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ONLINE SUPPLEMENT FOR:

SHIFTING VITAL RATE CORRELATIONS ALTER PREDICTED POPULATION RESPONSES TO INCREASINGLY VARIABLE ENVIRONMENTS

The American Naturalist

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Appendix S1

Part 1: Example of how increased environmental variability can influence vital rate correlations

To illustrate how a change in the variance of either a shared or non-shared environmental driver can impact the correlation between vital rates, consider two vital rates (per-capita fertility, F, and adult survival, S_A) that are each linearly related to an environmental driver, ENV_{shared}. Equations describing the vital rates are:

$$F(t) = \bar{F} + \beta_F \cdot ENV_{shared}(t) + \varepsilon_F(t) \quad \text{(S1)}$$

$$S_A(t) = \overline{S_A} + \beta_{S_A} \cdot ENV_{shared}(t) + \varepsilon_{S_A}(t), \quad \text{(S2)}$$

where $\bar{F}$ and $\overline{S_A}$ are the vital rate values in the mean environment (i.e., when $ENV_{share} = 0$), β_k is the slope of the relationship between vital rate k and the shared environmental driver, and ε_k is additional "residual" variation in the vital rate not explained by ENV_{shared}. The residual variation ε_k can be correlated (e.g., owing to joint influences of other environmental drivers) or uncorrelated among vital rates.

For illustrative purposes, assume both vital rates have the same mean ($\bar{F} = \overline{S_A} = 0.5$) and that both vital rates respond with the same strength and direction to ENV_{shared} ($\beta_F = \beta_{S_A} = 0.05$). In this example, ε_F and ε_{S_A} are independent and normally distributed (SD of ε_F and ε_{S_A} = 0.05). If ENV_{sha} initially has a SD of 1, both vital rates have a SD of 0.07 and their correlation is 0.50 (Fig. S1A). If the SD of ENV_{sha} increases to 2, the SD of each vital rate increases to 0.11 while the correlation between S_A and F increases to 0.80 (Fig. S1B). However, if the vital rates experience the same increase in total SD but this occurs through increases in their uncorrelated residual variation ε_F and ε_{S_A}, the overall correlation between the two vital rates decreases from 0.50 to 0.20 (Fig. S1C). As a final example, if the SD of ENV_{share} and the

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SD of residual variation in each vital rate experience identical proportional increases, the SD of both vital rates could increase while their correlation remains unchanged (Fig. S1D). Thus, environmentally-driven changes in vital rate variance will often be accompanied by shifts in the strength of vital rate correlations.

Estimating the relationships between vital rates and environmental drivers, such as equations S1 and S2, is a common goal of ecological research. If such relationships exist, increased environmental variability will affect both the variability of vital rates and their correlation with each other. Increased environmental variability could also affect other statistical moments of vital rates if responses are non-linear (e.g., increased environmental variability channeled through a convex vital rate relationship will increase both the mean and variance of the vital rate), but we omit this additional complexity in our current investigation.

Part 2: Expanded description of simulation methods used in main text

We conducted all analyses in R (R code presented below). We first randomly generated a life history with a constant population growth rate in a constant environment by drawing random values between 0 and 1 for adult survival (S_A), juvenile survival (S_J), and maturation probability (p). We then numerically solved for values of fertility (F) that would result in a value of λ_D equal to 1. This resulted, for example, in the following life history:

```
require(popbio)


set.seed(1)


# Randomly generated vital rates
Sj = 0.6502951  # Juvenile survival
```

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```
Sa = 0.1878522  # Adult survival

p = 0.8476384   # Maturation probability

F = 1.3273394   # Fertility


#Deterministic Matrix

A = matrix(c(Sj*(1-p), F,

             Sj*(p),   Sa),

           byrow=F,nrow=2,ncol=2)


#Lambda_D

lam_d = lambda(A) # lam_d = 0.9999821
```

We then randomly generated a coefficient of variation (and associated standard deviation) for adult survival and fertility between 0 and 0.3.

```
cv_Sa = runif(1,0,0.3) # cv_Sa = 0.0796526

sd_Sa = cv_Sa * Sa     # sd_Sa = 0.01496292

cv_F = runif(1,0,0.3)  # cv_F  = 0.1116372

sd_F = cv_F * F        # sd_F  = 0.1481804
```

In Scenario 1 of the main text, we generated a time-varying, standard normal environmental driver, $ENV(t) \sim Normal(0,1)$, that was linearly related to $S_A(t)$ but not to $F(t)$. In Scenario 2, $ENV(t)$ was linearly related to both $S_A(t)$ and $F(t)$. We allowed $ENV(t)$ to explain a random proportion (between 0 and 1) of the variation in related vital rates (in Scenario 2, $ENV(t)$ explained the same proportion of variation in both vital rates.

The total variance of a vital rate, for example $F(t)$, is the sum of variation due to the explicit environmental driver and residual "background" variation:

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$$\sigma^2_{total}(F) = \sigma^2_{ENV}(F) + \sigma^2_{resid}(F) \quad \text{(S3)}$$

In our analyses, we assumed a linear relationship between vital rates and the environmental drivers. Thus, if $ENV(t) \sim Normal(0,1)$ explained 75% of the SD in $F(t)$, the slope of the linear relationship between $ENV(t)$ and $F(t)$ was calculated as:

$$\sigma_{ENV}(F) = slope_{F(t)} = \sigma_{total}(F) \times proportion\ explained \quad \text{(S4)}$$

The standard deviation of residual "background" variation was thus calculated as:

$$\sigma_{resid}(F) = \sqrt{\sigma^2_{total}(F) - \sigma^2_{ENV}(F)}. \quad \text{(S5)}$$

The following R code generates these relationships:

```
####################
# Explicit environmental driver that affects Sa and F
####################
time = 1000000 # length of stochastic simulation


# Create standard normal environmental driver (which will be shared among F
and Sa)
env_shared1 = rnorm(time,0,1)
env_shared1 = (env_shared1 - mean(env_shared1))/sd(env_shared1)


# Proportion sd explained in each vital rate by shared environmental driver
prop_explained = runif(1,0.01,0.99) # prop_explained = 0.2111163
prop_sd_Sa = prop_explained # prop_explained = 0.2111163
prop_sd_F = prop_explained  # prop_explained = 0.2111163


#Slopes for vital rates
```

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```
slope_Sa = prop_sd_Sa * sd_Sa                    # slope_Sa = 0.003158915
slope_F = prop_sd_F * sd_F * sign(runif(1,-1,1)) # slope_F = 0.0312833


#Amount of 'background variation' in vital rates necessary to generate
appropriate standard deviation
bg_sd_Sa = sqrt(sd_Sa^2 - slope_Sa^2) # bg_sd_Sa = 0.01462567
bg_sd_F = sqrt(sd_F^2 - slope_F^2)    # bg_sd_F = 0.1448406


#Create a dataframe to store vital rate variation driven by env_shared
vr_env_shared1 = data.frame(Sa = Sa + slope_Sa * env_shared1,
                            F = F + slope_F * env_shared1)
```

Finally, we generated a random correlation ranging from -1 to 1 for the residual variance in $S_A(t)$ and $F(t)$; for example, caused by other "unexplained" environmental covariates or life history tradeoffs. A multivariate normal distribution was then used to generate correlated residual deviates of $S_A(t)$ and $F(t)$.

```
require(MASS) # for mvnorm() function


###################
# Correlated background ("residual") variation in F and Sa
###################


#Random background correlation between -1 and 1
bg_cor_Sa_F = runif(1,-1,1)  # bg_cor_Sa_F = -0.7063433


#Covariance (for background variation)
```

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```
cov_Sa_F = bg_cor_Sa_F*bg_sd_Sa*bg_sd_F # cov_Sa_F = -0.001496311


vcv_mat = matrix(c(bg_sd_Sa^2,
                   cov_Sa_F,
                   cov_Sa_F,
                   bg_sd_F^2),
                 nrow = 2, ncol = 2, byrow = TRUE)


bg_Sa_F = mvrnorm(n = time, mu = rep(0, 2), Sigma = vcv_mat)
colnames(bg_Sa_F) = c("Sa","F")


#Ensure this residual variance has mean = 0 and exactly correct sd
bg_Sa_F[,"Sa"] = (bg_Sa_F[,"Sa"] - mean(bg_Sa_F[,"Sa"]))/sd(bg_Sa_F[,"Sa"]) *
bg_sd_Sa
bg_Sa_F[,"F"] = (bg_Sa_F[,"F"] - mean(bg_Sa_F[,"F"]))/sd(bg_Sa_F[,"F"]) *
bg_sd_F
```

The overall variation in a vital rate is the sum of environmentally-driven variation and residual variation:

```
# Add the two dataframes together to get overall vital rate variation
vr_total_1 = vr_env_shared1 + bg_Sa_F


sd_Sa              # sd_Sa = 0.01496292
sd(vr_total_1$Sa)  # sd(vr_total_1$Sa) = 0.01496285; this is very close
```

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```
sd_F                # sd_F = 0.1481804

sd(vr_total_1$F)    # sd(vr_total_1$F) = 0.1481664; this is very close
```

The sequence of vital rates in the "reference environment" (i.e., when $ENV(t) \sim Normal(0,1)$) was used to calculate elasticities to vital rate variance. We then increased the total SD of vital rates by 5% in one of two ways, and examined whether E^{σ} correctly anticipated the fitness effect of this change. First, we increased the variance of $ENV(t)$ by a sufficient amount, or 2) we directly altered the variance of vital rates while artificially fixing their correlation. This was achieved as follows:

```
# Required increase in env_shared to achieve 5% increase in sd of vital rates


sd_increase_env = sqrt((sd_Sa*1.05)^2 - bg_sd_Sa^2)/sd(vr_env_shared1$Sa)

env_shared2 = env_shared1 * sd_increase_env

sd(env_shared2) # 1.816521 is the SD of ENV(t) required to increase the SD of
both vital rates by 5%


#Variation in vital rates caused by more variable environmental driver

vr_env_shared2 = data.frame(Sa = Sa + slope_Sa * env_shared2,

                            F = F + slope_F * env_shared2)


#Add original background variation to both vital rates (this is unchanged)

vr_total_2 = vr_env_shared2 + bg_Sa_F


#Check that vital rate sds have both increased by 5%

sd(vr_total_2$Sa)/sd(vr_total_1$Sa) # 1.049997; very close to 1.05

sd(vr_total_2$F)/sd(vr_total_1$F)   # 1.049936; very close to 1.05
```

