

Proceedings of the Royal Society B – Biological Sciences

“Why climate change invariably alters selection pressures on phenology”

Electronic Supporting Material 1

1. Detailed description of simulation model

Background

We constructed an individual-based simulation model that was based on our great tit-caterpillar consumer-resource system as a template. Great tits (*Parus major*) are small passerine birds that rely on caterpillars as a food source on which to raise their offspring [e.g. 1, 2]. These caterpillars develop during spring and their biomass peaks around mid May. To maximise their reproductive success, great tits strive to synchronise the nestling period with this peak in food abundance and to achieve this they need to initiate egg-laying about four weeks earlier. Consequently, the birds cannot use the temperatures that determine caterpillar growth as a cue to time egg-laying. Great tit breeding time correlates best with mean temperature from March 16 to April 20 [3] making this the likely cue environment E_1 . Caterpillar phenology responds to mean temperature from March 8 to May 17 (E_2) [2]. E_2 and E_1 vary across years and the interannual variance in E_2 (=0.90) is lower, however, than that in E_1 (=1.45), which is not surprising given that E_2 is measured over a longer period. The regression coefficient of E_2 against E_1 β_{E_2,E_1} , is 0.45.

There was no individual variation in caterpillar phenology as we here actually modelled the biomass peak of the caterpillars. The biomass peak reaction norm is described by:

$$(1) \quad P(E_2) = a_{caterpillar} + b_{caterpillar}E_2$$

Model structure

We used an individual-based model to simulate evolution of consumer reaction norms. In contrast to the phenology of caterpillars (i.e. the resource), which was fixed, the phenotypic plasticity of great tits (i.e. the consumer) could evolve. The consumer reaction norm was modelled assuming a linear function, with the elevation and slope parameters considered as two separate traits that were each affected by additive genetic variation and residual variation. An individual's phenotype dependent on E_1 is hence given by its genotypic value (additive genetic 'merit') for elevation, the residual variance in elevation, its genotypic value for slope plus the residual variation in slope multiplied by E_1 :

$$(2)P(E_1) = \mu_{elevation} + G_{elevation} + \epsilon(0, \sigma_{residual_{elevation}}) + (\mu_{slope} + G_{slope} + \epsilon(0, \sigma_{residual_{slope}}))E_1$$

The variation in $G_{elevation}$ and G_{slope} is the additive genetic variation (V_A) in elevation and slope, respectively.

Individuals were tracked throughout their 'lifetime' and their trait values, reproductive success, and survival recorded. At the beginning of each simulation run a consumer base population was set up with genotypic values for elevation and slope drawn randomly from a multivariate normal distribution with variances and covariance given by the additive genetic (co)variances. Then 100 'years' were simulated, which consisted of the following steps: (1) Temperatures affecting resource and consumer phenology were drawn from a multivariate normal distribution defined by the (co)variation in temperatures. (2) Random mating occurs. (3) Phenotypes of resource and consumers are predicted from these temperatures using eqs. (1) and (2), respectively. (4) Offspring are produced depending on the mismatch between the maternal phenotype and resource phenology (see below for details). The maternal phenotype was used to determine the pair's reproductive success because in great tits, our model system, males do not affect their females' egg-laying dates [4]. (5) Offspring genotypic values for reaction norm elevation and slope are calculated as mid-parent value plus segregation error [5]. (6) Random adult mortality occurs at a set rate. To keep population numbers constant recruitment rate of offspring is adjusted according to the number of surviving adults, which results in a constant population size over time. The breeding population in the next year will consist of surviving

adults and recruiting offspring. Space was assumed to be homogeneous and was not modelled explicitly. 1000 simulation runs of each scenario were performed.

The number of offspring produced in every 'year' depended on the mismatch between the maternal phenotype and the optimal phenotype following:

$$(3) \quad W = e^{\frac{-\text{mismatch}^2}{2\omega}}$$

where W is 'reproductive success' and ω the width of the fitness function. W was then converted into the number of offspring (recruits) by first scaling it appropriately to keep population size constant and then drawing random number from a Poisson distribution with this re-scaled W as mean:

$$(4) \quad \text{no. offspring} = \text{Poisson}\left(\frac{W(K-\text{survivors})}{\bar{W}n\text{pairs}}\right)$$

where K is the maximal population size, *survivors* is the number of surviving adults after random mortality, \bar{W} is mean 'reproductive success' and *n*pairs the number of breeding pairs in the given 'year'.

