A tradeoff between robustness to environmental fluctuations and speed of evolution

Max Schmid[1] (maxschmid@posteo.de), Maria Paniw[1,2] (maria.paniw@ieu.uzh.ch), Maarten Postuma[1,3] (maartenpostuma@outlook.com), Arpat Ozgul[1] (arpat.ozgul@ieu.uzh.ch), & Frédéric Guillaume[1]* (frederic.guillaume@ieu.uzh.ch)

[1] Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057, Zurich, Switzerland
[2] Ecological and Forestry Applications Research Centre (CREAF), Campus de Bellaterra (UAB) Edifici C, ES-08193 Cerdanyola del Vallès, Spain
[3] Plant Ecology and Nature Conservation Group, Wageningen University, 6700 AA Wageningen, the Netherlands
* corresponding author

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Abstract

Organisms must cope with both short- and long-term environmental changes to persist. In this study we investigated theoretically if life histories trade off between their robustness to short-term environmental perturbations and their ability to evolve directional trait changes. With mathematical models and stochastic individual-based simulations, we could confirm the tradeoff, at least for comparisons between standardized life histories. Offspring dormancy and high adult survival rates allowed large population sizes to be maintained in face of interannual environmental fluctuations but limited the speed of trait evolution with ongoing environmental change. In contrast, precocious offspring maturation and short-living adults promoted evolvability while lowering demographic robustness. This tradeoff had immediate consequences on extinction dynamics in variable environments. High evolvability allowed to cope best with long-lasting gradual environmental change, but came at the expense of more pronounced population declines from environmental variability and during the initial phase of environmental change.

Introduction

Environmental conditions are rarely constant but fluctuate between years and average conditions change gradually over time, and both dynamics pose a considerable challenge for species (Bürger and Lynch, 1995; Boyce et al., 2006; Van De Pol et al., 2010; Vázquez et al., 2015). Average global temperatures change successively in the course of long-term glacial cycles or during ongoing anthropogenic climate change, but also vary on shorter time scales, for instance with variations between years (Stocker et al., 2013; Ummenhofer and Meehl, 2017). Given that the environmental tolerance of all species is finite, the exposure to fluctuating environmental conditions can result in higher mortality, lower recruitment, and population declines. A dynamic environment thus demands species to constantly adapt and adjust. While several adaptive strategies exist to cope with environmental changes (Parmesan, 2006; Aitken et al., 2008; Bell and Gonzalez, 2009; Doak and Morris, 2010; Duputié et al., 2015; Cayuela et al., 2017; McDonald et al., 2017), some strategies might not be adaptive with every kind of temporal change. For instance life-history characteristics affect the robustness of a population against short-term environmental fluctuations (Caswell, 2001; Boyce et al., 2006; Morris et al., 2008; Tuljapurkar et al., 2009), and the speed of adaptive evolution in response to gradual environmental change (Engen et al., 2011; Barfield et al., 2011; Orive et al., 2017). However, the ability of life histories to cope with one kind of environmental variability might come at a cost to cope with another kind of dynamic environment.

Stochasticity in vital rates (survival and fecundity) from random environmental fluctuations reduces the long-run fitness of populations and may depress population sizes, thereby increasing extinction risks (Lande and Orzack, 1988; Tuljapurkar et al., 2003; Engen et al.,

2005; Sæther et al., 2013). How severely environmental variability feeds back on population growth then depends on the species' life cycle, especially on its position along the fast-slow continuum and its reproductive strategy. Theory shows that species with longer generation times are more robust to fluctuations than short lived species, as are more iteroparous compared to semelparous species (Tuljapurkar, 1990; Tuljapurkar et al., 2009; Salguero-Gómez et al., 2017). Empirically, Morris et al. (2008) found a relation between the life expectancy of 36 plant and animal species and their sensitivity to environmentally driven variation in vital rates. Life histories with long generation times experienced less pronounced demographic consequences from stochasticity in vital rates than short-lived species (see also Dalgleish et al., 2010; Sæther et al., 2013). The temporal patterning of fluctuations is also crucial for population dynamics (Engen et al., 2013b). The growth rates of fast life histories were shown to be more sensitive to temporal autocorrelation in environmental fluctuations than slow life histories (Paniw et al., 2017). A life history's robustness against environmental fluctuations further depends on the proportion of individuals exposed to environmental extremes. For instance, long-lived species often exhibit highly tolerant age or stage classes. Plant seeds or adult trees are good examples of such stages because of their high tolerance against extreme temperatures or drought events, and can overcome detrimental conditions much better than seedlings or juvenile plants (Petit and Hampe, 2006; Buoro and Carlson, 2014). Delayed maturation of seeds or egg dormancy then can allow species to cope with temporally fluctuating environments by "dispersal through time" (Evans and Dennehy, 2005; Buoro and Carlson, 2014). Consequently, a species' life history is a critical factor affecting population dynamics in fluctuating environments with interannual variation (Tuljapurkar, 1990; Tuljapurkar et al., 2009; Morris et al., 2008).

Life-history strategies also shape the rate of trait evolution when the environment changes gradually (Lande, 1982; Charlesworth, 1994; Ellner and Hairston, 1994; Engen et al., 2009, 2011; Barfield et al., 2011; Orive et al., 2017; Cotto et al., 2019). The generation time of a species, which affects the pace of life, is an indicator for how fast selection can translate into changes of the gene pool. The lower the generation time, the greater is the evolutionary response to environmental change per unit of time (Lande, 1982; Vander Wal et al., 2013; Carlson et al., 2014; Orive et al., 2017). With life stages highly tolerant to environmental variation, life-history strategies further control the proportion of individuals exposed to the environment. Those genotypes "hidden" in the seedbank or in highly tolerant adult stages are not under selection and thereby delay genetic changes at the population level, lowering its rate of evolutionary trait change (Templeton and Levin, 1979; Hairston and De Stasio Jr., 1988; Barfield et al., 2011; Orive et al., 2017). Together with the life-history effects on robustness mentioned above, we can expect that short-lived species will have faster evolutionary trait responses but will suffer more from a higher demographic sensitivity to random fluctuations in vital rates. In contrast, life histories with longer generation times should be demographically more robust but less evolutionarily responsive to changes in their environments. This tradeoff between demographic robustness and evolvability is in fact implicit from previous theoretical work. Lande (1982) and Barfield et al. (2011) described the evolutionary response to selection as a function of the growth rate sensitivity to vital rate changes, which is a quantity related to robustness against short-term fluctuations. The tradeoff was also suggested by the results of Hairston and De Stasio Jr. (1988) and Templeton and Levin (1979), who found that the presence of a seed bank, a mechanism to cope with stochastic environments, slowed down the rate of phenotypic trait evolution. In a study by Orive et al. (2017), elevated iteroparity (with

adults shielded from selection) favored population recovery after a sudden step change in the environment, but made evolutionary rescue with gradual environmental change less likely.

While several findings point towards a robustness-evolvability tradeoff for life-history strategies, other studies hint at potential mechanisms to overcome this tradeoff. Life histories with overlapping generations were suggested to harbour higher levels of additive genetic variance in fluctuating environments than life histories with non-overlapping generations, a process known as the genetic storage effect (Ellner and Hairston, 1994; Sasaki and Ellner, 1997; Svardal et al., 2015). Given that the likelihood of a successful evolutionary rescue increases with the extent of standing genetic variation (Carlson et al., 2014), life histories with highly robust life stages might be able to accumulate higher levels of genetic variance, and thus also evolve faster (Yamamichi et al., 2019). All in all, this shows that life-history strategies can have large effects on evolutionary and demographic dynamics, and on the success of evolutionary rescue. However, the exact resolution of the tradeoff between evolvability and robustness is not solved yet and will likely depend on the details of the species' life cycle and on the type of environmental variation.

Here, we first characterized the tradeoff between demographic robustness and evolvability for four 3-stage life histories spanning the fast-slow continuum and different levels of iteroparity in stage-structured populations. Our analytical analysis of the tradeoff is based on classical matrix population modeling (Caswell, 2001) and on the quantitative genetics formalism developed by Lande (1982) and Barfield et al. (2011) to compute the phenotypic response to selection in stage-structured populations. We show that a linear tradeoff exists between sensitivities of the equilibrium population size (and growth rate),

and the rate of evolution of a quantitative trait. In a second step, we used individual-based simulations to model the eco-evolutionary dynamics of a single population for the same four life histories subject to both random inter-annual fluctuations and long-term gradual changes of the optimum trait value. The population reached its carrying capacity from negative density dependent survival. Only juveniles were under selection such that only their survival rate varied with the environment, while offspring and adults had very high environmental tolerance levels. The simulations further allowed us to account for demographic and genetic stochasticity and evolving additive genetic variance. We could thus study the effect of the tradeoff between robustness and evolvability on the population extinction risk.

Models

We modeled a hermaphroditic species with three life stages (offspring (n_1), juveniles (n_2), and adults (n_3)) in a single random mating population. The population reached an equilibrium population size ($\hat{n}_t$) from intra-specific density regulation. Environmental fluctuations only affected juvenile survival via stabilizing selection on a quantitative trait. This corresponds to situations where the focal trait is only expressed at the juvenile stage (e.g., growth), and where offspring and adult individuals have much higher environmental tolerance (e.g., frost or drought tolerance), or dwell in much more stable habitats (e.g., Petit and Hampe, 2006; Van De Pol et al., 2010; Marshall et al., 2016). As a consequence of the negative density dependence, a reduction in juvenile survival from environmental variability or directional selection resulted in a lower equilibrium population size (Fig. 1d,e).

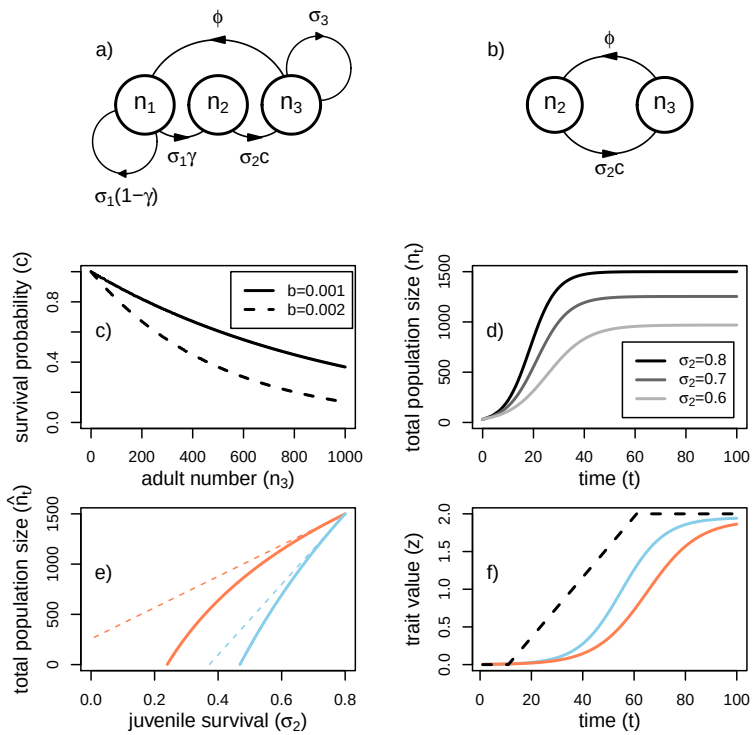

Figure 1: The life-history plot in a) illustrates the three-stage life cycle with delayed maturation and long-living adults (*del-sem*, *del-ite*, *pre-ite*), while b) shows the biennial two-stage life cycle (*pre-sem*), together with the relevant vital rates. Graph c) demonstrates the effect of negative density dependence on juvenile survival in the three-stage life cycle based on the Ricker function. Graph d) illustrates the temporal change of total population size over time following logistic growth such that an equilibrium mean population size is achieved from negative density dependence. By reducing the average juvenile survival σ_2, for instance from environmental perturbations, the population size at equilibrium $\hat{n}_t$ is reduced. We used the sensitivity of the equilibrium population size to juvenile survival ($\partial\hat{n}_t/\partial\sigma_2$) as a measure for environmental robustness. In graph e), two life histories are shown with the same equilibrium population size ($\hat{n}_t$, the two solid lines —) when environmental fluctuations are absent (at $\sigma_2 = 0.8$) but with different sensitivities to reductions in juvenile survival from interannual fluctuations. The slope of the dotted lines ($\cdots$) in graph e) represents $\partial\hat{n}_t/\partial\sigma_2$ as how quickly $\hat{n}_t$ responds to small reductions in σ_2. Graph f) illustrates the scenario with directional environmental change and the the corresponding trait evolution of two life histories (the two solid lines —). Environmental change is realized via directional changes of the phenotypic optima (θ, dashed line $--$).

We focused on four distinct life-history strategies along two axes, timing of maturation and degree of iteroparity, with two cases each: precocious (**pre**) and delayed (**del**) maturation, iteroparity (**ite**) and semelparity (**sem**). The life histories with combinations of delayed maturation and iteroparity (*del-sem*, *del-ite*, *pre-ite*) had three stages and overlapping generations (Fig. 1a). The precocious, semelparous life cycle (*per-sem*) had non-overlapping generations modeled with only two stages, juveniles (offspring maturing immediately) and adults reproducing once and dying (Fig. 1b).

Life-history parameters

Offspring, juvenile and adult individuals survived to the next year with probability σ_1, σ_2, and σ_3, respectively (Fig. 1a,b). Offspring exclusively resulted from the sexual reproduction of hermaphroditic adults with an average per capita fecundity of ϕ. Offspring matured to juveniles with a maturation probability γ and stayed in the offspring stage with probability $1 - \gamma$. Survival of juveniles was reduced by intra-specific competition c following the Ricker function ($c = exp(-b * n_3)$) and thus declined with increasing adult number n_3 for overlapping generations, and with juvenile number n_2 for non-overlapping generations, depending on the competition coefficient b. We also modeled a Beverton-Holt density regulation and present the results in the Supplementary Material.

The demographic dynamics of the three-stage life cycles *del-sem*, *del-ite*, and *pre-ite* were modeled by the following matrix population model (MPM):

$$A_3 = \begin{pmatrix} \sigma_1(1-\gamma) & 0 & \phi \\ \sigma_1(\gamma) & 0 & 0 \\ 0 & \sigma_2 \cdot c & \sigma_3 \end{pmatrix}, \tag{1}$$

and the two-stage life cycle *pre-sem* was represented by the following MPM:

$$A_2 = \begin{pmatrix} 0 & \phi \\ \sigma_2 \cdot c & 0 \end{pmatrix}. \tag{2}$$

Population sensitivity to environmental fluctuations

The robustness of a life history against environmental fluctuations can be seen as the sensitivity of the total equilibrium population size $\hat{n}_t$ to juvenile survival σ_2 ($\partial\hat{n}_t/\partial\sigma_2$, Fig. 1e). Assuming that the detrimental environmental conditions exclusively reduces average σ_2, but not σ_1 nor σ_3, $\partial\hat{n}_t/\partial\sigma_2$ is indicative of the effect of environmental fluctuations on the equilibrium population size (at $\lambda = 1$).

For the three-stage life cycle, we first derived the total population size at equilibrium $\hat{n}_t$ by solving $A_3 \cdot \hat{N} = \hat{N}$ with population vector $N = (n_1, n_2, n_3)^T$ (T meaning transposed, see Appendix A for the derivation):

$$\hat{n}_t = \frac{\phi + \phi\sigma_1\gamma - \sigma_1(1-\gamma) + 1}{b(\sigma_1(1-\gamma) - 1)} \cdot log\left(\frac{(1-\sigma_1(1-\gamma))(1-\sigma_3)}{\phi\sigma_1\gamma\sigma_2}\right). \tag{3}$$

From equation 3 we derived the partial derivative of $\hat{n}_t$ with respect to σ_2 (see Appendix A8):

$$\frac{\partial\hat{n}_t}{\partial\sigma_2} = \frac{\phi + \phi\sigma_1\gamma + (1-\sigma_1(1-\gamma))}{b\sigma_2(1-\sigma_1(1-\gamma))}. \tag{4}$$

The derivations for the two-stage life cycle are detailed in Appendix B. From equation (4), we can readily see that for a given match of the population to its local optimum (for a given σ_2), different life histories will have different rates of declines of their population size away from its equilibrium value depending mostly on the fecundity and less on other rates.

An alternative measure for the robustness to environmental variability is the sensitivity of the population growth rate λ to juvenile survival ($\partial\lambda/\partial\sigma_2$), which was shown to correlate with the sensitivity of the effective population size $\hat{n}_e$, instead of the total population size n_t (Grant and Benton, 2000, 2003; Caswell et al., 2004). Here, the effective population size represents the number of individuals weighted by the contribution of their stage class to density regulation and population growth (Takada and Nakajima, 1998). We present the results for $\partial\hat{n}_t/\partial\sigma_2$ together with those of $\partial\lambda/\partial\sigma_2$ (both estimated at equilibrium population density when λ=1), and discuss the differences between these two measures in Appendix C.