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Next, we generated a 5% increase in the SD of $S_A(t)$ and $F(t)$, but maintained their original correlation. We did this by z-standardizing them, multiplying by 1.05 times the original SD, and adding their original mean value:

```
vr_total_3 = vr_total_1

vr_total_3$Sa = 1.05 * sd(vr_total_1$Sa) * ( (vr_total_3$Sa -

mean(vr_total_3$Sa)) / sd(vr_total_3$Sa) ) + mean(vr_total_1$Sa)


vr_total_3$F = 1.05 * sd(vr_total_1$F) * ( (vr_total_3$F -

mean(vr_total_3$F)) / sd(vr_total_3$F) ) + mean(vr_total_1$F)


#Confirm that SDs are 1.05 times higher than in initial environment

sd(vr_total_3$Sa)/sd(vr_total_1$Sa) # 1.05; confirmed

sd(vr_total_3$F)/sd(vr_total_1$F)   # 1.05; confirmed


#Confirm that means are unchanged from initial environment

mean(vr_total_3$Sa)/mean(vr_total_1$Sa) # 1.000; confirmed

mean(vr_total_3$F)/mean(vr_total_1$F)   # 1.000; confirmed
```

The R commands and results below confirm that when an environmental driver becomes more variable, it affects vital rate variances *and* vital rate correlations.

```
###################################

# Environment 1: initial "reference" environment

###################################

# Original vital rate sds:

sd(vr_total_1$Sa) # sd(Sa) = 0.01496285

sd(vr_total_1$F)  # sd(F)  = 0.1481664
```

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```
# Original correlation:
cor(vr_total_1$Sa,vr_total_1$F) # -0.6304108

###################################
# Environment 2: Environmental driver causes SD of both vital rates to
increase by 5%
# This causes the correlation to shift
###################################
# New vital rate sds:
sd(vr_total_2$Sa) # sd(Sa) = 0.01571095
sd(vr_total_2$F)  # sd(F)  = 0.1555652

# Correlation after increased variance of env_shared:
cor(vr_total_2$Sa,vr_total_2$F) # -0.4789255

###################################
# Environment 3: SD of both vital rates increased by 5% but correlation
artificially fixed
###################################
# New vital rate sds:
sd(vr_total_3$Sa) # sd(Sa) = 0.01571099
sd(vr_total_3$F)  # sd(F)  = 0.1555747
```

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```
# Correlated is fixed at initial value

cor(vr_total_3$Sa,vr_total_3$F) # -0.6304108
```

To ensure no vital rates had "impossible" values (e.g., values of $S_A(t)$ larger than 1 or less than 0), we re-generated random CVs of $F(t)$ and $S_A(t)$ for each life history repeatedly until all vital rates had the correct support in all three environments.

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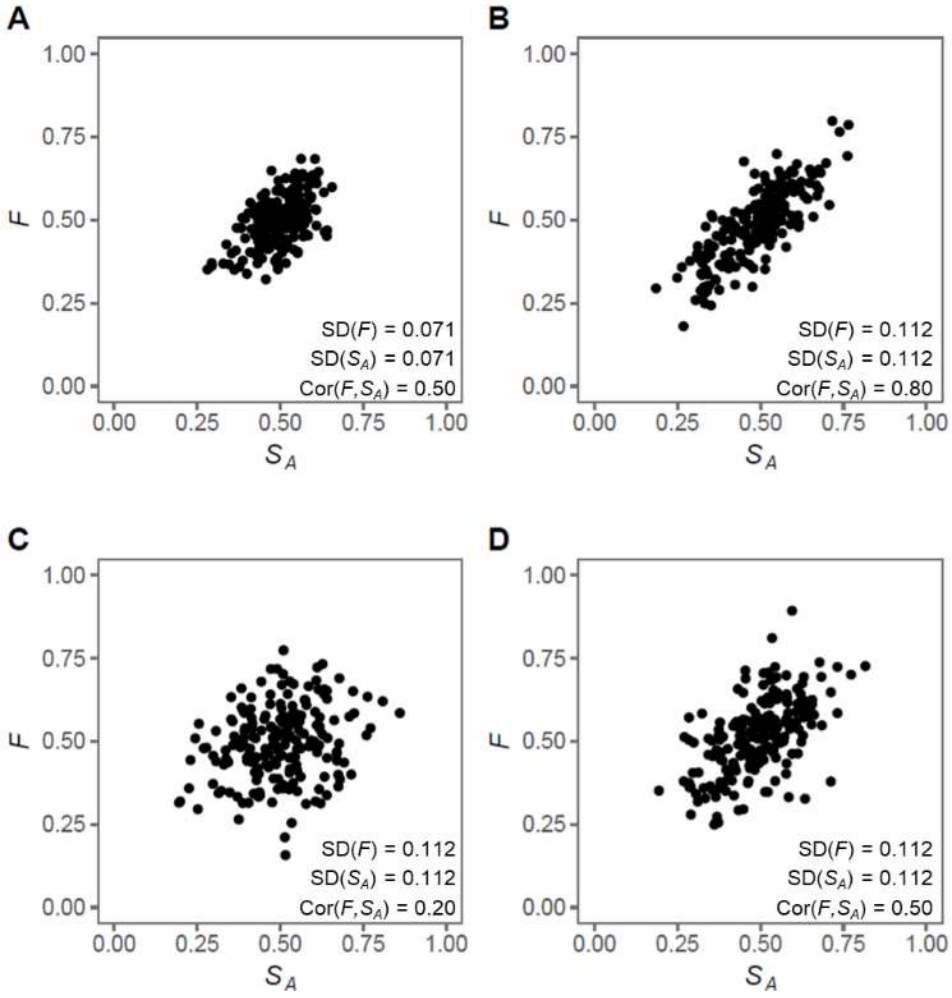