Since we were interested in evolution (i.e. the response to selection) but also selection itself, we first tracked annual mean genotypic values of reaction norm elevation and slope and, second, calculated annual selection differentials on these parameters. Annual selection on elevation and slope of the reaction norm was calculated by regressing relative fitness, i.e. individual fitness over (annual) mean fitness, against genotypic values instead of phenotypes as this allowed measuring selection on reaction norm slopes also in individuals that bred only once. This is equivalent to the standard approach of quantifying selection [6] except that we here used genotypes. While measuring selection on the genetic component using predicted breeding values from animal models is (highly) problematic [7], it does not result in biased selection estimates in our case because in our model true breeding/genotypic values are known.

Model parameterisation

Our model required the following input parameters: elevation and slope of the resource reaction norm (fixed over time) (parameters a and b in eq.1), population mean elevation and slope of the consumer reaction norm, genetic and residual variation in elevation and slope of the consumer reaction norm, mean and variances of temperatures affecting consumer and resource, E_1 and E_2 , the correlation between them, and the width of the fitness function (parameter ω in eq.3) which are given in Table S1. Since we assumed that consumer phenology was optimally adapted to match resource phenology before the onset of environmental change, we calculated μ_{slope} and $\mu_{elevation}$ for the consumer reaction norm as follows:

$$(5) \quad \mu_{slope} = b_{caterpillar} \rho \frac{\sigma_{E_2}}{\sigma_{E_1}}$$

$$(6) \quad \mu_{elevation} = b_{caterpillar} \bar{E}_2 - \mu_{slope} \bar{E}_1$$

where \bar{E}_1 and \bar{E}_2 are the means of the temperatures determining great tit and caterpillar phenology.

Temperatures affecting resource and consumer increased by 0.07°C/year and 0.06°C/year, respectively. Variances and correlation were however calculated based on de-trended temperature values from the years 1973 to 2012 and are hence unaffected by the changes in spring temperature.

The width of the fitness function (ω) indicates how quickly fitness declines with increasing distance of phenotypes from the optimal phenotype, i.e. mismatch in our case. To estimate it we first binned observed egg-laying dates, centred by annual mean egg-laying date, into 10 equally-spaced intervals and calculated the mean recruitment probability of an egg, i.e. the probability that an egg hatched, the chick fledged and recruited into the breeding population, for each bin. We then fitted a Gaussian function to these mean recruitment probabilities from which the width of the fitness function, ω , was taken as the estimated standard deviation [see 8 for more details].

Climate change scenarios

We explored a range of scenarios of linear environmental change with differential increases in the temperatures affecting consumer phenology (E_1) and temperatures affecting resource phenology (E_2). The increase in both E_2 and E_1 varied from no increase to an increase of $0.06^\circ\text{C}/\text{year}$, which corresponds to an 'extreme' scenario. However, the observed increases in E_2 in our great tit-study area are similar to this rate of increase [8]. Such a differential temperature increase can be expected under climate change, although the ratio will likely vary regionally and be hard to predict *a priori* [9].

Table S1 Values for all input parameters used in simulation model.

Parameter	value	Reference
$a_{caterpillar}$, elevation of resource reaction norm	0 days * ¹	
$b_{caterpillar}$, slope of resource reaction norm	-6.60 days/°C	[2]
$V_{Gelevation}$, genetic variation in consumer reaction norm elevation	1.08	[10]
V_{Gslope} , genetic variation in consumer reaction norm slope	0.069	[10]
$V_{Reselevation}$, residual variation in consumer reaction norm elevation	3.42	[10]
$V_{Reslope}$, residual variation in consumer reaction norm slope	0.161	[10]
\bar{E}_1 , mean of 'great tit' temperature	7.5°C	
\bar{E}_2 , mean of 'caterpillar' temperature	9.1°C	
σ_{E_1} , sd of 'great tit' temperature	1.20°C	
σ_{E_2} , sd of 'caterpillar' temperature	0.95°C	
ρ , correlation between 'great tit' and 'caterpillar' temperatures	0.57	
ω , width of the fitness function	14.7 days	[8]

*¹ The elevation was set to zero for reasons of numerical convenience but choosing any other value will not affect the results as simulations were always initiated with the optimal consumer reaction norm, which was calculated from the resource reaction norm.