The rate of trait evolution

We quantified the speed of evolution for a life history as the average trait change Δz per time step t from genetic evolution (not plasticity) in response to directional selection. The speed of evolution for quantitative traits in a stage-structured population was derived by Barfield et al. (2011):

$$\Delta\bar{\mathbf{z}} = \frac{1}{\bar{\lambda}} \sum_{i,j} v_i w_j \mathbf{G}_j \nabla_{\bar{\mathbf{z}}} \bar{a}_{ij} = \frac{1}{\bar{\lambda}} \mathbf{G} \sum_{i,j} \frac{\partial \bar{\lambda}}{\partial \bar{a}_{ij}} \nabla_{\bar{\mathbf{z}}} \bar{a}_{ij}, \tag{5}$$

where $\partial\bar{\lambda}/\partial\bar{a}_{ij} = v_i w_j / \mathbf{v}^{\mathrm{T}}\mathbf{w}$ is the sensitivity of the growth rate λ to changes in the vital rates a_{ij} (Caswell, 2001). Equation 5 (also known as Lande's theorem; Lande, 1982) was obtained under the assumption of weak selection and same mean phenotype $\bar{\mathbf{z}}$ and genetic variance $\mathbf{G}$ for all stages j (see discussion in Barfield et al., 2011, Appendix B). Importantly, equation 5 makes explicit the link between rate of evolution and population sensitivity to variation in vital rates. It also accounts for the changes of vital rates caused by changes in trait value z. We consider here that variation in survival is caused by the phenotypic mismatch of the population with its environment, which only affects the survival rate of juveniles. The relationship between phenotypic trait value z and juvenile survival σ_2 is given by a Gaussian fitness function: $w(z) = exp(-(z-\theta)^2/2\omega^2)$, where $\sigma_2(z) = w(z)$, with phenotypic optimum value θ, and variance of the fitness function ω^2, inversely related to the strength of selection on the trait.

For a species with three life-history stages, that reached the equilibrium population size from negative density dependence, with a stable stage distribution (SSD), and with one

trait under selection in juveniles (z_2), the asymptotic rate of evolution can be derived from Equation 5:

$$\Delta\bar{z} = G_2\ v_3\ w_2\ \sigma_2\ c\ \beta(z_2). \tag{6}$$

The asymptotic rate of trait change $\Delta\bar{z}$ thus varies with the additive genetic variance in juveniles G_2, the selection gradient on a single juvenile trait $\beta(z_2)$, the fraction of individuals exposed to selection $w_2 = \frac{\hat{n}_2}{\hat{n}_t}$, the survival probability of these individuals $\sigma_2 c = \sigma_2 exp(-b\hat{n}_3)$, and their contribution to the subsequent generations v_3 (the reproductive value of adults standardized such that $v^T w = 1$) (equation 8, Barfield et al., 2011). The rate of evolution ($\Delta\bar{z}$) can thus be expressed as a function of the vital rates by deriving expressions for w_2, c, and v_3:

$$\Delta\bar{z} = G_2\ \frac{(1-\sigma_3)(1-\sigma_1(1-\gamma))}{(1-\sigma_3)(1-\sigma_1(1-\gamma)) + (1-\sigma_3) + (1-\sigma_1(1-\gamma))}\ \beta(z_2), \tag{7}$$

as detailed in Appendix A. Equations 5–7 assume a population growth rate of $\lambda = 1$ at equilibrium population density, sexual (non-clonal) reproduction, weak selection, population dynamics that are faster than evolutionary dynamics, a Gaussian genotype-phenotype distribution, and the Gaussian fitness function mentioned above (Barfield et al., 2011; Orive et al., 2017). Under these assumptions, the selection gradient is: $\beta(z) = -(z-\theta)/(\omega^2 + P)$, a function of the distance between the phenotype z and its optimum θ, with P the phenotypic variance of the population (Via and Lande, 1985). Further assuming, for simplicity, that $\beta(z) = 1$, the evolvability of the population, de-

fined by Hansen et al. (2019) as $e = \Delta\bar{z}/\beta(z)$, becomes $e = \Delta\bar{z}$. We thus use the rate of change of the population mean phenotype as our measure of evolvability.

Standardization for numerical exploration

We standardized our generic life histories for uniform maximum population sizes ($\hat{n}_t$) in absence of environmental variation and for uniform maximum population growth rates (λ_{max}, the intrinsic population growth rate in absence of density regulation when *c=1*). With this standardization we could compare our four life histories while keeping key demographic properties constant (see Appendix C for a detailed discussion). Using a numeric approach, we adjusted the fecundity ϕ to reach equal λ_{max} across life histories, and a standardized form of the competition coefficient b (see Equations A9, B8) to reach equal $\hat{n}_t$. Using this standardization, Equation 4 becomes:

$$\frac{\partial \hat{n}_t}{\partial \sigma_2} = \frac{-\hat{n}_t}{\sigma_2} \cdot log\left(\frac{(1-\sigma_1(1-\gamma))(1-\sigma_3)}{\phi\sigma_1\gamma\sigma_2}\right)^{-1}. \tag{8}$$

Using Equations 7 and 8, we explored the effect of the vital rates σ_1, σ_3, and γ on the tradeoff between population size sensitivity $\partial\hat{n}_t/\partial\sigma_2$ and evolvability Δz (with $G = \beta(z_2) = 1$). As the sensitivity of the total population size varied with σ_2 (see equ. 8), $\partial\hat{n}_t/\partial\sigma_2$ was always quantified with $\sigma_2 = 0.8$. In addition we provide results for $\partial\lambda/\partial\sigma_2$ calculated for each combination of vital rates using the function sensitivity() from the *popbio* package (version 2.4.3, Stubben and Milligan, 2007) in R 3.4.2 (R Development Core Team, 2008).

Individual-based simulations

We ran individual-based simulations to test our mathematical derivations and account for genetic and demographic stochasticity, and an evolving additive genetic variance. Simulations were run with Nemo (Guillaume and Rougemont, 2006) extended for stage-structured populations (Cotto et al., 2017, 2020). We simulated a single panmictic population of hermaphroditic individuals. The population reached an equilibrium population size by density-dependent juvenile survival. A single quantitative trait was under hard selection in the juvenile stage such that changes in juvenile fitness (survival) translated into changes of the population size. The following life cycle events occurred consecutively each year: density-dependent regulation (of juvenile survival using the Ricker function), viability selection (removal of juveniles according to their survival probability which varied with the distance between trait value and environment), sexual reproduction (independent from the environmental state or population density), and stage transitions according to the MPM.

Life-history parameters

We modeled the four generic life-history strategies presented in the previous section. We standardized all four life-history strategies for the same total population size in absence of environmental fluctuations ($\hat{n}_{tmax} = 1500$ by adjusting b) and the same maximum population growth rate ($\lambda = 1.10$ or $\lambda_{max} = 1.15$, by adjusting ϕ). The single vital rates are listed in table 1.

With these simulation scenarios we tried to span a range of key life-history characteristics by accounting for differences in "pace of life" along the slow-fast continuum and for

Table 1: The following table lists the vital rates of the simulated life-history strategies, which are combinations of delayed (*del*, maturation probability $\gamma = 0.5$) or precocious (*pre*, $\gamma = 1.0$) offspring maturation, and semelparous (*sem*, adult survival $\sigma_3 = 0.0$) or iteroparous (*ite*, $\sigma_3 = 0.5$) adults, standardized for $\lambda_{max} = 1.10$ or $\lambda_{max} = 11.5$ via the annual fecundity ϕ. Offspring and juvenile survival were set to $\sigma_1 = \sigma_2 = 0.8$ for all life histories. The generation time (T) and the net reproductive rate (R_0) were calculated for the MPMs in absence of density regulation using the functions generation.time() and net.reproductive.rate() from the popbio package in R (Stubben and Milligan, 2007; R Development Core Team, 2008). The growth rate sensitivity ($\partial\lambda/\partial\sigma_2$) was calculated for the MPMs at $\hat{n}_t$ ($\lambda = 1$) using the function eigen.analysis() from the popbio package in R (Stubben and Milligan, 2007; R Development Core Team, 2008). The rate of evolution Δz was calculated with $G_2\beta(z_2) = 1$.

life history	λ_{max}	γ	σ_3	ϕ	b	$\partial\hat{n}_t/\partial\sigma_2[/10]$	$\partial\lambda/\partial\sigma_2$	Δz	T	R_0
del-ite	1.10	0.5	0.5	1.445	0.0012610	433.4	0.4129	0.21	4.53	1.54
del-sem	1.10	0.5	0.0	2.650	0.0016560	542.2	0.4818	0.27	3.62	1.41
pre-ite	1.10	1.0	0.5	1.134	0.0007550	503.5	0.4536	0.25	3.91	1.45
pre-sem	1.10	1.0	0.0	1.5125	0.0002111	983.6	0.6250	0.50	2.00	1.21
del-ite	1.15	0.5	0.5	1.750	0.0021100	301.1	0.5000	0.21	4.47	1.87
del-sem	1.15	0.5	0.0	3.100	0.0027600	372.9	0.5636	0.27	3.60	1.65
pre-ite	1.15	1.0	0.5	1.343	0.0012340	346.2	0.5372	0.25	3.88	1.72
pre-sem	1.15	1.0	0.0	1.6530	0.0002990	671.0	0.6250	0.50	2.00	1.32

differences in the reproductive strategy (see Fig. S13, and Stearns, 1983; Gaillard et al., 1989, 2005; Salguero-Gómez, 2017).

Genetic setup and selection model

We simulated the evolutionary dynamics of adaptation to a single environmental condition via the evolution of a single quantitative trait (z) under stabilizing selection in the juvenile stage using the classical Gaussian fitness function $w(z) = exp(-(z-\theta)^2/2\omega^2)$ (see above). We set the width of the fitness function to $\omega^2 = 4$ (corresponding to a stronger selection strength) or $\omega^2 = 16$ (representing a weaker selection strength). Each individual carried $l = 20$ unlinked loci, contributing additively to the trait z. We used a continuum-of-allele model where mutational effects, picked from a Gaussian distribution centered on zero with mutational variance $\alpha = 0.1$, were added to the existing allelic values. The mutation rate was $\mu = 0.0001$ so that the mutational phenotypic variance was $V_M = 2l\mu\alpha = 0.001$. We excluded random environmental effects on phenotype expression (e.g., developmental noise) such that the phenotype z was the sole product of the additive genetic effects for simplicity.

Environmental scenarios

We simulated environmental variation between years together with gradual changes of the average condition by perturbing the phenotypic optimum θ (e.g., see Chevin et al., 2017). Each year, the position of the phenotypic optimum for the entire population was picked from a Gaussian distribution $\theta \sim \mathcal{N}(\bar{\theta},\epsilon)$ with the average environment $\bar{\theta}$ and variance ϵ. We thus simulated environmental fluctuations between years that were independently and identically distributed (e.g., Caswell, 2001).

To allow the population genetic variance to reach mutation-selection-drift balance, we ran burn-in simulations for 50'000 years for each life history. Burn-in simulations were run with a constant average environment of $\bar{\theta} = 10$ for six different degrees of environmental fluctuations ($\epsilon = 0.0, 0.2, 0.5, 1.0, 1.5, 2.0$).

To asses the population size sensitivity of life-history strategies to interannual environmental stochasticity, we recorded population demographic characteristic (e.g., population size $\hat{n}_t$) every 10 years for an additional period of 500 years. A life history's population size sensitivity was assessed as the steepness of declining average population sizes ($\hat{n}_t = \frac{1}{51}\sum_{t=1}^{500} n_t$) with increasing degrees of interannual environmental fluctuations.

To asses the speed of trait evolution, we then initiated directional environmental change of the average environmental condition ($\bar{\theta}$) after burn-in, while still simulating interannual variation on top of the changing mean. The average phenotypic optimum started to change at t=100 with a rate of $\Delta\bar{\theta}$=+0.01, for 200 and 800 years. We quantified the speed of evolution as the time to reach 90% of the novel phenotypic optimum ($\bar{\theta}$=12, or $\bar{\theta}$=18). We did not use the maximum rate of phenotypic change per time step because all life histories either went extinct or adopted trait changes as fast as the rate of environmental change ($\Delta\bar{z} = \Delta\bar{\theta}$).

Results

Mathematical models

We found a tradeoff between life-history effects on the rate of evolution and their robustness against environmental perturbations, at least when comparing life histories with the

same maximum growth rate. The tradeoff is explicit in the positive, linear relationship between the rate of evolution (Δz) and the sensitivity of the population size to juvenile survival ($\partial n_t/\partial\sigma_2$ and $\partial\lambda/\partial\sigma_2$) for both the three-stage and the two-stage model (Fig. 2). Changes in vital rates that enhanced the rate of evolution also increased the sensitivity to environmental perturbations, and vice versa.

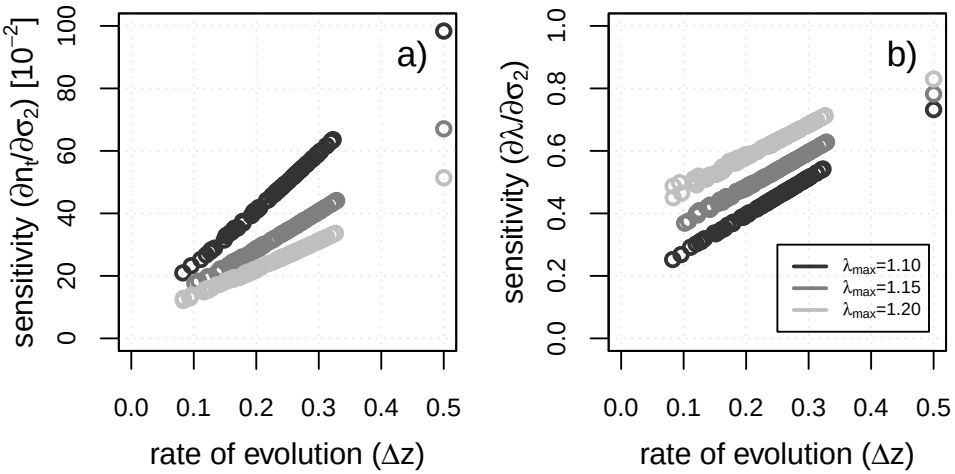

Figure 2: A life history's tradeoff between evolvability (Δz) and robustness ($\partial\hat{n}_t/\partial\sigma_2$ in a, and $\partial\lambda/\partial\sigma_2$ in b). Each circle illustrates a random combination of vital rates (with $0.2 \leq \sigma_1 \leq 1.0$, $\sigma_2 = 0.8$, $0.0 \leq \sigma_3 \leq 0.9$, $0.2 \leq \gamma \leq 1.0$). The fecundity (ϕ) and the strength of competition (b) were re-calculated for each vital rate combination to standardize the maximum population growth rate ($\lambda_{max} = 1.10 - black, \lambda_{max} = 1.15 - darkgray, \lambda_{max} = 1.20 - lightgray$) and the total population size at stable conditions (n_t=1'500). We then calculated the rate of evolution (Δz, with $G_2\beta(z_2) = 1$), the population size sensitivity ($\partial\hat{n}_t/\partial\sigma_2$), and the growth rate sensitivity ($\partial\lambda/\partial\sigma_2$) for each life-history variant. The three single points on the right of the plots were derived for the 2-stage life cycle (with $\sigma_2 = 0.8$), while the rest of the points illustrate parameter combinations for 3-stage life cycles.

A higher degree of iteroparity (high adult survival σ_3; Fig. 3a,d,g) and delayed maturation (low maturation rate γ; Fig. 3c,f) increased the robustness of the population size to environmental fluctuations, but reduced the rate of trait evolution. In contrast, precocious

maturation and semelparous adults allowed for fast evolution but reduced the robustness to environmental variability. We obtained qualitatively similar results for the sensitivity of the growth rate $\partial\lambda/\partial\sigma_2$, at least for a given maximal growth rate (Fig. 2).

The maximum rate of population growth (λ_{max}) shaped both the population size and growth rate sensitivity to environmental fluctuations, even though it had no effect on the rate of evolution. Higher λ_{max} reduced $\partial n_t/\partial\sigma_2$ and thus helped to maintain higher population densities with short-term environmental perturbations (Fig. 2, equation 8). However, higher λ_{max} increased $\partial\lambda/\partial\sigma_2$ (Fig. 2b). Therefore, vital rate changes that increased the populations' maximal growth rate and helped to maintain higher population sizes in the face of interannual environmental fluctuations caused stronger declines in the effective population size (Fig. 3h, Fig. 3g-i).