Figure S1. In increasingly variable environments, increased vital rate variability will often be accompanied by changes in vital rate correlations. A) Vital rate variance and correlations in an initial reference environment. B) Correlations strengthen if vital rates become more variable through increases in variability of a shared environmental driver. C) Correlations weaken if vital rates become more variable through increases in variability of uncorrelated background variation of each vital rate. D) Correlations only remain unchanged if increased vital rate variance caused by the shared environmental driver and background variation exactly counter-balance.

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Appendix S2 - Additional simulations using copulas to impose changes in variance of beta and lognormal distributions for vital rates

In the main text, we presented results of simulations where adult survival and fertility were normally distributed. This allowed us to impose strictly linear effects of an environmental driver on vital rates, ensuring that increased variance in an environmental driver did not alter vital rate means. However, a limitation of this approach is that large coefficients of variation could result in impossible values for vital rates (e.g., survival rates greater than 1), especially when mean survival is close to 1. We discarded simulations that resulted in impossible values, which implicitly constrained the range of vital rates we could consider.

A more formal alternative to the approach in the main text is to use a "copula" to generate non-normal multivariate vital rate distributions (see examples and further descriptions of this approach in Koons et al. 2008; de Valpine et al. 2014). This allows us examine the effects of increasingly variable environments on a wider range of life histories, including those with a much wider range coefficients of variation in vital rates.

This approach begins by using methods described in the main text. We again assumed $S_A(t)$ and $F(t)$ both responded linearly to an increasingly variable environmental driver, that a random proportion (between 0 and 1) of vital rate variance was explained by the driver, and that this proportion was the same for both vital rates. We again chose a random correlation for residual variation among vital rates. Because a copula ensures vital rates have appropriate support, we were able to allow larger variation in adult survival and fertility. For each life history, we randomly selected a CV for $S_A(t)$ between 0 and its maximum possible CV (Morris and Doak 2004). For fertility, we randomly selected a CV between 0 and 1. We again calculated the resulting vital rate correlations in a reference environment and a more variable

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environment in which the SD of $S_A(t)$ and $F(t)$ were 5% higher. We then standardized each vital rate distribution, resulting in correlated standard normal distributions in each environment.

A copula involves using a probability integral transformation to convert each normal distribution onto the scale of a standard uniform. To accomplish this, we used the *pnorm* function in R, resulting in correlated standard uniform distributions. We used a final transformation to convert the standard uniforms into distributions with appropriate support for each vital rate (e.g., beta for survival and lognormal for fertility), and with desired means and variances, using the *qlnorm* and *qbeta* functions in R. This approach allows an increasingly variable environmental driver to linearly affect the covariance of vital rates, on their appropriate scales, while not affecting their means.

Similar to results in the main text, the increasingly variable environmental driver altered $Cor(S_A, F)$ for many life histories (shading in Fig. S2A). This shift in vital rate correlations reduced the ability of vital rate elasticities (summed across vital rates; $\sum_{ij} E_{ij}^{\sigma}$) to reliably predict changes in λ_S (Fig. S2A). Conversely, $\sum_{ij} E_{ij}^{\sigma}$ was almost perfectly predictive of changes in λ_S when we artificially fixed the correlation between vital rates (Fig. S2B). These results are therefore quite general; vital rate variances and correlations are likely to shift concurrently when an environmental driver becomes more variable, which impacts fitness and the reliability of elasticities to vital rate variance.