2. Detailed results from simulation model

We here present detailed results from simulation model runs for four scenarios of temperature change: 1) no change, 2) stronger increase the temperatures affecting resource phenology (E_2) than in the temperatures affecting consumer phenology (E_1), 3) equal increase in E_1 and E_2 , and 4) a combination of increases in E_1 and E_2 that leads to equal advances in phenology and hence no selection. We would however like to point out here that these detailed results are meant to illustrate how the simulation model works. A much larger range of scenarios has actually been explored and is presented in Fig.2 in the main text.

In scenario 1 temperatures affecting consumer and resource (Fig.S1A) did not increase over time. Since phenologies of consumer and resource were set to be matched (Fig.S1B) and did not advance, mismatch (Fig.S1C) was on average zero and did not increase. Consequently, there was on average no selection on reaction norm elevation (Fig.S1D) or slope (Fig.S1E) and neither genotypic values for reaction norm elevation (Fig.S1F) nor slope (Fig.S1G) changed consistently. Additive genetic variation in reaction norm elevation (Fig.S1H) and slope (Fig.S1I) initially declined due to stabilising selection and then equilibrated at a lower level.

In scenario 2 the temperature affecting the consumer (E_1) increased by 0.02°C/year while the temperature affecting the resource (E_2) increased by 0.04°C/year (Fig.S2A). The consumer phenology initially increased at a slower rate than the resource (Fig.S2B) leading to a phenological mismatch (Fig.S2C). After about 50 years consumer phenology started advancing at the same rate (due to evolution) and a stable 'evolutionary lag' developed. Accordingly, selection on reaction norm elevation (Fig.S2D) and slope (Fig.S2E) initially increased but plateaued when this stable lag was reached. Genotypic values for elevation (Fig.S2F) and slope (Fig.S2G) advanced as a response to this selection. Additive genetic variation in elevation (Fig.S2H) and slope (Fig.S2I) initially declined due to selection but equilibrated before the phase of stable evolutionary lag was reached.

In scenario 3 the temperatures affecting the consumer (E_1) increased by 0.02°C/year while the temperature affecting the resource (E_2) increased at the same rate (0.04°C/year). The results are generally similar to scenario 2 with unequal increases. The only difference is that the consumer

started to 'catch up' with the resource around year 70 (Fig.S3C) as a consequence of the somewhat smaller mismatch.

In scenario 4 the rates of increase in temperatures affecting the consumer (E_1) and in the temperature affecting the resource (E_2) were tuned such that no mismatch and hence no directional selection would arise. To fulfil this condition (while assuming unchanged (co)variances in E_1 and E_2) consumer temperature would need to increase at 2.22-times the rate of the resource temperature. The increases in E_1 and E_2 hence were 0.04°C/year and 0.018°C/year, respectively. The other results are similar to scenario 1 without change in E_1 and E_2 , except that phenologies advanced (Fig.S4B) but at the same rate.