Results for a Beverton-Holt instead of a Ricker function for density regulation were qualitatively similar. The linear robustness-evolvability tradeoff remained (Fig. S5). Only the population size sensitivity $\partial\hat{n}_t/\partial\sigma_2$ was higher with a Beverton-Holt regulation function (Fig. S6).

Individual-based simulations

We could confirm the tradeoff between evolvability and robustness also in our individual-based simulations as the genetic storage effect was not strong enough to overcome the tradeoff. Life-history strategies with high robustness had the slowest rates of evolution, and vice versa. The average population size maintained at constant average conditions during burn-in declined with increasing environmental fluctuations for all life cycles below $\hat{n}_{tmax} = 1'500$, while life-history strategies differed from each other in the extent of $\hat{n}_t$

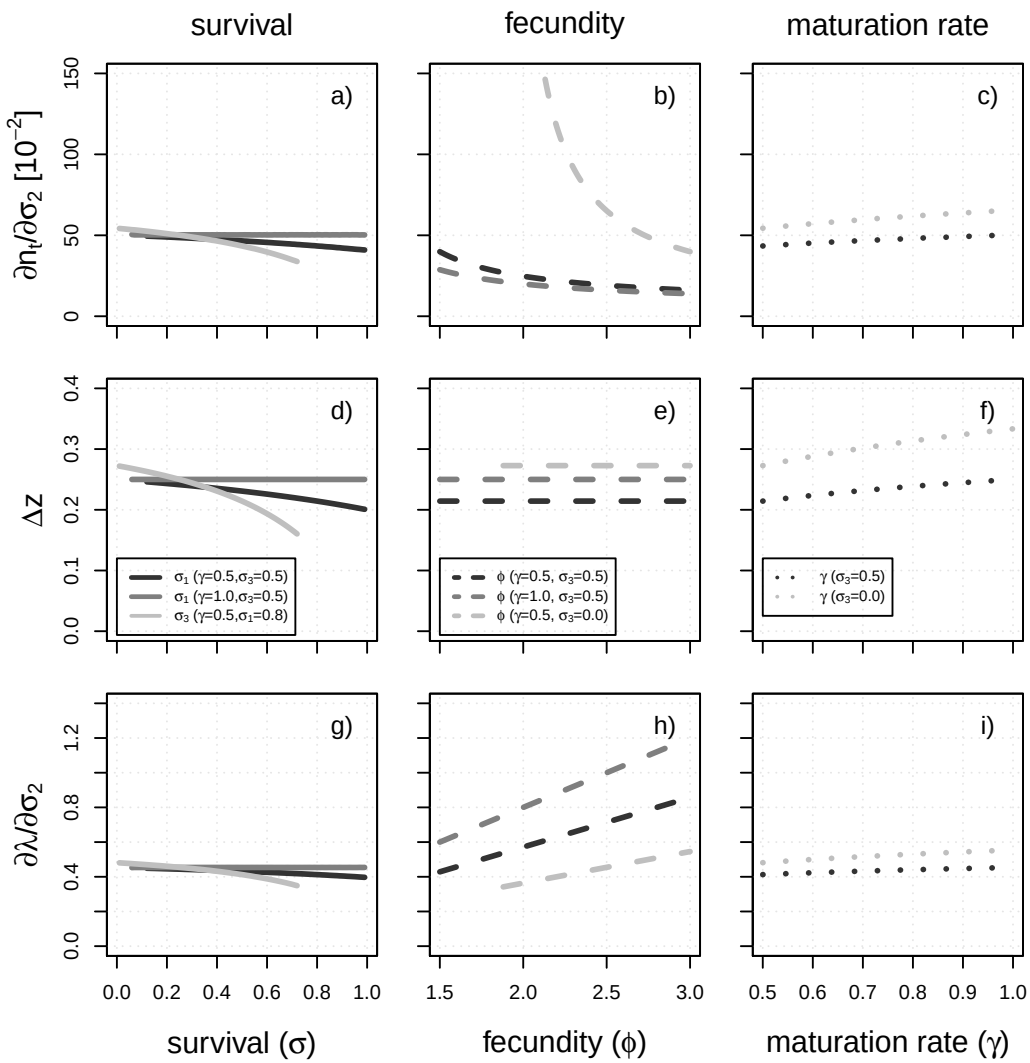

Figure 3: The graphs illustrate the analytical results for the sensitivity of the total population size to juvenile survival ($\partial\hat{n}_t/\partial\sigma_2 10^{-2}$, a-c), the rate of evolution (Δz, d-f), and the sensitivity of the population growth rate ($\partial\lambda/\partial\sigma_2$, g-i) for three-stage life cycle depending on survival rate (σ_1, σ_3), fecundity (ϕ), and maturation probability (γ). The sensitivity measures ($\partial\lambda/\partial\sigma_2$, $\partial\hat{n}_t/\partial\sigma_2$) were estimated at equilibrium population size in absence of interannual environmental variation at $\sigma_2 = 0.8$. The maximum growth rate has been standardized for $\lambda_{max} = 1.10$ by fecundity adjustments, except for the case with varying fecundity (b,e,h). Each parameter combination has been standardized for the same equilibrium population size in absence of interannual environmental fluctuations ($\hat{n}_t$=1500) via adjustments of the strength of competition (b). If not specified otherwise, the following parameter values have been used : $\sigma_1 = 0.8$, $\sigma_3 = 0.5$, $\gamma = 0.5$, $G_2 = 1$, and $\beta(z_2) = 1$.

reductions (Fig. 4b, Fig. 5a). The onset of gradual environmental change further reduced juvenile survival and evoked a decline in juvenile number and total population size (Fig. 4b,d), before trait evolution allowed to adapt to the changing conditions (Fig. 4a) and recover in a later phase of environmental change (Fig. 4d). Evolutionary rescue resulted in a u-shaped curve in total population size n_t, with a population size recovery already during environmental change or only after environmental change has stopped (Fig. 4b).

Population size sensitivity to environmental variability

The sensitivity of the total population size n_t to juvenile survival (Fig. 5a,b) matched with our analytical predictions (Tab. 1). The biennial, two-stage life cycle (*pre-sem*) had the greatest sensitivity, shown in the decline of n_t with the strength of interannual environmental fluctuations (ϵ, Fig. 5a) and in the fluctuations of n_t over time when the population was under stabilizing selection (i.e., 90% quantile of total population size, Fig. 5b). Sensitivity of n_t to fluctuations decreased among life histories as iteroparity (σ_3) and maturation time ($1 - \gamma$) increased (see Table 1), from *pre-sem* to *pre-ite*, *del-sem*, and *del-ite* life histories. The standardization of the life histories for maximum growth rate λ_{max} did not affect the rank order of life-history strategies. Overall, the sensitivity and the temporal fluctuations of n_t decreased when we increased λ_{max} from 1.10 to 1.15 (Fig. 5a,b). A weaker strength of selection ($\omega^2 = 16$) also attenuated the sensitivity and stochasticity of population size for all life histories (Fig. S11).

Rate of directional trait evolution

As expected from our analytical predictions (Table 1), the biennial life cycle (*pre-sem*) had the fastest evolutionary trait response to directional environmental change, while the

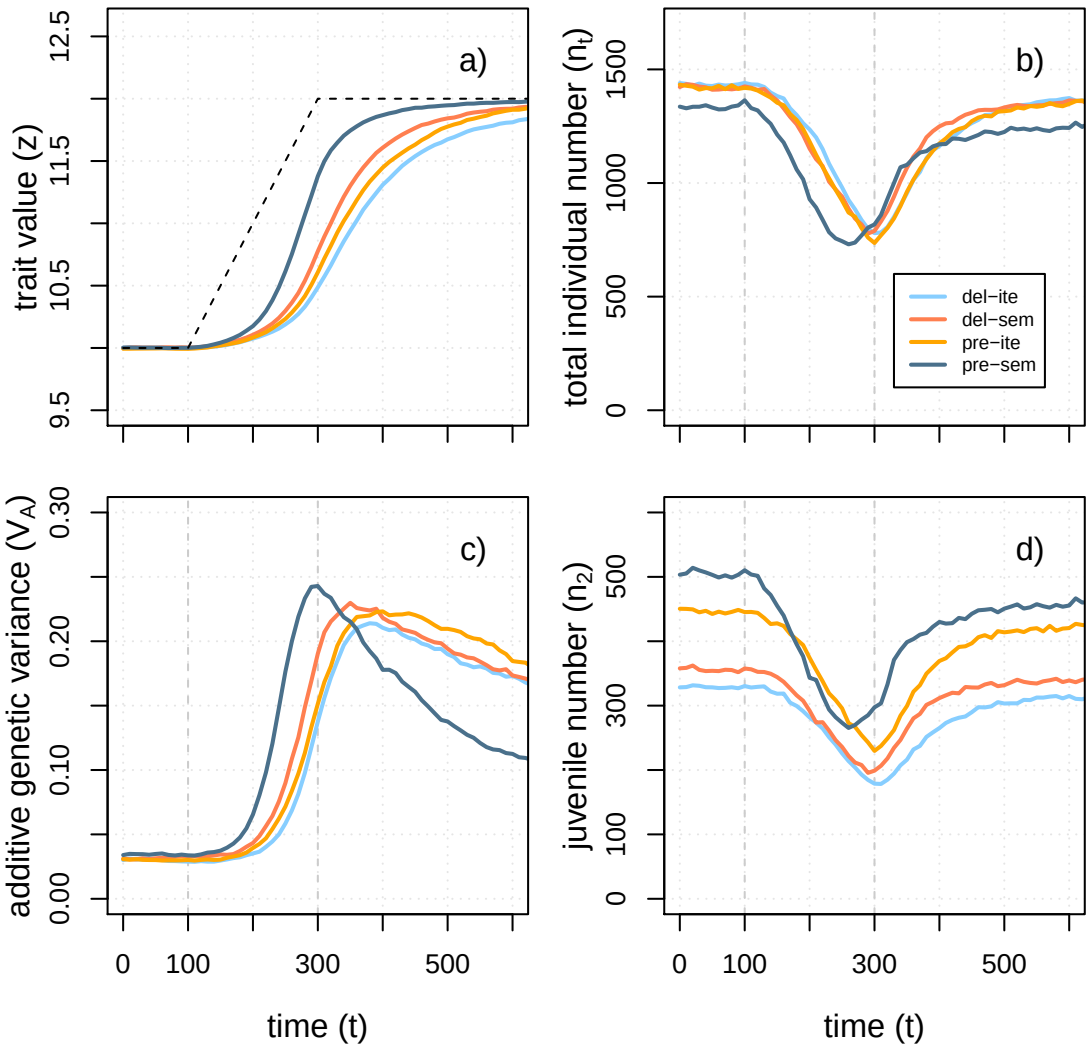

Figure 4: The graphs show the results of individual-based simulations for the mean trait value z (a), the total population size n_t (b), the additive genetic variance G_2 (c), and the juvenile number n_2 (d) for the four life histories (*del-sem*, *del-ite*, *pre-ite*, *pre-sem*) over 600 years. Environmental change started at t=100 and was realized by a gradual shift in the phenotypic optimum (−− black dashed lines) from $\theta = 10$ to $\theta = 12$ by t=300 (a). The between-year environmental fluctuations were set to $\epsilon = 0.2$ and life histories were standardized for $\lambda_{max} = 1.15$. Average population sizes (n_t) were standardized to $n_t = 1500$ in absence of interannual environmental fluctuations, and were depressed as result of between-year fluctuations and directional environmental change as result of a fitness reduction in juveniles (a). All values of the total population size and trait values represent the arithmetic means over all of the 100 replicates that did not go extinct.

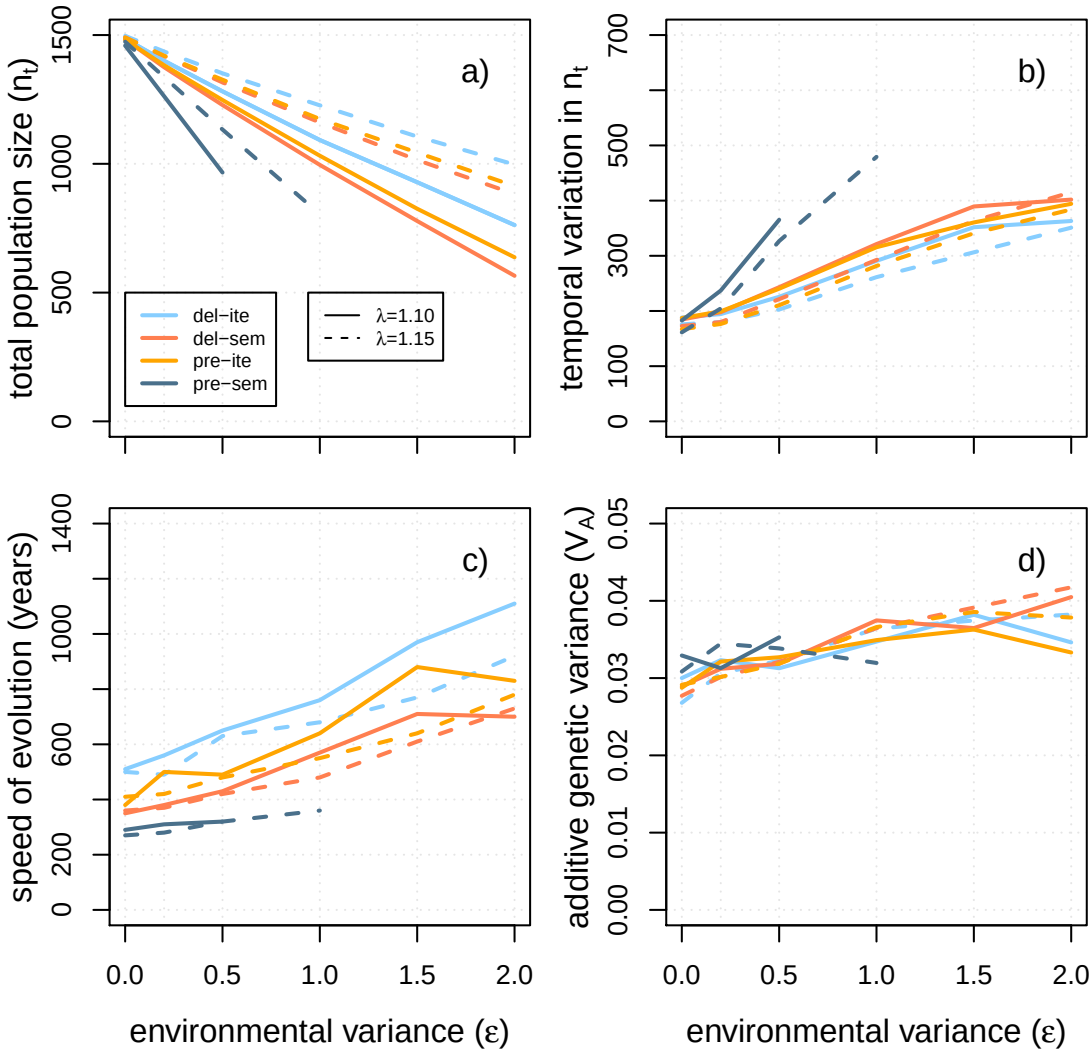

Figure 5: The graphs illustrate the total population size n_t (a), the variability in n_t over time (90 % quantile of n_t over 500 years, b), the speed of evolution (the average number of years to reach the trait value $z = 11.8$, c), and the additive genetic variance (G_2, d) are shown depending on the interannual environmental variability (ϵ). The simulation results are shown for four life histories (*del-sem*, *del-ite*, *pre-ite*, *pre-sem*) that have been standardized for two maximal population growth rates ($\lambda_{max} = 1.10$, $\lambda_{max} = 1.15$) with environmental change lasting for 200 years.

del-ite life history evolved the slowest (Fig. 5c). However, even though the differences were small, life histories standardized for $\lambda_{max} = 1.15$ evolved faster than life histories with $\lambda_{max} = 1.10$ (Fig. 5c), which was a deviation from the analytical predictions. Nevertheless,

differences in evolvability were mainly found on a yearly, absolute time scales. Once scaled to generation time, all life histories took a similar number of *generations* to reach the same phenotypic threshold (Fig. S10c).

Although standing genetic variation G_2 was similar across life-history strategies after burn-in (Fig. 5d), its temporal dynamics was strongly affected by the degree of iteroparity and delayed maturation. G_2 increased fastest during adaptation to new average local conditions in the *pre-sem* and slowest in the *del-ite* life cycle (Fig. 4c). The dynamics of G_2 were also slowed down by delayed maturation (Fig. 4c). Overall, larger interannual fluctuations tended to increase standing genetic variation in all life histories (Fig. 5d).