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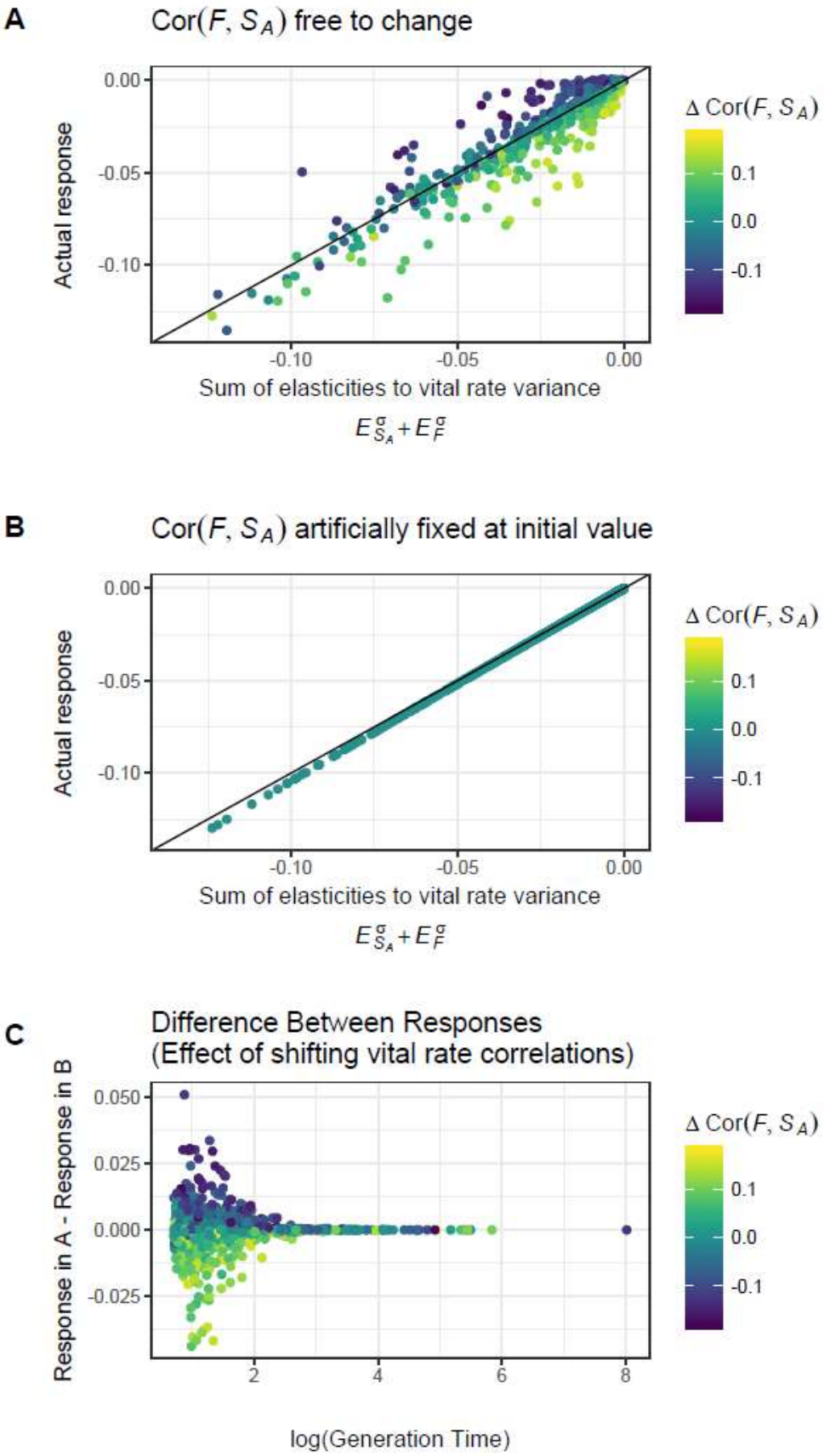

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Figure S2. The relationship between the sum of elasticity to variance across two vital rates ($E_F^{\sigma} + E_{S_A}^{\sigma}$; calculated in an initial reference environment) and the actual proportional change in λ_S that occurs when the *sd* of both $S_A(t)$ and $F(t)$ increases by 5%, calculated numerically using $\Delta\lambda_S/\lambda_S \times \frac{1}{2}(sd(S_A)/\Delta sd(S_A) + sd(F)/\Delta sd(F))$. In this scenario the environmental driver explained the same proportion of variation in both vital rates, but this proportion differed among life histories. A) Relationship when vital rate correlations are free to shift naturally ($R^2 = 0.694$). Black line represents perfect 1:1 relationship. B) Relationship when vital rate correlations were artificially fixed ($R^2 = 0.999$). C) Differences between responses in panels A and B, plotted against each life history's generation time. Note that while shifts in vital rate correlations occurred for all life histories (colored shading in panels A and C), these shifts had the largest fitness effects for life histories with short to medium generation times.

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Appendix S3 – Results when environmental driver explains a different proportion of variation in vital rates

In all of our previous simulations, we ensured that the shared environmental driver explained the same proportion of the variation in each affected vital rate. This is a key assumption of using the summed elasticities of individual vital rates to predict population responses to increased environmental variation. However, in reality, environmental drivers are likely to explain different proportions of the variation in vital rates. To examine the effect of this variation on the predictive ability of summed elasticities, we allowed $ENV(t)$ to explain a random proportion of the variation in each of $F(t)$ and $S_A(t)$, ranging from 0 to 1. We then increased the variance of $ENV(t)$ by a sufficient amount to increase the *sd* of $F(t)$ by 5%. Because $ENV(t)$ did not explain the same proportion of variation in both vital rates, this caused the *sd* of $S_A(t)$ to increase anywhere from 1 (i.e., no increase) to 15 times its initial value. In this case, summed stochastic elasticities do not strongly predict population responses to increased environmental variation whether vital rate correlations shift (Fig. S3A) or are artificially fixed (Fig. S3B). Note that in this figure, we plot the $\Delta\lambda_S/\lambda_S$ on the y axis, and have not rescaled it to place it on the same scale as elasticities by multiplying it by $\frac{1}{2}(sd(S_A)/\Delta sd(S_A) + sd(F)/\Delta sd(F))$.This is because the proportional change in the *sd* of S_A is occasionally extremely large. Nevertheless, if elasticities predicted proportional population responses to increasing vital rate variation, we would expect a tight linear relationship.

