Scaled@letpos],
      Rotate[Text[Style["", LabelSize], Scaled@ylabpos], 90 Degree]
     },
    ImagePadding → Pad,
    FrameTicksStyle →
     {{Directive[FontColor → White], Black}, {Directive[FontColor → White], Black}},
    PlotRangeClipping → False
   ];

 (*popn growth rate*)
 plot3 = Show[
    Table[ListPlot[Table[{gens[i][[1, j]], ns[i][[1, j]] / numparents[i][[1, j]] - 1},
       {j, imin[i], imax[i]}], Joined → True,
      PlotRange → {{mintime, maxtime}, {-1, 2}}, Axes → False,
      PlotStyle → Black], {i, 0, maxrep}],
    Plot[0, {t, mintime, maxtime}, PlotStyle → {Black, Thick}],
    Frame → {True, True, False, False},
    PlotRangePadding → None,
    FrameLabel → {"", Style["", LabelSize]},
    FrameStyle → Directive[FontSize → TickSize],
    Epilog → {
```

```
      Text[Style["G", LabelSize, Bold], Scaled@letpos],
      Rotate[Text[Style["", LabelSize], Scaled@ylabpos], 90 Degree]
     },
    ImagePadding → Pad,
    FrameTicksStyle →
     {{Directive[FontColor → White], Black}, {Directive[FontColor → White], Black}},
    PlotRangeClipping → False
   ];

(*survivors of viability selection*)
plot4 = Show[
    Table[ListPlot[Table[{gens[i][[1, j]], ns[i][[1, j]]}, {j, imin[i], imax[i]}],
      Joined → True, PlotRange → {{mintime, maxtime}, {0, 1300}}, Axes → False,
      PlotStyle → Black, PlotRangeClipping → True], {i, 0, maxrep}],
    Plot[KK, {t, mintime, maxtime}, PlotStyle → {Black, Thick}],
    (*Plot[2B/(2B-1) KK,{t,mintime,maxtime},PlotStyle→{Thick,Black}],*)
    Frame → {True, True, False, False},
    PlotRangePadding → None,
    FrameLabel → {Style["Generation", LabelSize], Style["", LabelSize]},
    FrameStyle → Directive[FontSize → TickSize],
    Epilog → {
      Text[Style["H", LabelSize, Bold], Scaled@letpos],
      Rotate[Text[Style["", LabelSize], Scaled@ylabpos], 90 Degree]
     },
    ImagePadding → Pad,
    FrameTicksStyle → {{Directive[FontColor → White], Black}, {Black, Black}},
    PlotRangeClipping → False
   ];

GraphicsGrid[{{plot1}, {plot2}, {plot3}, {plot4}(*,{plot5}*)},
 ImageSize → FigureSize, Spacings → 0]

Export[imagedir <> "AltHysteresisSnapshotLarge.pdf", %];

Clear[KK, B, ω, μ, α, n, k, rep, σθ]
```

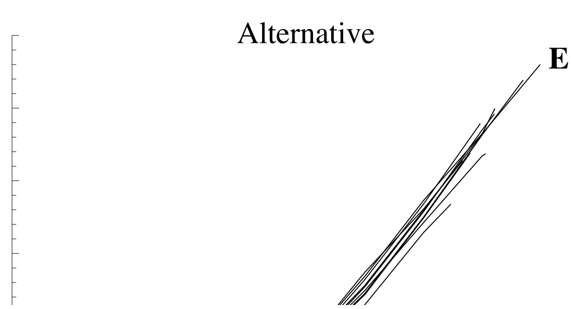
NSolve::ifun : Inverse functions are being used by NSolve, so
some solutions may not be found; use Reduce for complete solution information. ≫

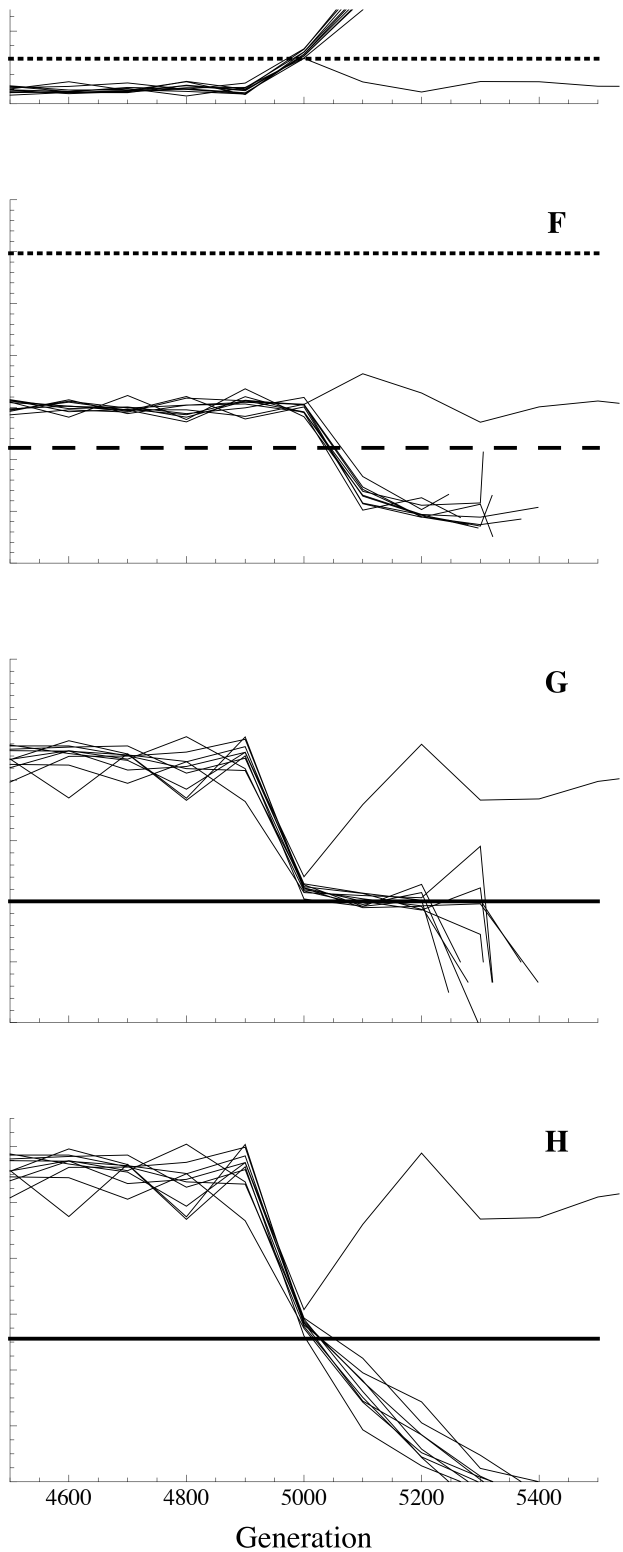
Part::partw : Part 1 of {} does not exist. ≫

Part::partw : Part 1 of {} does not exist. ≫

Part::partw : Part 1 of {} does not exist. ≫

General::stop : Further output of Part::partw will be suppressed during this calculation. ≫




F
G
H
4600
4800
5000
5200
5400
Generation