Extinction risk

The extinction risk of the population, evaluated as the total number of extinct replicates at a given time during the simulations (Fig. 6), varied among life histories. In general, population extinctions were delayed relative to the onset of directional environmental change and still occurred after the environmental change stopped (Fig. 6a,c). The less robust life-history strategies (e.g., *pre-sem*) experienced earlier extinction because of larger demographic stochasticity leading to earlier declines in n_t than robust life histories (e.g., *del-ite*; Fig. 4b,d). Nevertheless, the iteroparous life histories (*pre-ite, del-ite*) had larger extinction risks when we prolonged the period of environmental change from 200 to 800 years, at least at low rate of random environmental fluctuations (Fig. 6c). Under these conditions, the semelparous life cycles could adapt faster to the shifting trait optimum and reduce their phenotypic lag with it (results not shown). However, at high rates of interannual fluctuations, the bi-annual life cycle *pre-sem* always had the highest rate

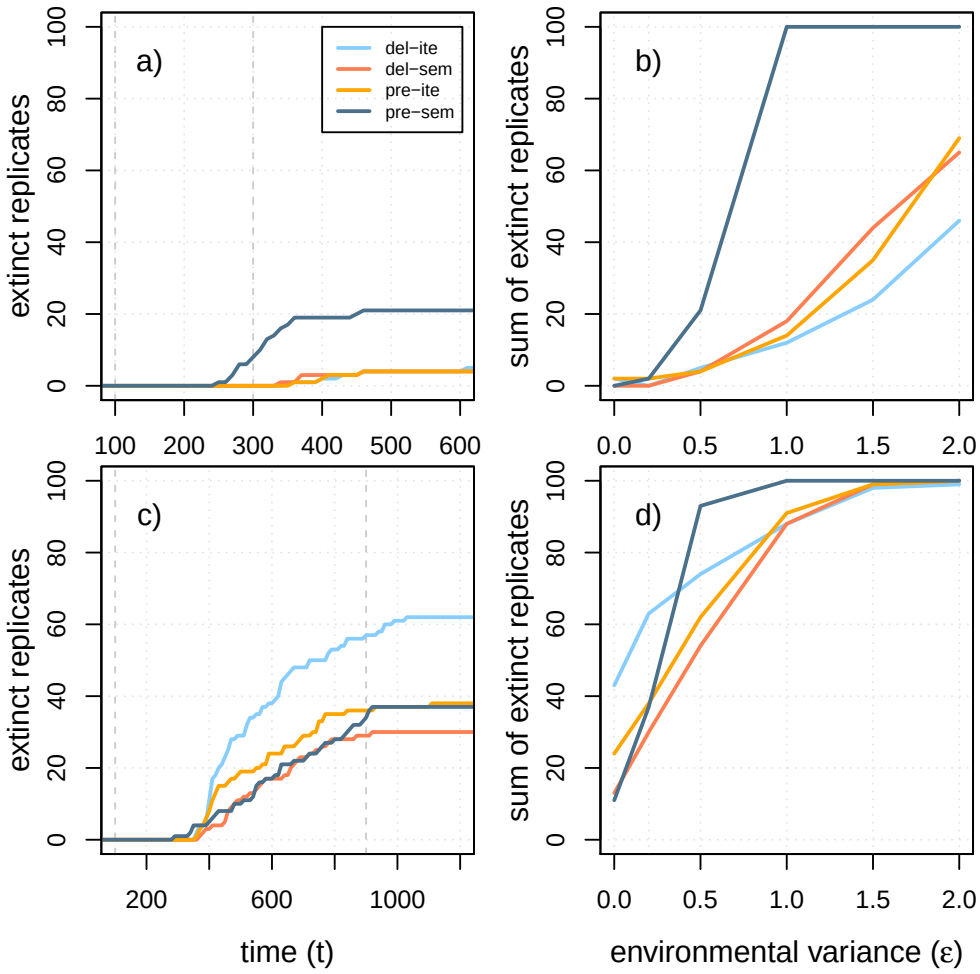

Figure 6: These graphs show the number of extinct replicates over time t (a,c) and the total number of extinct replicates depending on environmental variability ϵ (b,d) for each of the four life histories. Extinction dynamics are shown for two different scenarios with environmental change either lasting for 200 years (a,b) or for 800 years (c,d). The gray dashed lines indicate the start of environmental change ($t = 100$) and its end ($t = 300$ for a,b; $t = 900$ for c,d). In both scenarios, the rate of environmental change per year was set to $\Delta\bar{\theta} = 0.01$ and all life histories were standardized for a maximum growth rate of $\lambda = 1.10$. The temporal dynamics are shown for an environmental variability of $\epsilon = 0.5$ (a) and $\epsilon = 0.2$ (c).

of extinction (Fig. 6b,d). Overall, extinction risks were attenuated by having larger fecundity when setting $\lambda_{max} = 1.15$ (Fig. S9) and when reducing the strength of selection to $\omega^2 = 16$, where no extinction occurred (Fig. S12).

Discussion

Life-history strategies can impact a species' persistence in a dynamic environment, especially by helping it to cope with short-term interannual fluctuations and by shaping its evolutionary response to long-term gradual changes (Lande, 1982; Hairston and De Stasio Jr., 1988; Barfield et al., 2011). In this study, we asked (i) whether a tradeoff between a life history's demographic robustness against environmental variability and its rate of trait evolution exists, (ii) how life-history characteristics determine the position of a species along the robustness-evolvability tradeoff, focusing on fast versus slow life cycles in species with overlapping generations, different degrees of iteroparity and timing of offspring maturation (dormancy), (iii) whether a genetic storage effect could alleviate the tradeoff, and (iv) how the tradeoff affects species persistence in fluctuating environments. Using existing theory from matrix population modeling and quantitative genetics, we confirmed numerically that a tradeoff exists. However, current theory does not account for stochasticity, density dependence, and demographic feedback on the genetic composition of a population. For these reasons, we ran stochastic individual-based simulations for a single population reaching a carrying capacity under negative density dependence. Here too, we could confirm the hypothesized tradeoff between a life history's robustness and evolvability. Overall, we could show that, along the fast-slow continuum, short-lived semelparous species were more "evolvable" and could cope best with long-lasting directional environmental change, but experienced the highest extinction risk from interannual fluctuations and during the initial phase of environmental changes. They should thus suffer more from rapid anthropogenic climate changes than long-lived iteroparous species. We now discuss the effects and implications of the details of our models.

A higher robustness against random and uncorrelated between-year environmental fluctuations was achieved by three life-history characteristics: Offspring dormancy, higher adult survival (leading to iteroparity), and a larger maximum growth rate. Offspring dormancy and higher adult survival helped to tolerate a variable environment by shielding a higher proportion of individuals from detrimental environmental conditions and spreading the risk of failed survival across years (e.g., see also Orzack and Tuljapurkar, 1989; Tuljapurkar, 1990; Koons et al., 2008; Zeineddine and Jansen, 2009). In our simulations, offspring dormancy and iteroparity allowed the population to maintain larger sizes in face of fluctuations, reducing its demographic stochasticity, and thereby helping the population to cope with reduced offspring survival caused by interannual environmental variation. In addition, a larger maximum growth rate improved the robustness to environmental variability by helping to recover faster from extreme events (Hallett et al., 2018).

Opposed to the means of promoting robustness, evolvability of life-history strategies benefited from lower dormancy in offspring and reduced adult survival, following two main effects. First, the rate of trait evolution in stage-structured populations generally increases when exposing more individuals to selection and improving their contribution to the next generation. From Equations 5 and 6, these two factors maximize the weight put on the amount of additive genetic variation G_2 available for selection (i.e, the evolvability of the trait, see Houle, 1992; Hansen and Houle, 2008). Therefore, life-histories without dormancy could mobilize a larger amount of genetic variation per unit of time and adapt faster to shifting environmental conditions. Increased adult mortality has a similar effect by increasing the rate of juvenile recruitment. Kuparinen et al. (2010) also showed this

effect when simulating the evolution of a quantitative trait in Scots pine and Silver birch in populations with a fixed age structure. A higher mortality in adult trees (e.g., from senescence or forest management) favored faster recruitment of adapted juvenile trees and accelerated trait evolution in their simulations. A second effect favoring evolvability was shorter generation times (also described in Barfield et al., 2011; Orive et al., 2017). In our case, increased generation time, mostly controlled by the degree of iteroparity, was the main factor lowering the pace of adaptation to the shifting environment. Per unit of generation time, long-lived species experienced larger environmental shifts causing larger maladaptation and thus lower growth rate, eventually reducing juvenile recruitment rates sufficiently to cause larger extinction rates than for fast evolving, short-lived species. Osmond et al. (2017) described this mechanism in predator-prey systems when predation reduced the generation time of the prey species and thus helped the prey to better adapt to novel environmental conditions. Overall, we could thus confirm our initial hypothesis that those life-history changes favoring evolvability simultaneously reduce robustness to interannual environmental variability, and vice versa.

In our simulations, the genetic storage effect did not affect the amount of standing genetic variation at the start of directional environmental change and did not help to overcome the tradeoff between robustness and evolvability in long-lived species. Although all life histories had same standing genetic variation, they differed markedly in the evolution of additive genetic variance G_2 during environmental change. The genetic variance G_2 increased during directional selection in all simulations, as expected from the increase of allele frequencies of rare variants during adaptation towards a new trait optimum (Bürger, 1999; Kopp and Matuszewski, 2014). This rise in G_2 happened most rapidly

for the biennial life cycle and slowest for the life history with offspring dormancy and iteroparity. When a higher proportion of juveniles under selection allowed for faster allele frequency changes over time, the additive genetic variance rose more quickly, which further boosted evolution. Life histories thus shaped the rate of evolution via G_2 differently from our initial expectations, in fact in the opposite direction, such that the tradeoff was not mitigated but enforced. Yet, the storage effect has been shown to speed up evolution with overlapping generations for very large levels of environmental fluctuations ϵ (Yamamichi et al., 2019). We could not impose such high levels of ϵ without driving populations to extinction. In our case, populations were under hard selection such that decreases in mean fitness translated into reduced offspring numbers, while Yamamichi et al. (2019) simulated a yearly offspring production that was insensitive to ϵ.

To overcome the tradeoff, a higher maximum growth rate could allow life-history strategies to be more robust and at the same time more evolvable. In our models, a higher population growth rate λ_{max} improved robustness against environmental fluctuations by helping to recover faster from detrimental environmental events and avoid extinction, in line with previous theory (Lynch and Lande, 1993; Lande, 1993; Bürger and Lynch, 1995; Bürger, 1999). Interestingly, a higher growth rate also caused faster trait evolution in our simulations, even though it had no effect on Δz in our mathematical models. In the simulations, a higher λ_{max}, when realized by larger fecundity, was associated with more frequent mutation and recombination events. This effect of life-history parameters on the amount of mutational input (Fig. S8) is a process not accounted for in previous analytical models, but should be of importance in natural systems.

In conclusion, our results show that the feedback between evolutionary and demographic

processes are critical for species persistence. A similar conclusion can be reached from models of evolutionary rescue (i.e., adaptation to single-shift environmental scenarios: Lynch et al., 1991; Lynch and Lande, 1993; Bürger and Lynch, 1995; Gomulkiewicz and Holt, 1995; Gomulkiewicz and Houle, 2009; Chevin, 2013), or from models of species persistence on temporally shifting environmental gradients (i.e., models of species' range evolution: Polechová et al., 2009; Duputié et al., 2012). However, these models often ignore short-term perturbations (but see Orive et al., 2017), assume constant population growth (i.e., with density-independent growth, but see Boulding and Hay, 2001), and do not incorporate explicit life cycles. On the other hand, quantitative genetics models of trait evolution in stage-structured populations with (Engen et al., 2011, 2013a) or without (Barfield et al., 2011) stochastic environmental fluctuations do not model species persistence, to a few recent exceptions (Marshall et al., 2016; Cotto et al., 2019). Importantly, no study to date explicitly addressed the tradeoff between evolvability and demographic robustness. We have shown that such a tradeoff exists and may limit the odds of evolutionary rescue in fast life-histories, while slow life-histories may persist longer while accumulating large adaptation lags at the cost of increased extinction debts (Dullinger et al., 2012; Cotto et al., 2017).

Implications

We highlighted a fundamental property of eco-evolutionary dynamics whereby maximizing the evolutionary response of a population adapting to a fluctuating environment comes at the expense of its demographic robustness to variation in vital rates. Our conclusions are based on comparisons of eco-evolutionary dynamics of standardized life cycles. However, life-history strategies in natural systems are not standardized. In fact, systematic

differences in more than one life-history characteristic exist. Species with low generation times often exhibit systematically higher population sizes ($\hat{n}_t$), greater intrinsic growth rates, larger dispersal abilities, but lower competitive abilities than species with long generation times (Petit and Hampe, 2006; Buoro and Carlson, 2014; Beckman et al., 2018). They might thus be more robust to changes than predicted here. Similarly, long-lived species may suffer more from climate changes if adult mortality is increased, reducing their robustness. For instance, adult trees may be sensitive to extreme weather events such as drought or forest fires (e.g., Van Mantgem and Stephenson, 2007). As we have shown, reducing adult survival would decrease robustness by modifying the life history strategy of the species towards semelparity. By simplifying the action of selection on a single life stage (e.g., on tree seedlings), we have not incorporated possible feedback between environmentally induced selection and life history characteristics. Such feedback could change the life history of the species, as shown by Cotto et al. (2019), and move the species along the fast-slow life history tradeoff between evolvability and robustness. Instead, we have characterized archetype life-history strategies that span the fast-slow continuum and exemplified those possible outcomes. Our work thus shows the importance of merging population ecology with evolutionary quantitative genetics in a dynamical and stochastic modelling framework to characterize species' vulnerability to environmental changes.

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Conflicts of interest

The authors declare no conflict of interest.

Appendix

Appendix A: 3-stage model

Equilibrium population size

The populations' demographic dynamics were modeled via the population vector

$$N = \begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix} \tag{A1}$$

and the matrix population model

$$A = \begin{bmatrix} \sigma_1(1-\gamma) & 0 & \phi \\ \sigma_1(\gamma) & 0 & 0 \\ 0 & \sigma_2 \cdot exp(-bn_3) & \sigma_3 \end{bmatrix} \tag{A2}$$

such that $N(t+1) = AN(t)$. By solving for the stage densities at equilibrium when $\hat{N} = A\hat{N}$,with $\hat{N} = (\hat{n}_1, \hat{n}_2, \hat{n}_3)^T$, the individual numbers within the offspring, juvenile, and adult stage at equilibrium could be derived as

$$\hat{n}_1 = \frac{\phi}{b(\sigma_1(1-\gamma)-1)} \cdot log\left(\frac{(1+\sigma_1\gamma-\sigma_1)(1-\sigma_3)}{\phi\sigma_1\gamma\sigma_2}\right), \tag{A3}$$

$$\hat{n}_2 = \frac{\phi\sigma_1\gamma}{b(\sigma_1(1-\gamma)-1)} \cdot log\left(\frac{(1+\sigma_1\gamma-\sigma_1)(1-\sigma_3)}{\phi\sigma_1\gamma\sigma_2}\right), \tag{A4}$$

$$\hat{n}_3 = \frac{1}{-b} \cdot log\left(\frac{(1+\sigma_1\gamma-\sigma_1)(1-\sigma_3)}{\phi\sigma_1\gamma\sigma_2}\right). \tag{A5}$$

The total population size at equilibrium was computed from $\hat{n}_t = \hat{n}_1 + \hat{n}_2 + \hat{n}_3$ as

$$\hat{n}_t = \frac{\phi+\sigma_1\gamma(\phi+1)-\sigma_1+1}{b(\sigma_1(1-\gamma)-1)} \cdot log\left(\frac{(1+\sigma_1\gamma-\sigma_1)(1-\sigma_3)}{\phi\sigma_1\gamma\sigma_2}\right). \tag{A6}$$

Sensitivity of total population size to juvenile survival

The partial derivative of the total population size at equilibrium ($\hat{n}_t$) to juvenile survival (σ_2) was calculated as

$$\frac{\partial\hat{n}_t}{\partial\sigma_2} = \frac{\phi+\sigma_1\gamma(\phi+1)-\sigma_1+1}{b(\sigma_1(1-\gamma)-1)} \cdot \frac{\phi\sigma_1\gamma\sigma_2}{(1+\sigma_1\gamma-\sigma_1)(1-\sigma_3)} \cdot \left(\frac{-1\phi\sigma_1\gamma(1+\sigma_1\gamma-\sigma_1)(1-\sigma_3)}{(\phi\sigma_1\gamma\sigma_2)^2}\right), \tag{A7}$$

which could be simplified to

$$\frac{\partial\hat{n}_t}{\partial\sigma_2} = \frac{\sigma_1(1-\gamma)-1-\phi(1+\sigma_1\gamma)}{b\sigma_2(\sigma_1(1-\gamma)-1)}. \tag{A8}$$