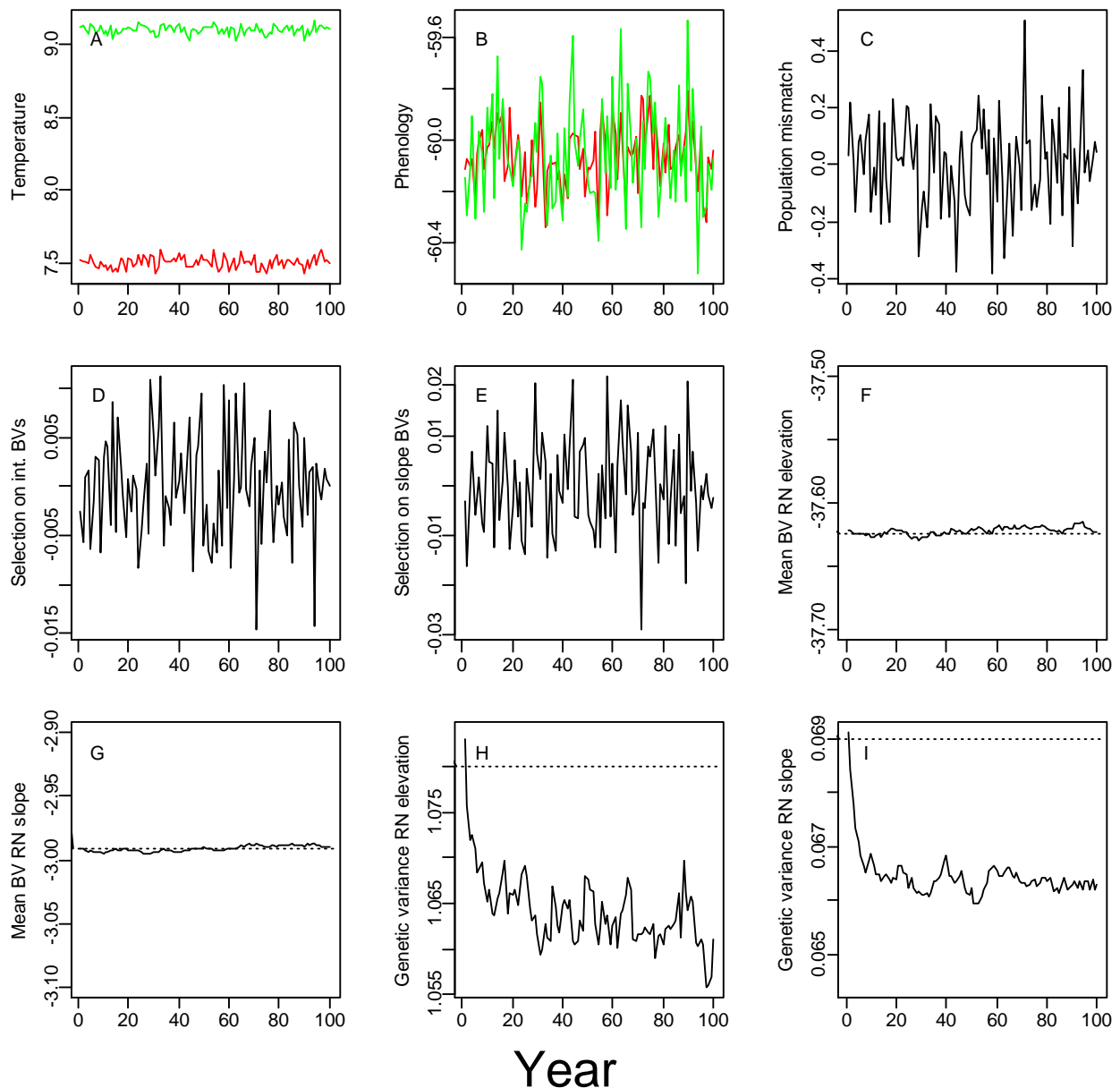


Figure S1. Changes over 100 simulated years in (A) temperatures affecting consumer (red) and resource (green), (B) phenologies of consumer (red) and resource (green), (C) population mean mismatch between consumer and resource, (D) selection on breeding values (BV) for reaction norm intercept, (E) selection on breeding values (BV) for reaction norm slope, (F) annual mean breeding value (BV) for reaction norm (RN) elevation, (G) annual mean breeding value (BV) for reaction norm (RN) slope, (H) genetic variation in reaction norm (RN) elevation and (I) genetic variation in reaction norm (RN) slope. Note that scaling of the y-axis in panels D to I is very different from the scaling in Figs. S2 and S3. Parameter values were averaged per year over 1000 simulation runs and plotted against year. Dotted horizontal lines in panels H and I indicate initial values for reaction norm elevation and slope as well as genetic variance in elevation and slope, respectively.