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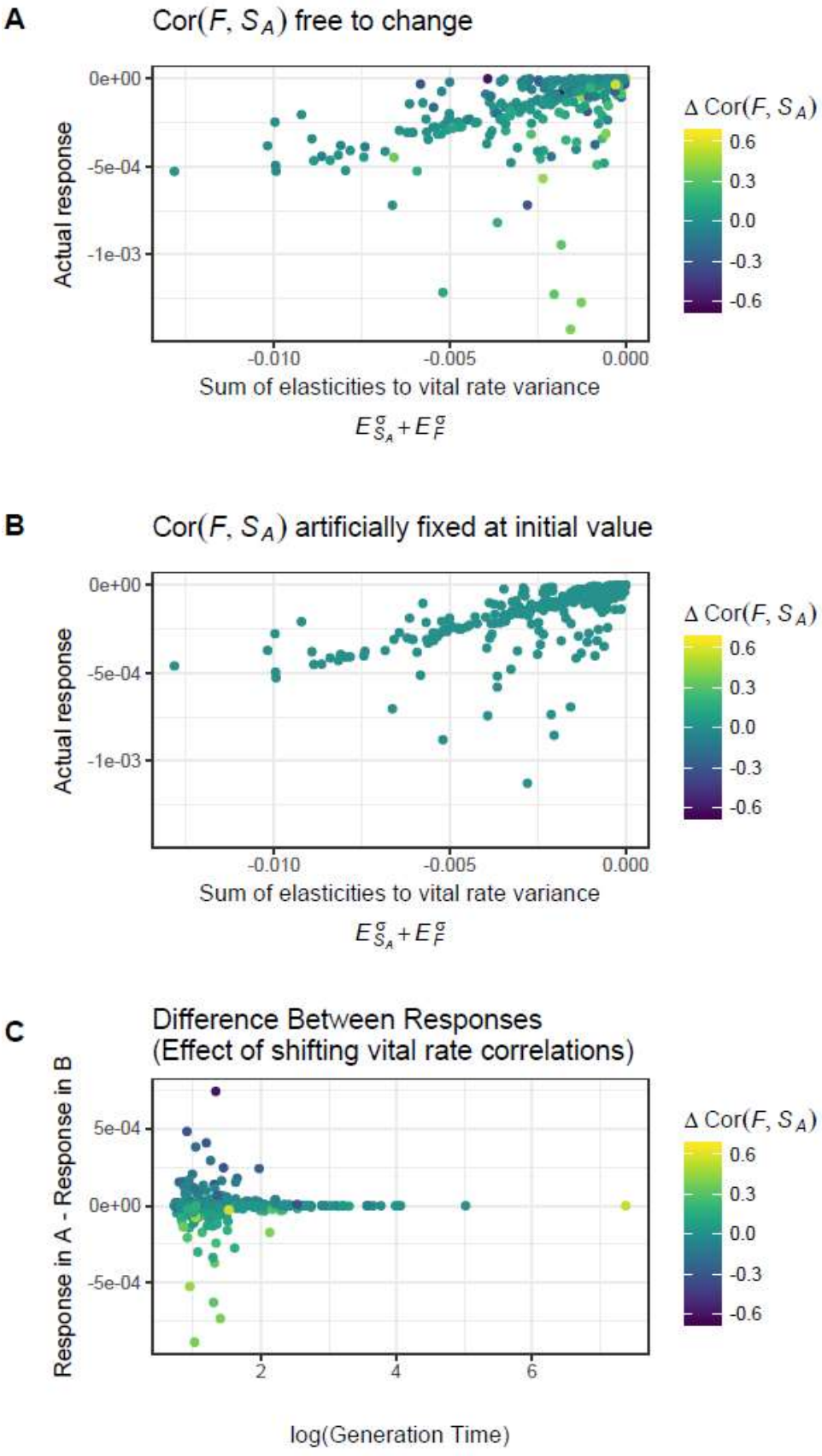

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Figure S3. The ability of elasticities to vital rate variance (summed across vital rates; $\sum_{ij} E_{ij}^{\sigma}$) to predict the effects of increased variance in two vital rates, $S_A(t)$ and $F(t)$, when an increase in the SD of each is driven by a shared environmental driver (note that $\Delta\lambda_S/\lambda_S$ is on the y-axis in panels A and B). A) Relationship when vital rate correlations are free to shift naturally. B) Relationship when vital rate correlations were artificially fixed. In this scenario the environmental driver explained a different (and random) proportion of variation in both vital rates, and these proportions differed between life histories. C) Differences between responses in panels A and B, plotted against each life history's generation time.