To standardize a life history for a specific total equilibrium population size ($\hat{n}_t$) the strength of intra-specific competition was adjusted as follows

$$b = \frac{\phi+\sigma_1\gamma(\phi+1)-\sigma_1+1}{\hat{n}_t(\sigma_1(1-\gamma)-1)} \cdot log\left(\frac{(1+\sigma_1\gamma-\sigma_1)(1-\sigma_3)}{\phi\sigma_1\gamma\sigma_2}\right). \tag{A9}$$

By inserting equation A9 in equation A8, the population size sensitivity can be expressed

depending on the equilibrium population size as

$$\frac{\partial \hat{n}_t}{\partial \sigma_2} = \frac{\sigma_1(1-\gamma) - 1 - \phi(1+\sigma_1\gamma)}{\sigma_2(\sigma_1(1-\gamma)-1)} \cdot \frac{\hat{n}_t(\sigma_1(1-\gamma)-1)}{\phi + \sigma_1\gamma(\phi+1) - \sigma_1 + 1} \cdot log\left(\frac{(1+\sigma_1\gamma-\sigma_1)(1-\sigma_3)}{\phi\sigma_1\gamma\sigma_2}\right)^{-1}, \tag{A10}$$

such that the following partial derivative is obtained

$$\frac{\partial \hat{n}_t}{\partial \sigma_2} = \frac{-\hat{n}_t}{\sigma_2} \cdot log\left(\frac{(1+\sigma_1\gamma-\sigma_1)(1-\sigma_3)}{\phi\sigma_1\gamma\sigma_2}\right)^{-1}. \tag{A11}$$

Rate of evolution at equilibrium population size

We adapted equation 8 from Barfield et al. (2011) for our three-stage life cycle to describe the rate of evolution depending on the juvenile proportion (w_2), juvenile survival (σ_2), competition survival (c), the reproductive value of adults (v_3), the additive genetic variance in juveniles (G_2), and the selection gradient on a juvenile trait ($\beta(z_2)$) as

$$\Delta\bar{z} = G_2\ v_3\ w_2\ \sigma_2\ c\ \beta(z_2). \tag{A12}$$

The juvenile proportion (w_2) could be derived from equation A4 and A6 as

$$w_2 = \frac{\hat{n}_2}{\hat{n}_t} = \frac{\phi\sigma_1\gamma}{\phi + \sigma_1\gamma(\phi+1) - \sigma_1 + 1}. \tag{A13}$$

The probability of surviving intra-specific competition (c) was derived by combining the Ricker function $c = exp(-bn_3)$ and equation A5 as

$$c = \frac{(1-\sigma_3)(1+\sigma_1\gamma-\sigma_1)}{\phi\sigma_1\gamma\sigma_2}. \tag{A14}$$

The reproductive value of adults (v_3) could be derived from the left eigenvector (v) of the matrix population model (A) when solving $vA = \lambda v$ (Caswell, 2001, equation 4.81). For

a population at equilibrium population size ($\lambda = 1$) the reproductive value of adults can be derived as

$$v_3 = \frac{\phi}{(1 - \sigma_3)}, \tag{A15}$$

and normalized to

$$v_3 = \frac{\phi + \sigma_1\gamma(\phi + 1) - \sigma_1 + 1}{(1 - \sigma_3)(1 - \sigma_1(1 - \gamma)) + (1 - \sigma_3) + (1 - \sigma_1(1 - \gamma))} \tag{A16}$$

such that $v * w = 1$ (as in Barfield et al., 2011). The rate of evolution depending on the single vital rates then could be expressed as

$$\Delta\bar{z} = G_2 \, \frac{(1 - \sigma_3)(1 - \sigma_1(1 - \gamma))}{(1 - \sigma_3)(1 - \sigma_1(1 - \gamma)) + (1 - \sigma_3) + (1 - \sigma_1(1 - \gamma))} \, \beta(z_2). \tag{A17}$$

Appendix B: 2-stage model

Equilibrium population size

The demographic dynamics for a 2-stage life history with non-overlapping generations were modeled by the population vector

$$N = \begin{pmatrix} n_2 \\ n_3 \end{pmatrix} \tag{B1}$$

and the matrix population model

$$A = \begin{bmatrix} 0 & \phi \\ \sigma_2 exp(-bn_2) & 0 \end{bmatrix} \tag{B2}$$

such that $N(t+1) = AN$. By solving for the individual numbers within stages at equilibrium when $\hat{N} = A\hat{N}$ and $\hat{N} = (\hat{n}_2, \hat{n}_3)^T$ the juvenile and adult numbers at equilibrium were derived as

$$\hat{n}_2 = \frac{-\phi}{b\phi} \cdot log\left(\frac{1}{\phi\sigma_2}\right). \tag{B3}$$

$$\hat{n}_3 = \frac{-1}{b\phi} \cdot log\left(\frac{1}{\phi\sigma_2}\right). \tag{B4}$$

(with natural logarithm log()). The total population size at equilibrium was computed from $\hat{n}_t = \hat{n}_2 + \hat{n}_3$ as

$$\hat{n}_t = \frac{-1-\phi}{b\phi} \cdot log\left(\frac{1}{\phi\sigma_2}\right). \tag{B5}$$

Sensitivity of total population size to juvenile survival

The partial derivative of the total population size at equilibrium $\hat{n}_t$ to juvenile survival σ_2 was derived as

$$\frac{\partial \hat{n}_t}{\partial \sigma_2} = \frac{(-\phi - 1)}{b\phi} \cdot \frac{\sigma_2 \phi}{1} \cdot \frac{-\phi}{\phi^2 \sigma_2^2}, \tag{B6}$$

which could be simplified to

$$\frac{\partial \hat{n}_t}{\partial \sigma_2} = \frac{\phi + 1}{b\sigma_2 \phi}. \tag{B7}$$

To reach a certain total equilibrium population size ($\hat{n}_t$) the strength of intra-specific competition (b) was standardized as follows

$$b = \frac{-1 - \phi}{n_t \phi} \cdot log\left(\frac{1}{\phi \sigma_2}\right). \tag{B8}$$

Given that the maximum growth rate λ_{max} could be calculated from

$$\lambda_{max} = \sqrt{\sigma_2 \phi}, \tag{B9}$$

life histories could be standardized for λ_{max} via ϕ adjustments as

$$\phi = \frac{\lambda_{max}^2}{\sigma_2}, \tag{B10}$$

such that the sensitivity $\partial \hat{n}_t / \partial \sigma_2$ could be generalized to

$$\frac{\partial \hat{n}_t}{\partial \sigma_2} = \frac{-n_t}{\sigma_2} \cdot log\left(\frac{1}{\lambda_{max}^2}\right)^{-1}. \tag{B11}$$

Rate of evolution at stable population size

To describe the rate of evolution we adapted equation 8 from Barfield et al. (2011) for our two-stage life cycle as

$$\Delta\bar{z} = G_2\ v_3\ w_2\ \sigma_2\ c\ \beta(z_2). \tag{B12}$$

The juvenile proportion could be derived from equation B3 and B5:

$$w_2 = \frac{\hat{n}_2}{\hat{n}_t} = \frac{\phi}{1+\phi}. \tag{B13}$$

The probability of surviving intra-specific competition (c) was derived by combining the Ricker function $c = exp(-bn_2)$ and equation B3:

$$c = exp(-bn_2) = \frac{1}{\phi\sigma_2}. \tag{B14}$$

The reproductive value of adults (v_3) could be derived from the left eigenvector (v) of the matrix population model (A) when solving $vA = \lambda v$ (Caswell, 2001, equation 4.81). For a population at equilibrium ($\lambda = 1$) the reproductive value of adults could be derived as

$$v_3 = \phi \tag{B15}$$

and normalized to

$$v_3 = \frac{1+\phi}{2} \tag{B16}$$

such that $v * w = 1$ (as in Barfield et al., 2011). The rate of evolution depending on the

single vital rates then could be expressed as

$$\Delta \bar{z} = \frac{1}{2}\, G_2 \beta(z_2) \tag{B17}$$

Appendix C: The standardization of life-history strategies

standardization

A critical aspect for the interpretation of our model and simulation results was the standardization of life-history strategies for uniform total population sizes $\hat{n}_t$ at stable conditions and for homogeneous maximum growth rates λ_{max}. The population size standardization was necessary for two reasons. First, the environmental sensitivity $\partial n_t/\partial \sigma_2$ varied with the total population size (see equation 8), such that we had to measure it in the mathematical models at the same $\hat{n}_t$ to achieve informative comparisons between life histories. Second, the population size standardization allowed us to make $\partial n_t/\partial \sigma_2$ an informative proxy for extinction risk from short-term environmental variability. The population size reduction from environmental fluctuations determined the distance to critically low population sizes, the levels of genetic and demographic stochasticity, and thus fed back on the success rate of evolutionary rescue (Gomulkiewicz and Holt, 1995; Willi and Hoffmann, 2009; Lanfear et al., 2014; Carlson et al., 2014; Orive et al., 2017). While we are convinced that a population size standardization was necessary for this kind of study, we want to highlight that other kinds of standardization, for instance for the effective population size $\hat{n}_e$ (Caswell et al., 2004) or for uniform adult numbers $\hat{n}_3$, could make sense as well.

A life-history standardization for uniform maximum population growth rates was not mandatory, but highly useful. While the growth rate at population size equilibrium is always unity ($\lambda = 1$), the maximum population growth rate λ_{max} is an important demographic parameter with regard to a populations' recovery subsequent to detrimental environmental conditions (Lynch and Lande, 1993; Chevin et al., 2010). By running two

sets of simulations with distinct levels of λ_{max} we could study the levels of robustness and evolvability not only along the axis of the fast-slow continuum (e.g., generation time T) but also along the axis of reproductive strategy as well (e.g., net reproductive rate R_0). This distinction revealed that the tradeoff between robustness and evolvability was only present when life histories with the same λ_{max} were compared to each other. Instead, both properties could be increased or decreased simultaneously when changes in vital rates translated into changes in λ_{max} (e.g., when moving to the bottom right or top-left corner in Fig. 2a). Thus, some life histories could be more evolvable and, at the same time, more robust than others. We thus conclude that the described tradeoff is not a "hard" tradeoff but could be overcome, at least partly, by life-history evolution towards higher maximum growth rates (λ_{max}) along the reproductive strategy axis of life histories.

Two measures to quantify robustness against environmental variability

Even though we used two different robustness measures, $\partial\hat{n}_t/\partial\sigma_2$ and $\partial\lambda/\partial\sigma_2$, we suggest to not use them interchangeably given that they responded in opposite directions to some vital rate changes (see also Takada and Nakajima, 1998; Grant and Benton, 2000; Caswell et al., 2004). In our mathematical models, increasing a life history's maximum growth rate (e.g., to λ_{max}=1.15) resulted in a lower sensitivity of total population size ($\partial\hat{n}_t/\partial\sigma_2$) but in a higher sensitivity of the effective population size ($\partial\lambda/\partial\sigma_2$), such that one measure indicated an increase in robustness, and the other a decrease. Hence, it is unclear which measure is better suited to quantify a life history's robustness against interannual environmental fluctuations. On the one hand, $\partial\hat{n}_t/\partial\sigma_2$ was much better correlated to the extinction risk from short-term environmental variation than $\partial\lambda/\partial\sigma_2$ levels. On the other hand, this correlation might vanish, or even be reversed, when

life-history strategies would have been standardized for the same 'effective' population size, instead of the same 'total' population size. We thus don't suggest to favor one measure over the other, but recommend a careful interpretation and further theoretical investigations.

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Supplementary Material

Supp A: 3-stage model with Beverton-Holt density regulation

Equilibrium population size

The demographic dynamics were modeled via the population vector

$$N = \begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix} \tag{S1}$$

and the MPM

$$A = \begin{bmatrix} \sigma_1(1-\gamma) & 0 & \phi \\ \sigma_1(\gamma) & 0 & 0 \\ 0 & \sigma_2 \cdot 1/(1+bn_3) & \sigma_3 \end{bmatrix} \tag{S2}$$

such that $N(t+1) = AN(t)$. At equilibrium $\hat{N} = A\hat{N}$ with $\hat{N} = c(\hat{n}_1, \hat{n}_2, \hat{n}_3)^T$. The number of offspring, juveniles, and adults at equilibrium then could be derived as

$$\hat{n}_1 = \frac{\phi}{b(1-\sigma_1(1-\gamma))} \cdot \left(\frac{\sigma_2\sigma_1\gamma\phi}{(1-\sigma_3)(1-\sigma_1(1-\gamma))} - 1 \right), \tag{S3}$$

$$\hat{n}_2 = \frac{\phi\sigma_1\gamma}{b(1-\sigma_1(1-\gamma))} \left(\frac{\sigma_2\sigma_1\gamma\phi}{(1-\sigma_3)(1-\sigma_1(1-\gamma))} - 1 \right), \tag{S4}$$

$$\hat{n}_3 = \frac{1-\sigma_1(1-\gamma)}{b(1-\sigma_1(1-\gamma))} \cdot \left(\frac{\sigma_2\sigma_1\gamma\phi}{(1-\sigma_3)(1-\sigma_1(1-\gamma))} - 1 \right). \tag{S5}$$

The total population size at equilibrium was computed from $\hat{n}_t = \hat{n}_1 + \hat{n}_2 + \hat{n}_3$ as

$$\hat{n}_t = \frac{\phi + \phi\sigma_1\gamma + 1 - \sigma_1(1-\gamma)}{b(1-\sigma_1(1-\gamma))} \cdot \left(\frac{\sigma_2\sigma_1\gamma\phi}{(1-\sigma_3)(1-\sigma_1(1-\gamma))} - 1 \right). \tag{S6}$$

Sensitivity of total population size to juvenile survival

The partial derivative of the total population size at equilibrium ($\hat{n}_t$) to juvenile survival (σ_2) was calculated as

$$\frac{\partial \hat{n}_t}{\partial \sigma_2} = \frac{\phi + \phi\sigma_1\gamma + 1 - \sigma_1(1-\gamma)}{b(1-\sigma_1(1-\gamma))} \cdot \left(\frac{\sigma_1\gamma\phi(1-\sigma_3)(1-\sigma_1(1-\gamma) - 0}{((1-\sigma_3)(1-\sigma_1(1-\gamma))^2} - 0) \right) \tag{S7}$$

and could be simplified to

$$\frac{\partial \hat{n}_t}{\partial \sigma_2} = \frac{\phi + \phi\sigma_1\gamma + 1 - \sigma_1(1-\gamma)}{b(1-\sigma_1(1-\gamma))} \cdot \left(\frac{\sigma_1\gamma\phi}{(1-\sigma_3)(1-\sigma_1(1-\gamma))} \right). \tag{S8}$$

To reach a certain total equilibrium population size ($\hat{n}_t$) the strenght of intra-specific competition can be standardized as follows

$$b = \frac{\phi + \phi\sigma_1\gamma + 1 - \sigma_1(1-\gamma)}{\hat{n}_t(1-\sigma_1(1-\gamma))} \cdot \left(\frac{\sigma_2\sigma_1\gamma\phi}{(1-\sigma_3)(1-\sigma_1(1-\gamma))} - 1 \right). \tag{S9}$$

By inserting equation S9 in S8 the population size sensitivity to juvenile survival could be standardized for $\hat{n}_t$ as

$$\begin{aligned} \frac{\partial \hat{n}_t}{\partial \sigma_2} = & \frac{\phi + \phi\sigma_1\gamma + 1 - \sigma_1(1-\gamma)}{(1-\sigma_1(1-\gamma))} \cdot \left(\frac{\sigma_1\gamma\phi}{(1-\sigma_3)(1-\sigma_1(1-\gamma))} \right) \cdot \\ & \frac{\hat{n}_t(1-\sigma_1(1-\gamma))}{\phi + \phi\sigma_1\gamma + 1 - \sigma_1(1-\gamma)} \cdot \left(\frac{(1-\sigma_3)(1-\sigma_1(1-\gamma))}{\sigma_2\sigma_1\gamma\phi - (1-\sigma_3)(1-\sigma_1(1-\gamma))} \right), \end{aligned} \tag{S10}$$

such that the following partial derivative is obtained

$$\frac{\partial \hat{n}_t}{\partial \sigma_2} = \frac{\hat{n}_t \sigma_1 \gamma \phi}{\sigma_2 \sigma_1 \gamma \phi - (1-\sigma_3)(1-\sigma_1(1-\gamma))}, \tag{S11}$$