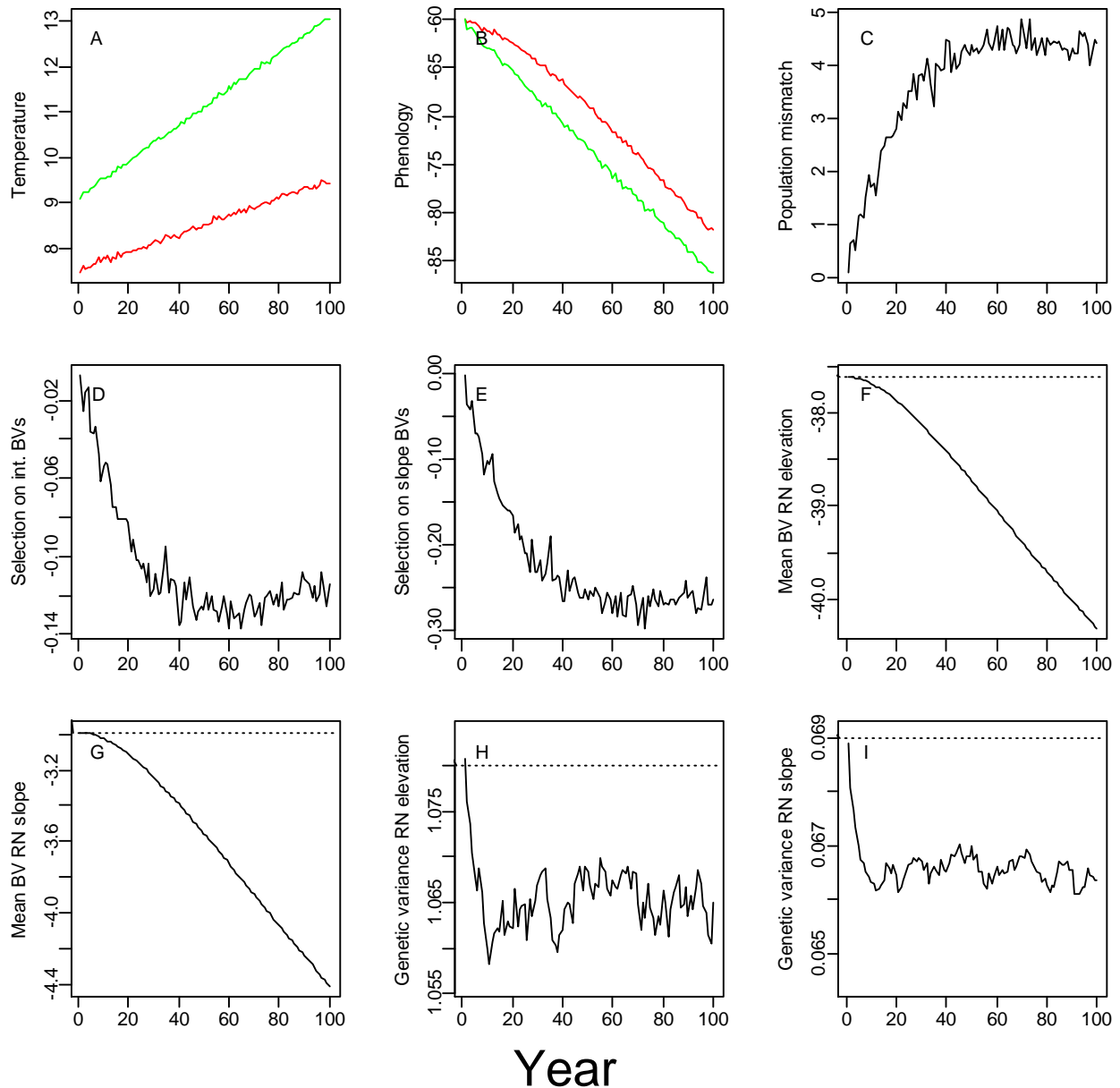


Figure S2. Changes over 100 simulated years in (A) temperatures affecting consumer (red) and resource (green), (B) phenologies of consumer (red) and resource (green), (C) population mean mismatch between consumer and resource, (D) selection on breeding values (BV) for reaction norm intercept, (E) selection on breeding values (BV) for reaction norm slope, (F) annual mean breeding value (BV) for reaction norm (RN) elevation, (G) annual mean breeding value (BV) for reaction norm (RN) slope, (H) genetic variation in reaction norm (RN) elevation and (I) genetic variation in reaction norm (RN) slope. Parameter values were averaged per year over 1000 simulation runs and plotted against year. Dotted horizontal lines in panels H and I indicate initial values for reaction norm elevation and slope as well as genetic variance in elevation and slope, respectively.