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Appendix S4 – Relationships between life history generation time and sensitivity to changes in vital rate correlations

In the main text and appendices above, we present results showing life histories with short generation times were disproportionately sensitive to changes in vital rate correlations that inevitably occur when environments become more variable. This is because the proportional fitness effect of a change in correlation between two vital rates is described by equation 6b from Doak et al. (2005):

$$E_{\rho_{v_i,v_j}} \approx \frac{-\rho_{v_i,v_j}}{\overline{\lambda_1}^2} \bar{S}_{v_i} \bar{S}_{v_j} \sigma_{v_i} \sigma_{v_j}$$

Thus, all else being equal (i.e., same initial correlation between vital rates ρ_{v_i,v_j}, and same deterministic growth rate $\overline{\lambda_1}$), the quantity $\bar{S}_{v_i} \bar{S}_{v_j} \sigma_{v_i} \sigma_{v_j}$ describes the effect of changes in vital rate correlations on fitness. The theoretical maximum variance of probability (or "zero-to-one") vital rates is attained at intermediate values of the vital rate (Morris and Doak 2004). Yet, variance of fertility is not affected by this constraint, and variance of fertility is therefore highest for life histories with high mean fertility. This occurs in real populations (e.g., Fig. S1.1 in Jongejans et al. 2010) and in our simulations:

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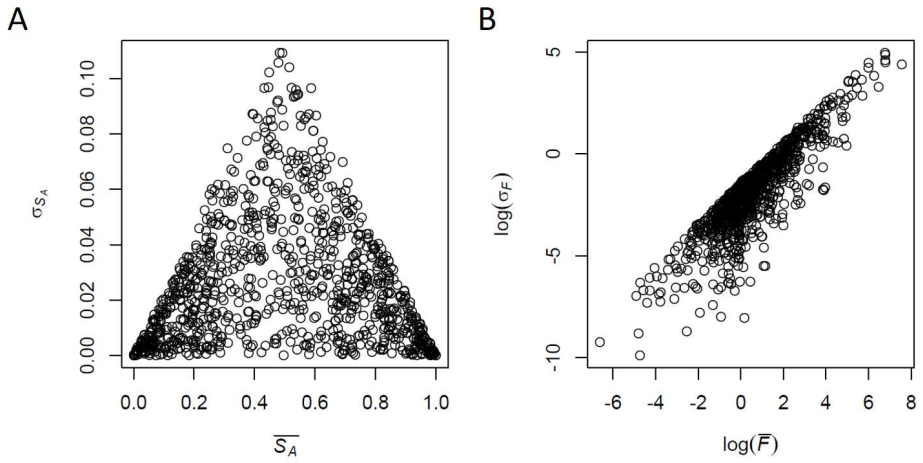

Figure S4. Mean-variance relationships between vital rates in our simulations (presented in main text). These relationships were qualitatively similar when using the copula method outlined in Appendix S2.

Life histories with short to medium generation times are characterized by high fertility and low to medium adult survival:

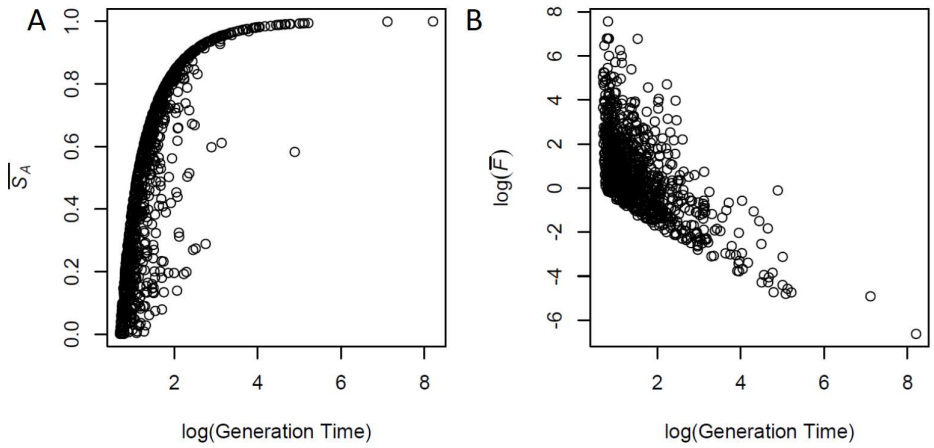

Figure S5. Relationship between generation time and mean vital rates across life histories.

The quantity $\sigma_{v_i}\sigma_{v_j}$ is therefore highest for life histories with short generation times:

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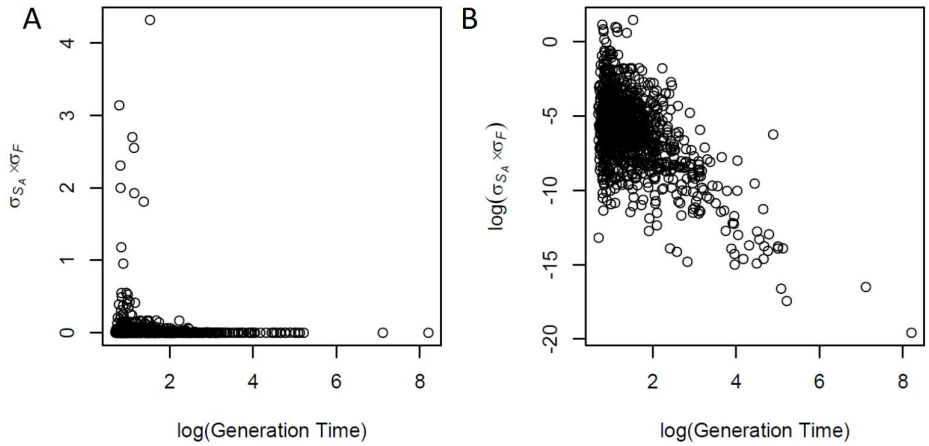