Rate of evolution at stable population size

The equation from Barfield et al. (2011) could be adapted for our 3-stage life cycle as

$$\Delta \bar{z} = w_2 \ \sigma_2 \ c \ v_3 \ G_2 \beta(z_2). \tag{S12}$$

The juvenile proportion (w_2) can be derived from equation S4 and A6 as

$$w_2 = \frac{\hat{n}_2}{\hat{n}_t} = \frac{\phi \sigma_1 \gamma}{\phi + \sigma_1 \gamma(\phi + 1) - \sigma_1 + 1}. \tag{S13}$$

The probability of surviving intra-specific competition (c) can be derived by combining the Beverton-Holt function $c = 1/(1 + bn_3)$ and equation S5

$$c = \frac{(1-\sigma_3)(1-\sigma_1(1-\gamma))}{\sigma_2 \sigma_1 \gamma \phi} \tag{S14}$$

The reproductive value of adults (v_3) can be derived from the left eigenvector (v) of the matrix population model (A) when solving $v^T A = \lambda v^T$ (Caswell 2001, chapter 4.6, equation 4.81). For a population at its stable population size ($\lambda = 1$) the reproductive value of adults is

$$v_3 = \frac{\phi}{(1-\sigma_3)} \tag{S15}$$

The normalization of v_3 such that $v^T w = 1$ could be achieved as

$$v_3 = \frac{\phi + \sigma_1 \gamma(\phi + 1) - \sigma_1 + 1}{(1-\sigma_3)(1-\sigma_1(1-\gamma) + (1-\sigma_3) + (1-\sigma_1(1-\gamma))} \tag{S16}$$

The rate of evolution then can be expressed as

$$\Delta\bar{z} = \frac{(1-\sigma_3)(1-\sigma_1(1-\gamma)}{(1-\sigma_3)(1-\sigma_1(1-\gamma)+(1-\sigma_3)+(1-\sigma_1(1-\gamma))}\ G_2\beta(z_2) \tag{S17}$$

Supp B: 2-stage model with Beverton-Holt density regulation

Equilibrium population size

Population dynamics were modeled with the population vector

$$N = \begin{pmatrix} n_2 \\ n_3 \end{pmatrix} \tag{B1}$$

and the matrix population model

$$A = \begin{bmatrix} 0 & \phi \\ \dfrac{\sigma_2}{(1+bn_2)} & 0 \end{bmatrix} \tag{B2}$$

such that $N(t+1) = An$ with equilibrium $\hat{N} = A\hat{N}$.

The number of juveniles and adults at equilibrium then could be derived as

$$\hat{n}_2 = \frac{\phi(\phi\sigma_2 - 1)}{b\phi}, \tag{B3}$$

and

$$\hat{n}_3 = \frac{\phi\sigma_2 - 1}{b\phi}, \tag{B4}$$

with a total population size at equilibrium of

$$\hat{n}_t = \frac{(\phi+1)(\phi\sigma_2 - 1)}{b\phi}. \tag{B5}$$

Sensitivity of total population size to juvenile survival

The partial derivative of the total population size at equilibrium ($\hat{n}_t$) with respect to juvenile survival (σ_2) can be computed as

$$\frac{\partial \hat{n}_t}{\partial \sigma_2} = \frac{b\phi \cdot (\phi(\phi+1) - 0}{(b\phi)^2}, \tag{B6}$$

and simplified to

$$\frac{\partial \hat{n}_t}{\partial \sigma_2} = \frac{\phi(\phi+1)}{b\phi}. \tag{B7}$$

The strength of intra-specific competition (b) could be standardized to reach a certain equilibrium population size ($\hat{n}_t$) via

$$b = \frac{(\phi+1)(\phi\sigma_2 - 1)}{n_t\phi}, \tag{B8}$$

while the fecundity (ϕ) could be used to standardize a life history for a specific maximum growth rate (λ_{max}) when

$$\lambda_1 = \sqrt{\sigma_2\phi}, \tag{B9}$$

and

$$\phi = \frac{\lambda_1^2}{\sigma_2}. \tag{B10}$$

The sensitivity $\partial\hat{n}_t/\partial\sigma_2$ then could be reformulated as

$$\frac{\partial \hat{n}_t}{\partial \sigma_2} = \frac{\hat{n}_t}{\sigma_2} \cdot \frac{\lambda_1^2}{(\lambda_1^2 - 1)}. \tag{B11}$$

847 **Rate of evolution at stable population size**

The equation from Barfield et al. (2011) can be adapted for our two-stage life cycle as

$$\Delta\bar{z} = w_2\ \sigma_2\ c\ v_3\ G_2\beta(z_2). \tag{B12}$$

The juvenile proportion can be derived from equation B3 and B5:

$$w_2 = \frac{\hat{n}_2}{\hat{n}_t} = \frac{\phi}{1+\phi}, \tag{B13}$$

and the probability of surviving intra-specific competition (c) can be derived by combining the Beverton-Holt function $c = 1/(1 + b\hat{n}_2)$ and equation B3:

$$c = 1/(1 + b\hat{n}_2) = \frac{1}{\phi\sigma_2}. \tag{B14}$$

The reproductive value of adults for the 2-stage life history with Beverton-Holt density regulation is

$$v_3 = \phi \tag{B15}$$

and can be normalize ($v^T w = 1$) to

$$v_3 = \frac{1+\phi}{2}. \tag{B16}$$

The rate of evolution for two-stage life history at population size equilibrium with BH density regulation then can be expressed as

$$\Delta\bar{z} = \frac{1}{2}\ G_2\beta(z_2). \tag{B17}$$

Supp C: Plots mathematical model

Figure S1: 3 stages (standardized for $n_t + \lambda_{max}$)

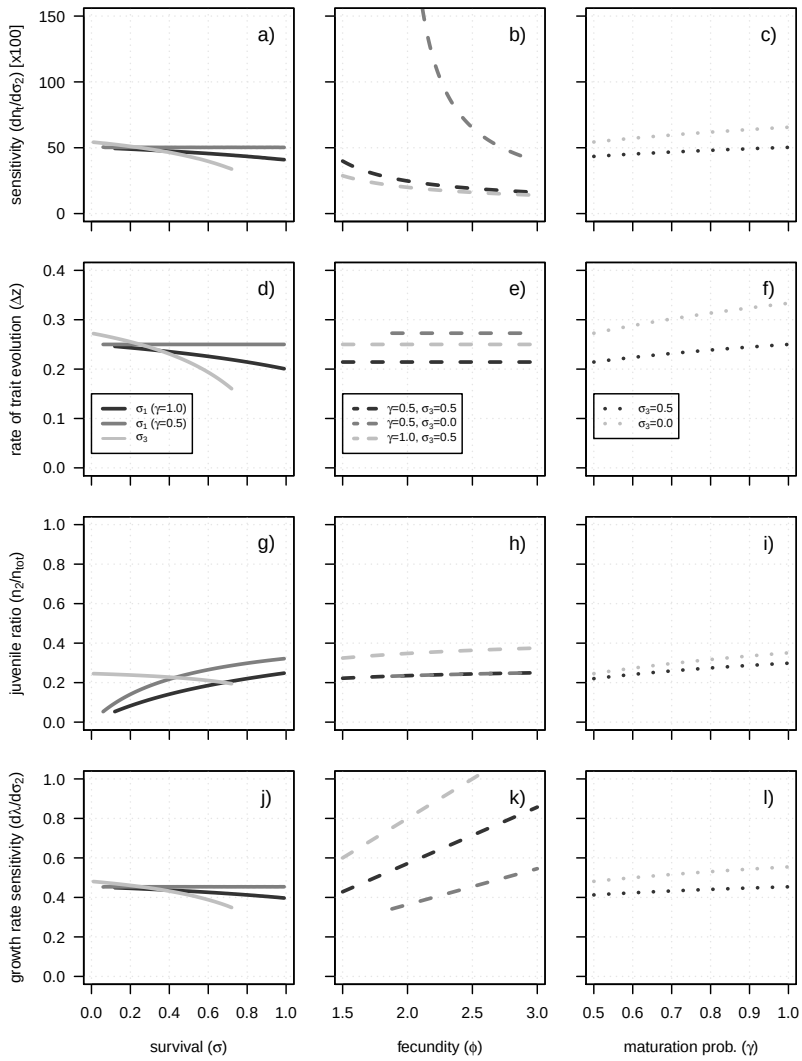

Figure S1: The model results for the sensitivity of the total population size ($\partial\hat{n}_t/\partial\sigma_2$, a-c), the rate of evolution (Δz, d-f), the juvenile ratio ($\hat{n}_2/\hat{n}_t$, g-i), and the sensitivity of the max. growth rate ($\partial\lambda/\partial\sigma_2$, j-l) are shown depending on a life histories' survival rate (σ_1,σ_3), fecundity (ϕ), and maturation probability (γ). The maximum growth rate has been standardized for $\lambda_{max} = 1.1$ by fecundity adjustments, except for the case when we varied fecundity (b,e,h,k). Each parameter combination has been standardized for the same equilibrium population size in absence of interannual environmental fluctuations ($\hat{n}_t$=1500) via adjustments of the strength of competition (**b**). The following parameter values have been used if not other specified: $\sigma_1 = 0.8$, $\sigma_2 = 0.8$, $\sigma_3 = 0.5$, $\gamma = 0.5$, $G = 1$, and $\beta(z_2) = 1$. This graph is identical to figure 3 but shows additionally the juvenile ratio.

Figure S2: 2 stages (standardized for $n_t + \lambda_{max}$)

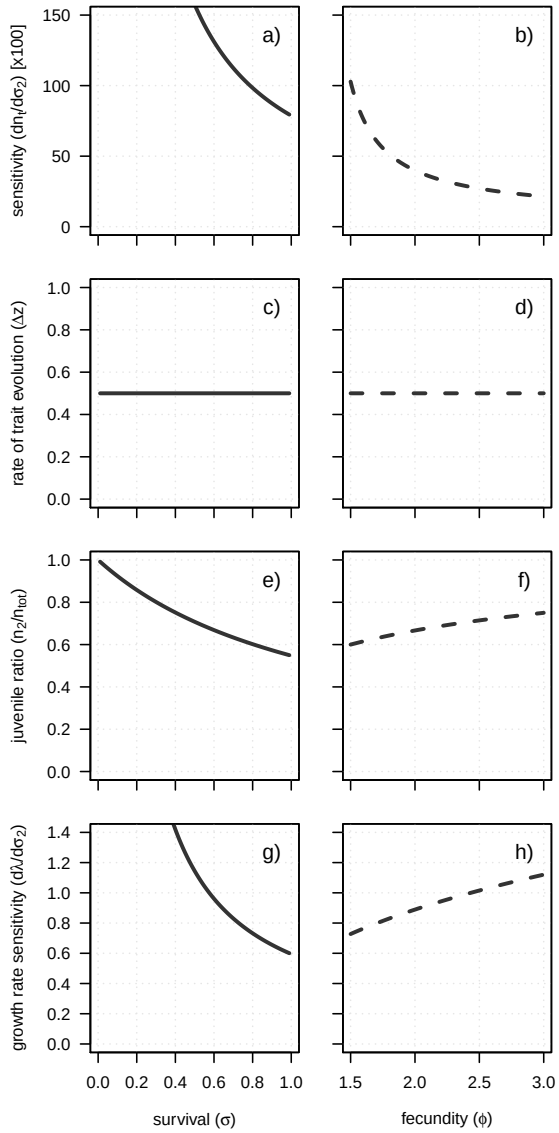

Figure S2: The sensitivity of the total population size ($\partial \hat{n}_t / \partial \sigma_2$, a-b), the rate of evolution (Δz, c-d), the juvenile ratio ($\hat{n}_2/\hat{n}_t$, e-f), and the sensitivity of the max. growth rate ($\partial \lambda / \partial \sigma_2$, g-h) are shown depending on the two-stage life cycles' survival rate (σ_2) and fecundity (ϕ). The maximum growth rate has been standardized for $\lambda_{max} = 1.1$ by fecundity adjustments, except for the case when we varied fecundity (b,d,f,h). Each parameter combination has been standardized for the same equilibrium population size in absence of interannual environmental fluctuations ($\hat{n}_t$=1500) via adjustments of the strength of competition (**b**). , $G = 1$, and $\beta(z_2) = 1$

Figure S3: 3 stages (standardized for n_t only)

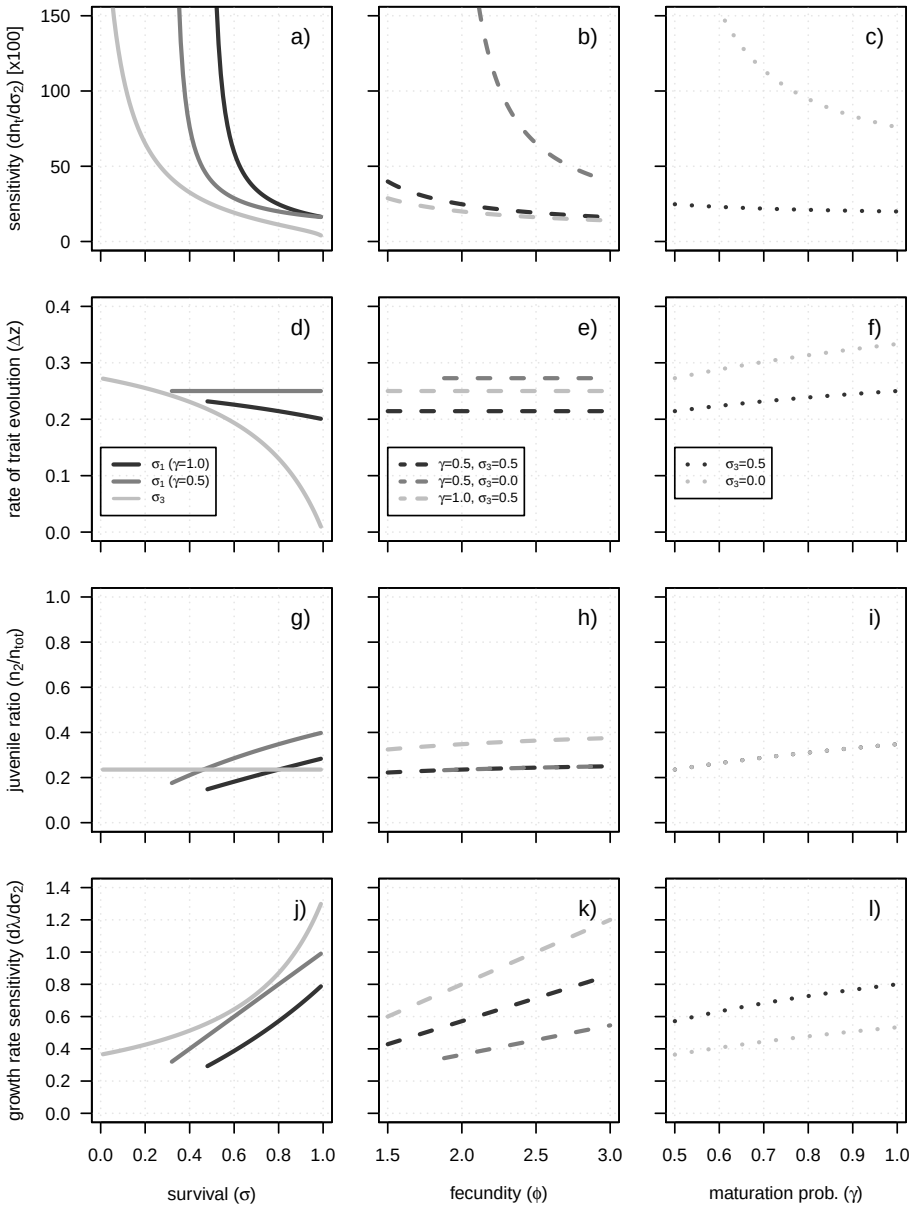

Figure S3: The model results for three-stage life cycles are shown for the sensitivity of the total population size ($\partial\hat{n}_t/\partial\sigma_2$, a-c), the rate of evolution (Δz, d-f), the juvenile ratio ($\hat{n}_2/\hat{n}_t$, g-i), and the sensitivity of the max. growth rate ($\partial\lambda/\partial\sigma_2$, j-l) depending on a life histories' survival rate (σ_1,σ_3), fecundity (ϕ), and maturation probability (γ). Each parameter combination has been standardized for the same equilibrium population size in absence of interannual environmental fluctuations ($\hat{n}_t$=1500) via adjustments of the strength of competition (**b**). However, the maximum growth rate has NOT been standardized in this case. The following parameter values have been used if not other specified: $\sigma_1 = 0.8$, $\sigma_2 = 0.8$, $\sigma_3 = 0.5$, $\phi = 2$, $G = 1$, and $\beta(z_2) = 1$. This figure shows the same results as figure 3 but adds the proportion of juveniles (g-i).