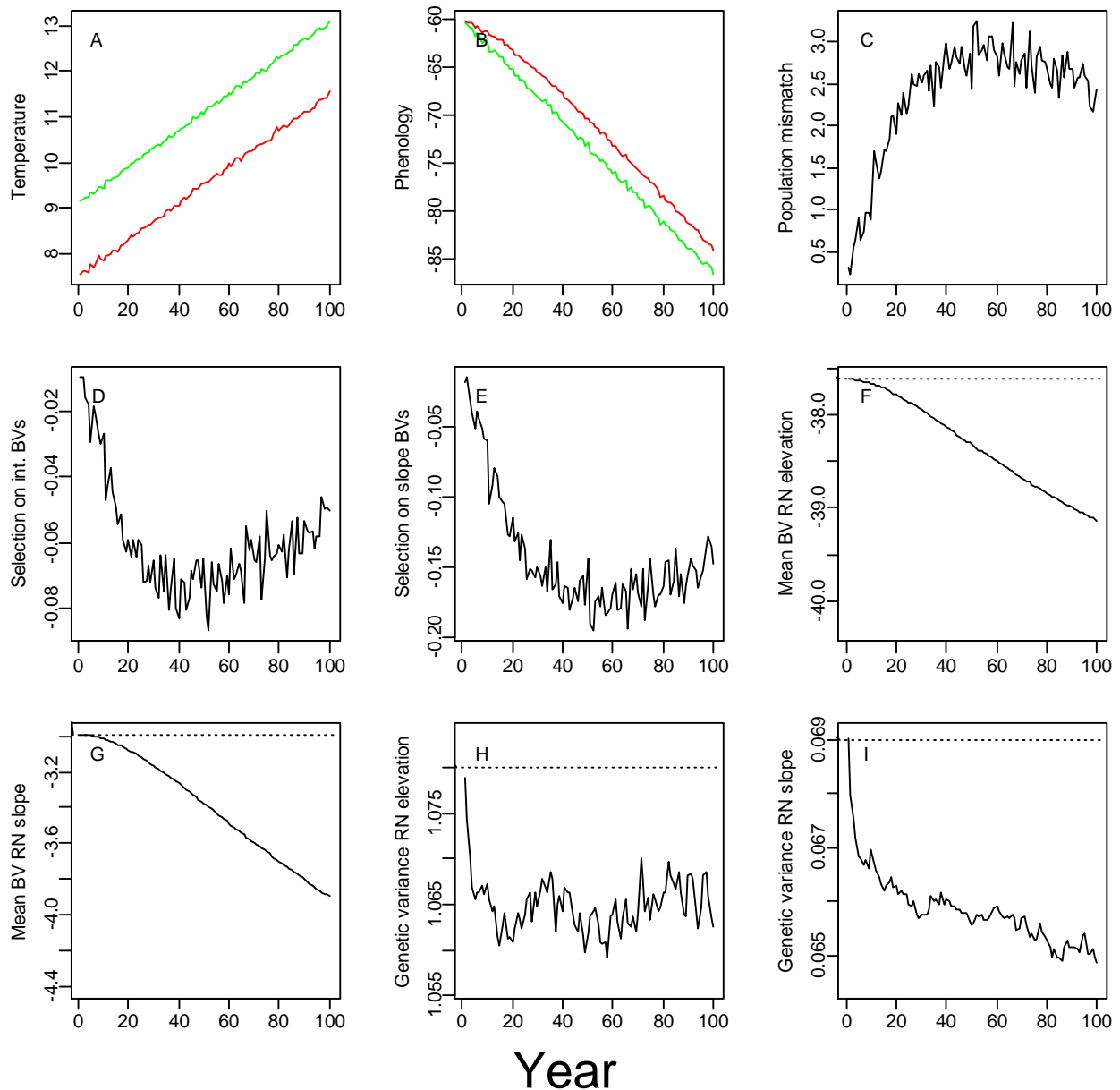


Figure S3. Changes over 100 simulated years in (A) temperatures affecting consumer (red) and resource (green), (B) phenologies of consumer (red) and resource (green), (C) population mean mismatch between consumer and resource, (D) selection on breeding values (BV) for reaction norm intercept, (E) selection on breeding values (BV) for reaction norm slope, (F) annual mean breeding value (BV) for reaction norm (RN) elevation, (G) annual mean breeding value (BV) for reaction norm (RN) slope, (H) genetic variation in reaction norm (RN) elevation and (I) genetic variation in reaction norm (RN) slope. Parameter values were averaged per year over 1000 simulation runs and plotted against year. Dotted horizontal lines in panels H and I indicate initial values for reaction norm elevation and slope as well as genetic variance in elevation and slope, respectively.