Figure S6. Relationship between the product of vital rate standard deviations and generation time. In Panel A, we present the raw product. In panel B, we log-transform this quantity, allowing it to be visualized on a proportional scale.

The product of vital rate sensitivities, $\bar{S}_{v_i}\bar{S}_{v_j}$, also impacts the fitness consequences of shifts in vital rate correlations. However, there is a weak positive relationship between generation time and the product of the sensitivities of fertility and adult survival ($R^2 = 0.20$):

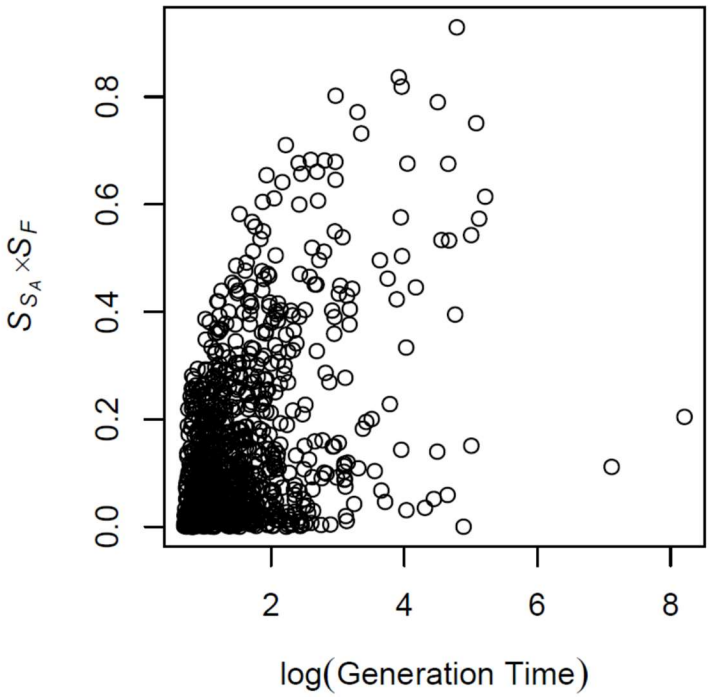

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Figure S7. Relationship between the product of vital rate sensitivities and generation time. There is a weak positive relationship ($R^2 = 0.20$).
As a result, the term $S_{S_A} S_F \sigma_{S_A} \sigma_F$ is maximized at low to medium generation times:

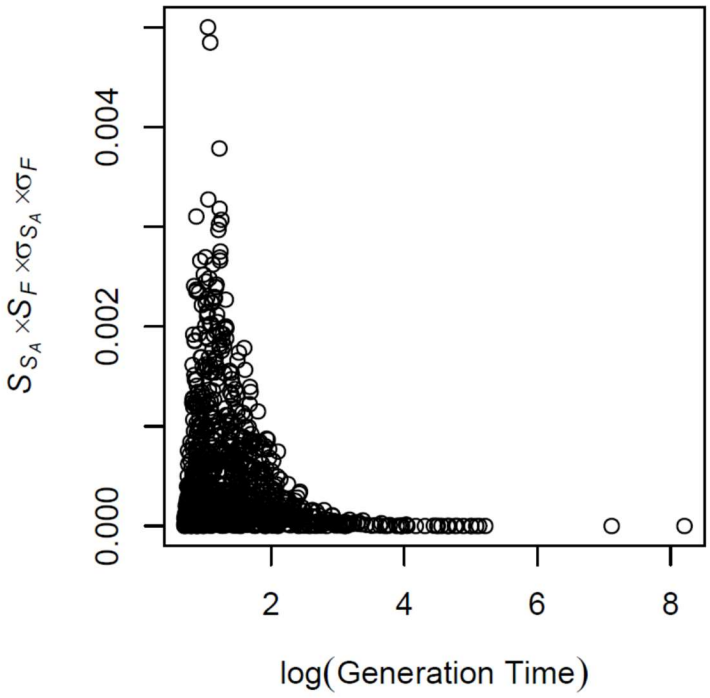

Figure S8. Relationship between $S_{S_A} S_F \sigma_{S_A} \sigma_F$ and generation time. The quantity $S_{S_A} S_F \sigma_{S_A} \sigma_F$ determines the proportional effect of shifts in vital rate correlations on fitness, all else being equal. Life histories with short to medium generation times are most sensitive to shifts in correlation between adult survival and fertility. Beyond a log(generation time) of 3 (actual generation time = exp(3) = 20 years), life histories are highly insensitive to changes in vital rate correlations.

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