852 **Figure S4: 2 stages (standardized for n_t only)**

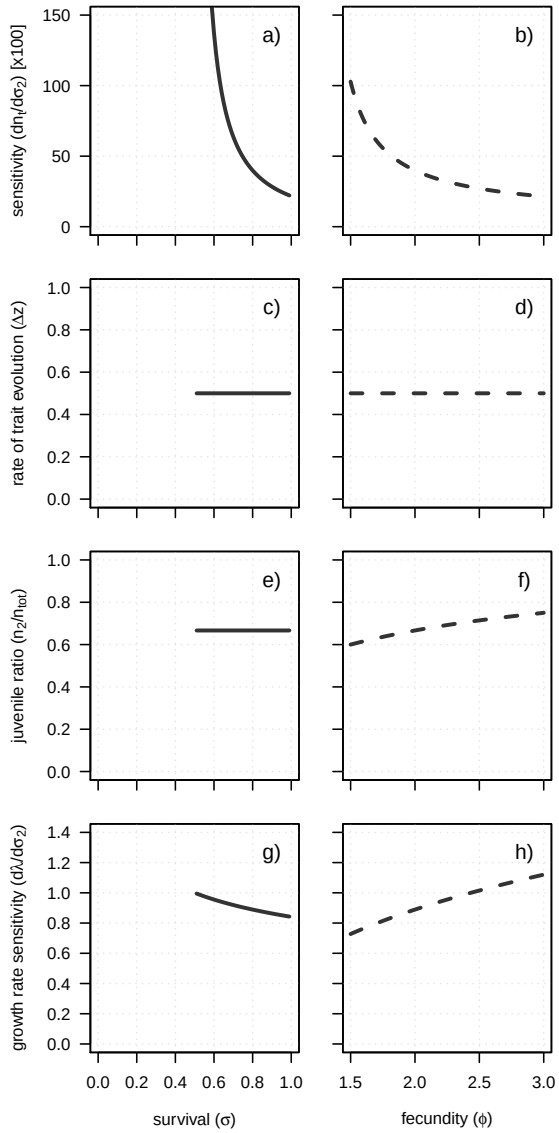

Figure S4: The model results for two-stage life cycles illustrate the sensitivity of the total population size ($\partial\hat{n}_t/\partial\sigma_2$, a-b), the rate of evolution (Δz, c-d), the juvenile ratio ($\hat{n}_2/\hat{n}_t$, e-f), and the sensitivity of the max. growth rate ($\partial\lambda/\partial\sigma_2$, g-h) depending on a life histories' survival rate (σ_2) and fecundity (ϕ). Each parameter combination has been standardized for the same equilibrium population size in absence of interannual environmental fluctuations ($\hat{n}_t$=1500) via adjustments of the strength of competition (**b**). However, the maximum growth rate has NOT been standardized for $\lambda_{max} = 1.1$ by fecundity adjustments. Juvenile survival was fixed to $\sigma_2 = 0.8$ with varying fecundity (b,d,f,h) and fecundity was set to $\phi = 2$ with varying σ_2 (a,c,e,g).

Figure S5: evolvability-robustness tradeoff with Beverton-Holt density regulation

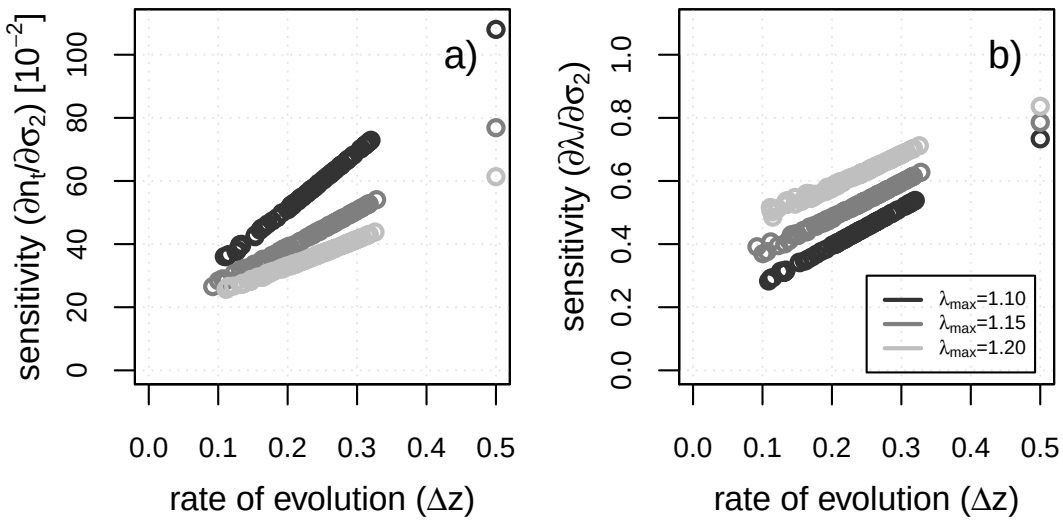

Figure S5: A life history's tradeoff between evolvability (Δz) and robustness ($\partial \hat{n}_t / \partial \sigma_2$ in a, and $\partial \lambda / \partial \sigma_2$ in b) using a Beverton-Holt function for density regulation. Each circle illustrates a random combination of vital rates (with $0.2 \leq \sigma_1 \leq 1.0$, $\sigma_2 = 0.8$, $0.0 \leq \sigma_3 \leq 0.9$, $0.2 \leq \gamma \leq 1.0$). The fecundity (ϕ) and the strength of competition (b) were re-calculated for each vital rate combination to standardize the maximum population growth rate ($\lambda_{max} = 1.10 - black, \lambda_{max} = 1.15 - darkgray, \lambda_{max} = 1.20 - lightgray$) and the total population size at stable conditions (n_t=1'500). We then calculated the rate of evolution (Δz, with $G_2 \beta(z_2) = 1$), the population size sensitivity ($\partial \hat{n}_t / \partial \sigma_2$), and the growth rate sensitivity ($\partial \lambda / \partial \sigma_2$) for each life-history variant. The three single points on the right of the plots were derived for the 2-stage life cycle (with $\sigma_2 = 0.8$), while the rest of the points illustrate parameter combinations for 3-stage life cycles.

Figure S6: compare results for Δz, $\partial \hat{n}_t / \partial \sigma_2$, and $\partial \lambda / \partial \sigma_2$ between models with Beverton-Holt and Ricker density regulation

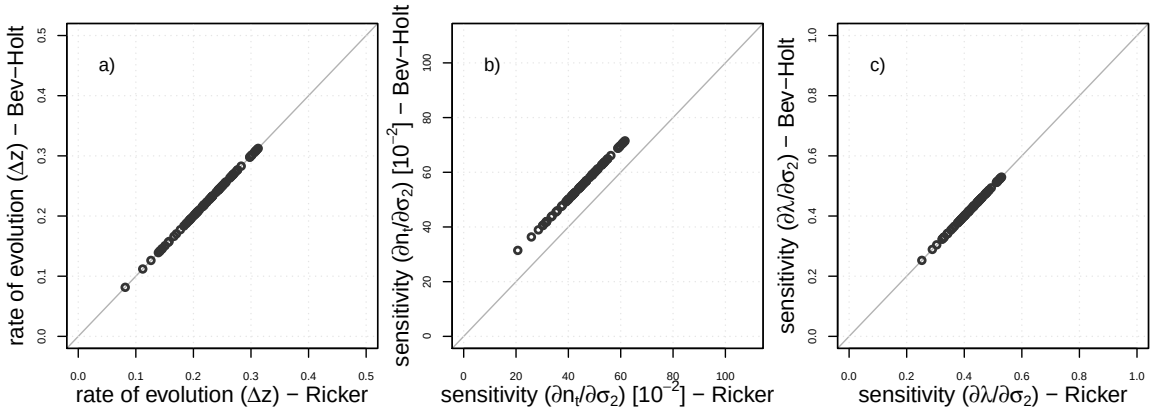

Figure S6: These graphs compare the model results for density regulation based on the Ricker function with the models based on the Beverton-Holt function, contrasting the rate of evolution (Δz), the sensitivity of the total population size to juvenile survival ($\partial \hat{n}_t / \partial \sigma_2$), and the sensitivity of the population growth rate to juvenile survival ($\partial \lambda / \partial \sigma_2$). Each dot is a random combination of vital rates with $0.2 \leq \sigma_1 \leq 1.0$, $\sigma_2 = 0.8$, $0.0 \leq \sigma_3 \leq 0.9$, $0.2 \leq \gamma \leq 1.0$.

Figure S7: Population growth over time for all four life histories and both levels of λ_{max}

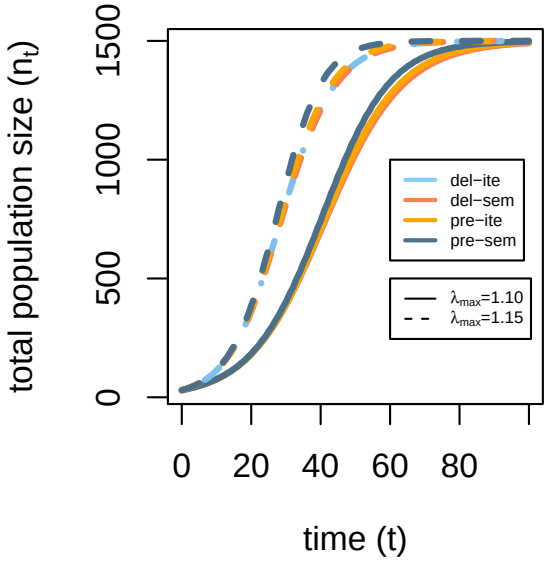

Figure S7: This graph illustrates the growth trajectories for all four life histories (*del-ite*, *del-sem*, *pre-sem*, *pre-ite*) and both maximum growth rates ($\lambda_{max} = 1.10$ and $\lambda_{max} = 1.15$) over time. All life histories here start at the same total population size ($n_t = 30$) and grow to the same carrying capacity of 1500 individuals ($n_t = n_1 + n_2 + n_3$). The population growth trajectories are quite similar across life histories with the same λ_{max}, while $\lambda_{max} = 1.15$ results in a faster increase in n_t than a standardization for $\lambda_{max} = 1.10$. In the beginning, stage structure was adjusted to the SSD of the respective life history.

Supp D: Plots individual-based simulations

Figure S8: Evolution of G_2 with $\lambda = 1.15$

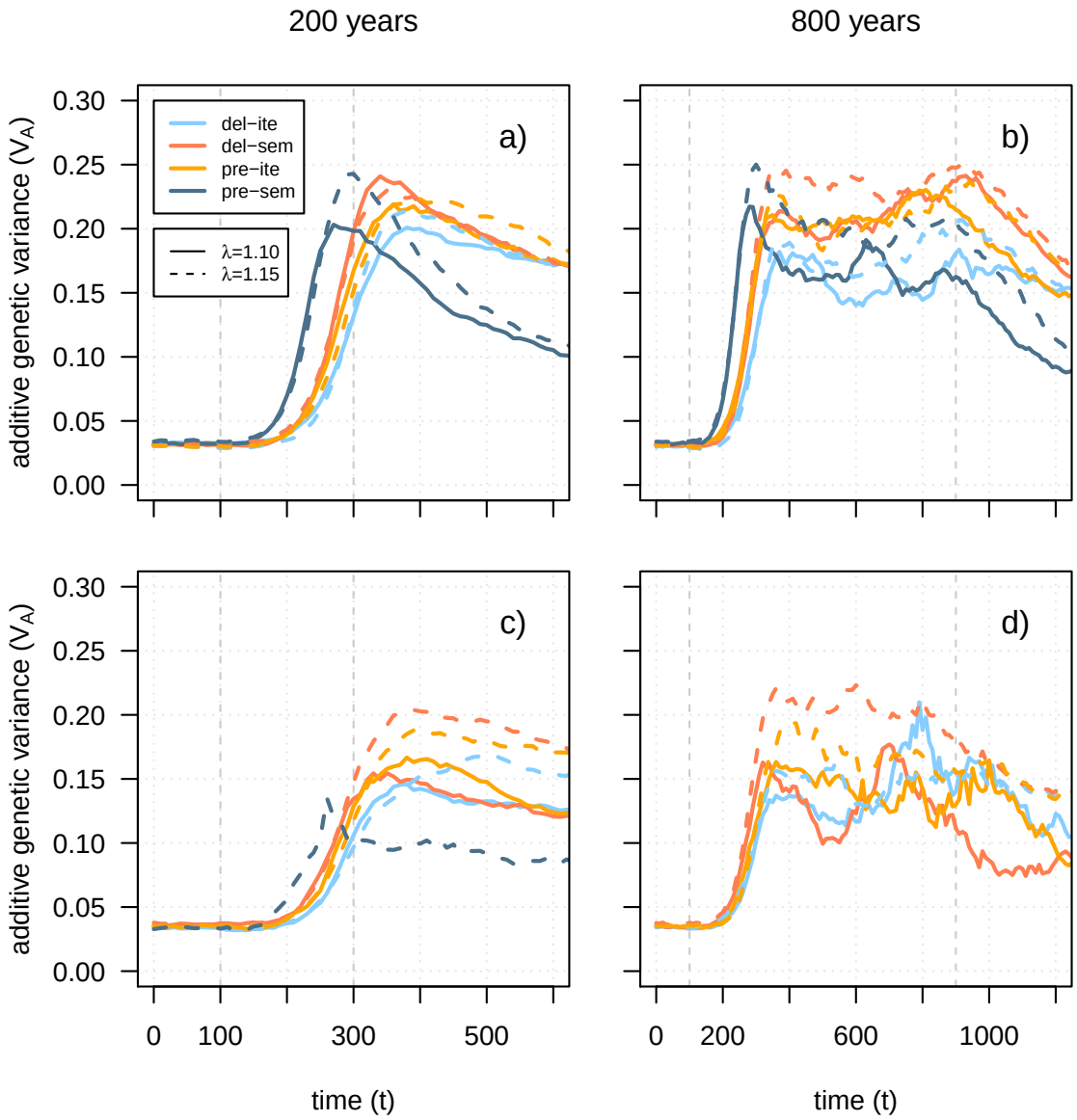

Figure S8: Simulation results for the evolution of additive genetic variance during environmental change are shown for the four life histories, the two different duration of environmental change (200 years - a,c; 800 years - b,d) and two degrees of interannual environmental variability ($\epsilon = 0.2$ - a,b; $\epsilon = 1.0$ - c,d). The simulation results were averaged over all of the 100 replicates that did not go extinct.