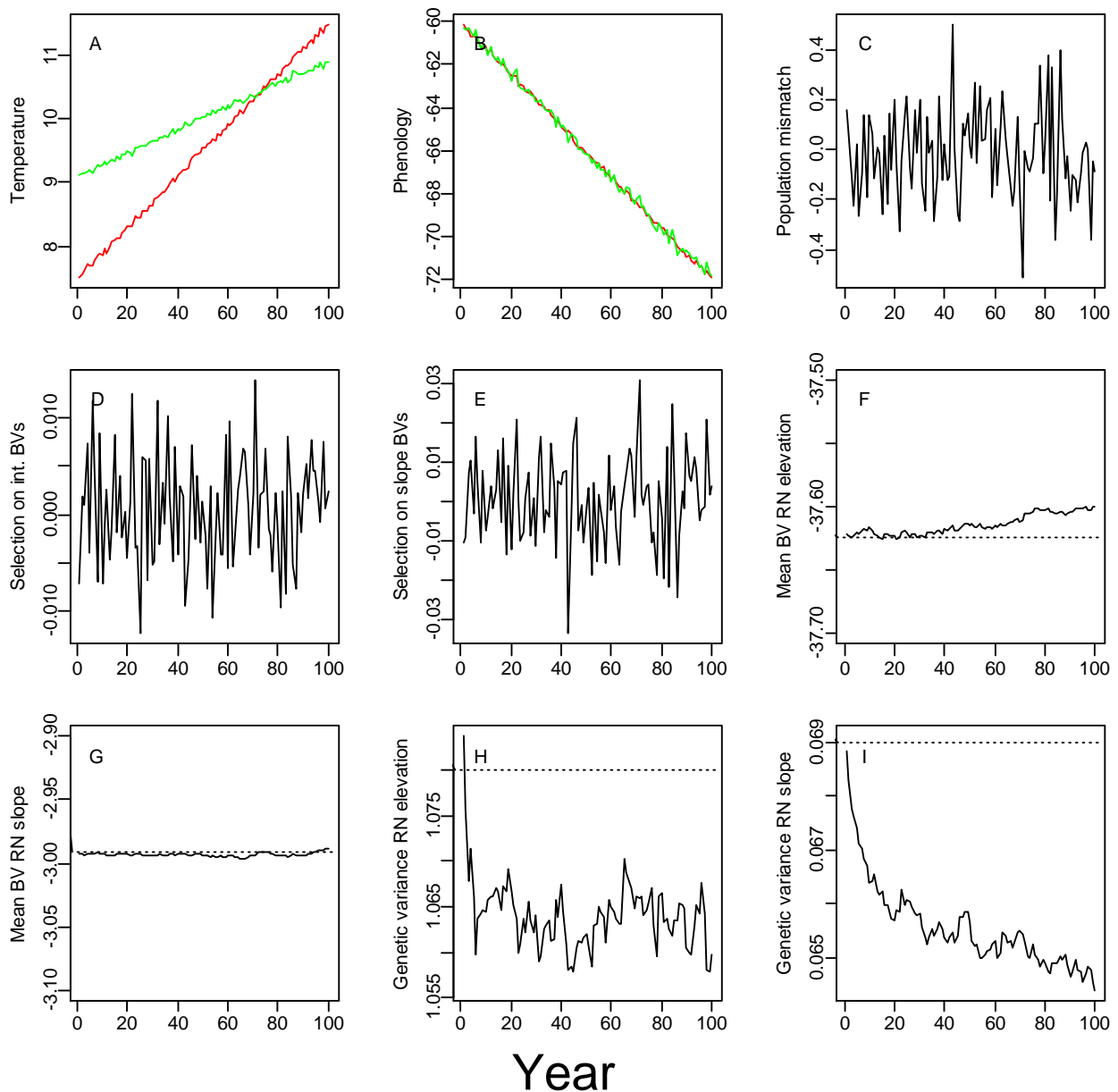


Figure S4. Changes over 100 simulated years in (A) temperatures affecting consumer (red) and resource (green), (B) phenologies of consumer (red) and resource (green), (C) population mean mismatch between consumer and resource, (D) selection on breeding values (BV) for reaction norm intercept, (E) selection on breeding values (BV) for reaction norm slope, (F) annual mean breeding value (BV) for reaction norm (RN) elevation, (G) annual mean breeding value (BV) for reaction norm (RN) slope, (H) genetic variation in reaction norm (RN) elevation and (I) genetic variation in reaction norm (RN) slope. Note that scaling of the y-axis in panels D to I is very different from the scaling in Figs. S2 and S3. Parameter values were averaged per year over 1000 simulation runs and plotted against year. Dotted horizontal lines in panels H and I indicate initial values for reaction norm elevation and slope as well as genetic variance in elevation and slope, respectively.

3. Running the simulation model

The individual based simulation model was programmed using standard R programming language [11]. The supplied code (ESM2) can simply be copied into the console or editor and run from there. A more convenient alternative when exploring ranges of parameter values would be to run a slightly altered version (see in-text comments on which parts need to be changed) in 'batch mode' by submitting e.g. the following code from the console.