Figure S9: Extinction dynamics with $\lambda = 1.15$

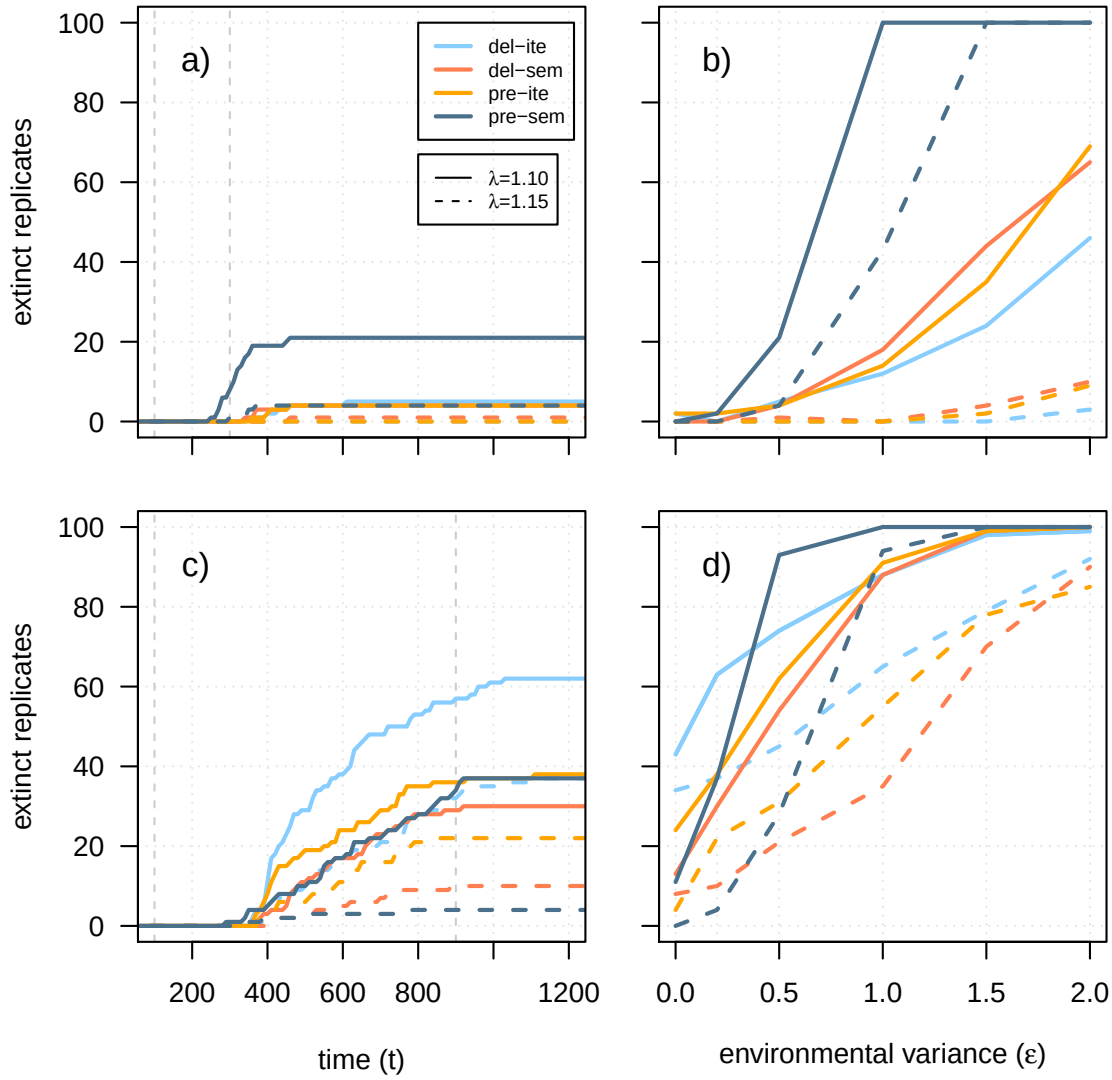

Figure S9: These graphs show the same simulation results on the number of extinct replicates as figure 6, but illustrate additionally the results for the life-history standardization of $\lambda_{max} = 1.15$. These graphs show for each of the four life histories the number of extinct replicates over time t (a,c) and the total number of extinct replicates depending on environmental variability ϵ (b,d). Extinction dynamics are shown for two different scenarios with environmental change either lasting for 200 years (a,b) or for 800 years (c,d). The gray dashed lines indicate the start of environmental change ($t = 100$) and its end ($t = 300$ for a,b; $t = 900$ for c,d). In both scenarios, the rate of environmental change per year was set to $\Delta\bar{\theta} = 0.01$. The temporal dynamics are shown for an environmental variability of $\epsilon = 0.5$ (a) and $\epsilon = 0.2$ (c).

Figure S10: Evolvability per generation

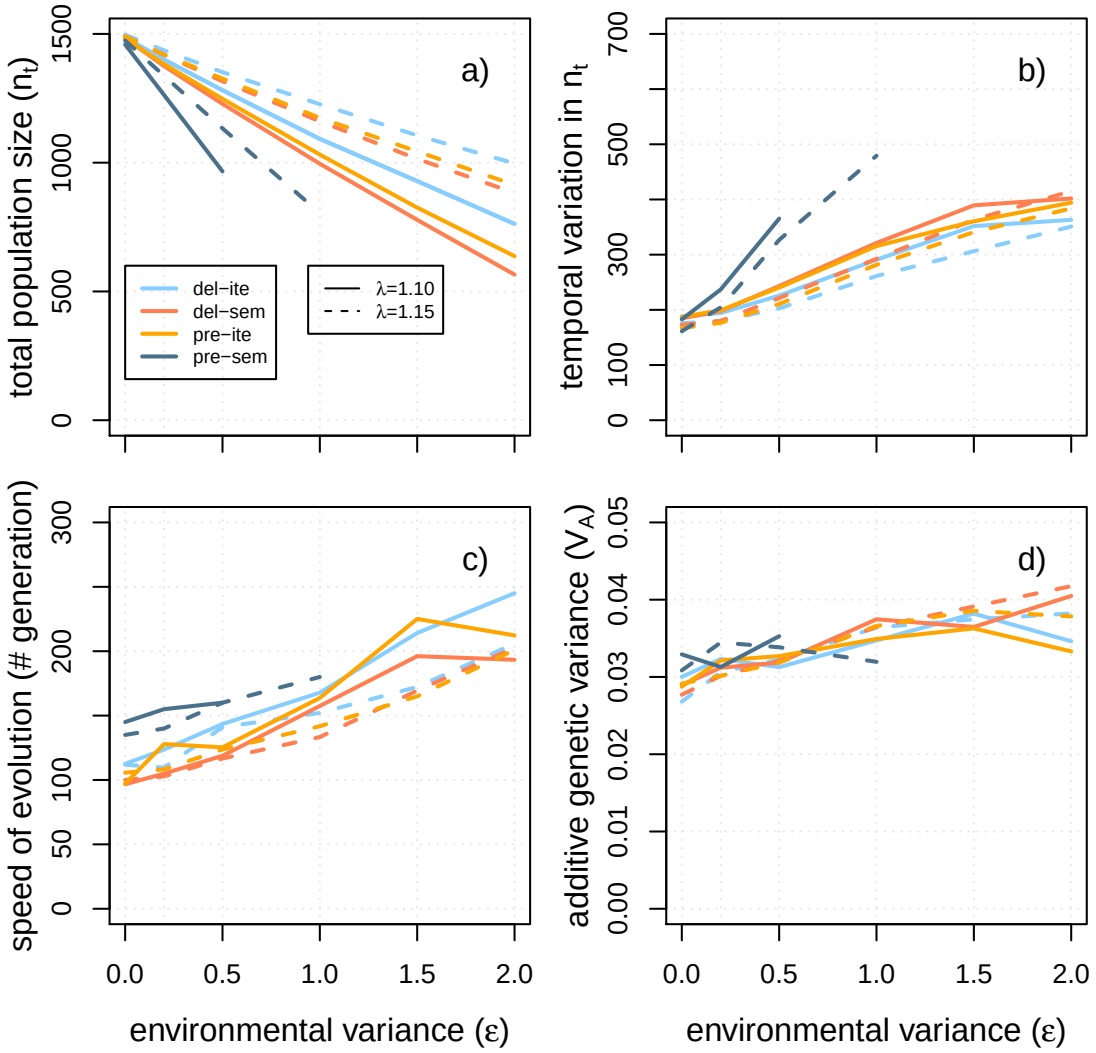

Figure S10: These graphs are identical to Fig. 5, except that the speed of evolution (c) is quantified as the number of generations (not years!) to reach 90% of the novel phenotypic optimum after climate change. For this purpose, the number of years to reach the threshold was divided by the average generation time of each life-history strategy at stable conditions from table 1. Please not that the realized generation time in the course of environmental change might differ from these estimates that have been calculated at equilibrium.

Figure S11: Robustness and evolvability with $\omega^2 = 16$

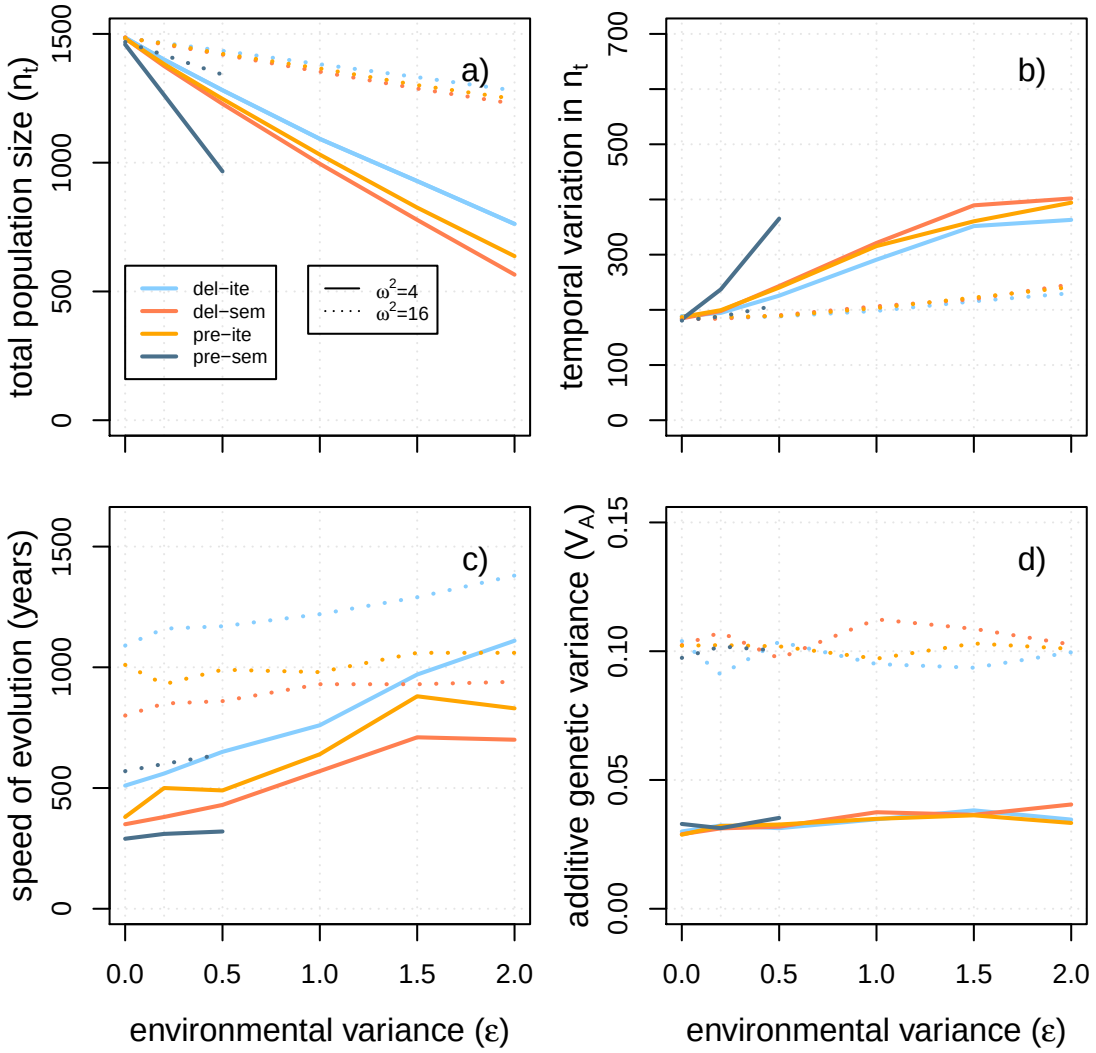

Figure S11: The simulation results for strong selection ($\omega^2 = 4$) are plotted together with the results for weak selection ($\omega^2 = 16$). Weaker selection strength leads to higher population sizes after burn-in (a), lower stochasticity in total population sizes over time (b), a slower speed of evolution (c), and higher levels of additive genetic variance in the juvenile trait (d). However, the rank order of life-history strategies with regard to robustness and evolvability is preserved.

Figure S12: Extinction dynamics with $\omega^2 = 16$

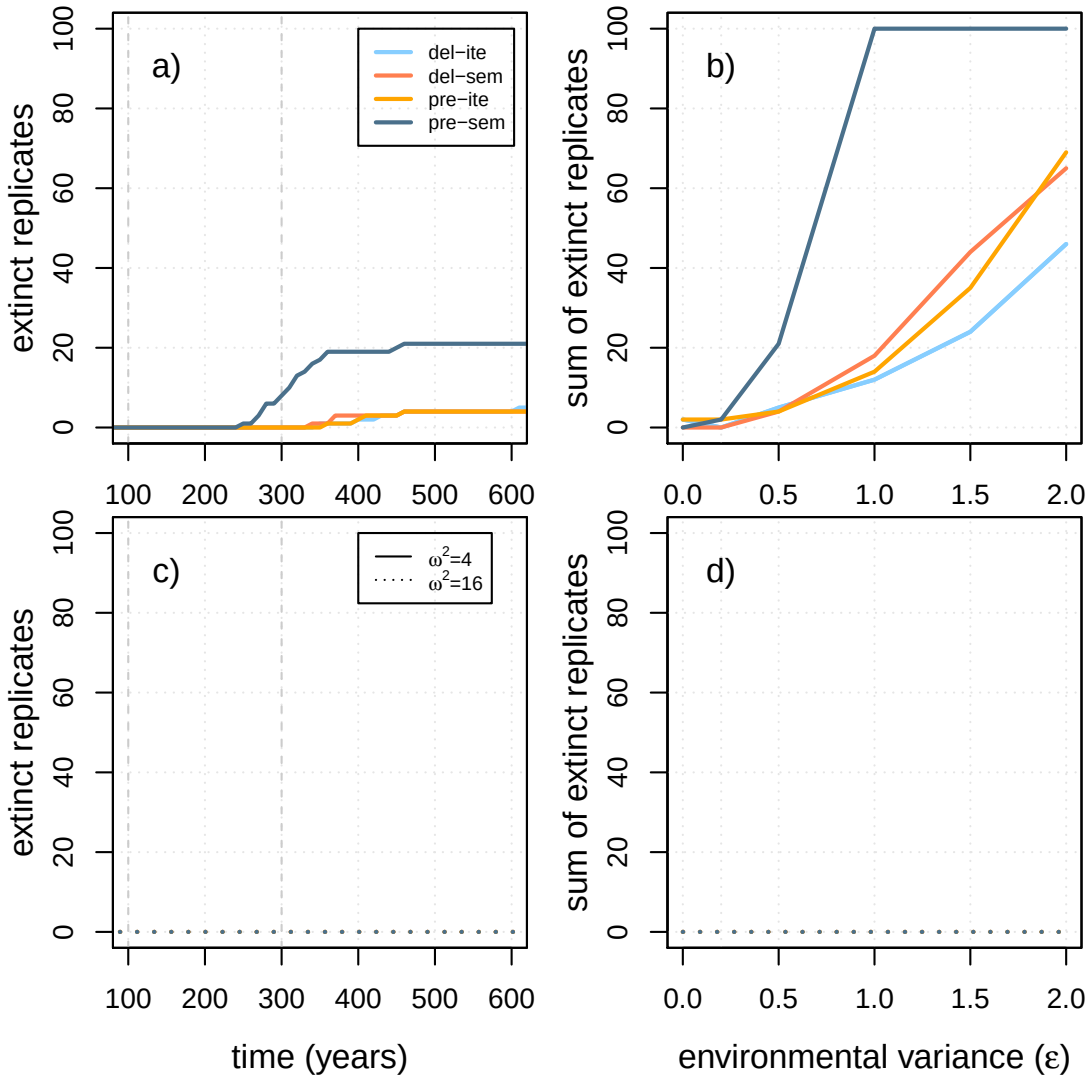

Figure S12: The effects of a stronger ($\omega^2 = 4$, a-b) versus weaker ($\omega^2 = 16$, c-d) selection on extinction probabilities is shown for the environmental change scenario over 200 years, similar to Fig. 6.

Figure S13: Simulated life histories along fast-slow continuum and reproductive strategy

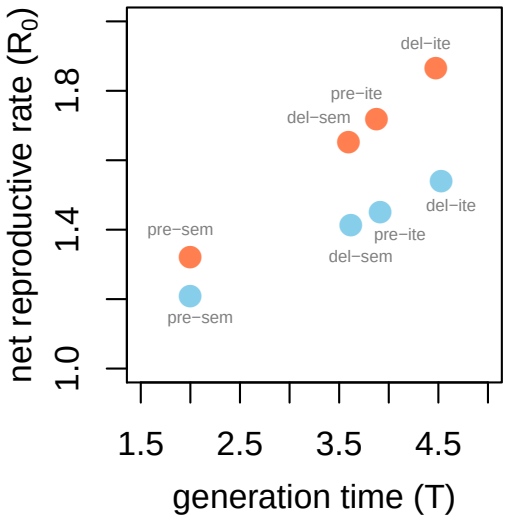

Figure S13: The generation time (T) of each simulated life history is plotted against its net reproductive rate (R_0) from table 1. While the blue circles illustrate life histories standardized for $\lambda_{max} = 1.10$, orange dots represent life histories with $\lambda_{max} = 1.15$. While the x-axis could be interpreted to represent the fast-slow continuum, the y-axis might rather illustrate the reproductive strategy axis as described in meta-analyses (Salguero-Gómez et al., 2017). Please note that both quantities (T and R_0) were computed in absence of density regulation.