```
#####
### This code sets the input parameters for the IBM of plasticity evolution
### and calls 'IBM_plast_evol.R' to actually run the simulation

### Set workspace, load libraries and clear workspace
setwd("YOUR CONVENIENT DIRECTORY")

library(MASS)
rm(list=ls())

#####
### set base parameters to standard values

nY <- 100           # number of years
nreps <- 500

V.Tc <- 1.445       # variance in consumer temperatures
V.Tf <- 0.901       # variance in food temperatures
r.init <- 0.574     # correlation between V.Tc and V.Tf

#####
### create empty vectors to store output
kTf <- c()
kTc <- c()
```

```

mP <- c()
sdP <- c()
mG1 <- c()
sdG1 <- c()
mG2 <- c()
sdG2 <- c()

#####

### cycle over increases in E1
for (k.Tc in seq(0.02,0.04,0.05) )
{
### cycle over increase in E2
for (k.Tf in seq(0.02,0.04,0.05) )
{
source("baseline_modelv2a.R")
kTf <- c(kTf,k.Tf)
kTc <- c(kTc,k.Tc)
mP <- c(mP,m.iP)
sdP <- c(sdP,sd.iP)
mG1 <- c(mG1,m.iG1)
sdG1 <- c(sdG1,sd.iG1)
mG2 <- c(mG2,m.iG2)
sdG2 <- c(sdG2,sd.iG2)
}
}

r1 <- data.frame(kTf,kTc,mP,sdP,mG1,sdG1,mG2,sdG2)
write.csv(r1,"results_IBM_plast_evol.txt",row.names=F)

```

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