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# Fluctuating population size, phylogenetic inertia and the *r-K* gradient: a model.

## Harmonic mean of *N* and phylogenetic inertia

Consider that population size, $N$, fluctuates over time. The instantaneous rate of coalescence between two random gene copies at time $t$ is proportional to $1/N(t)$, and the average coalescence rate during the last T generations is proportional to $\frac{1}{T}\int_0^T dt / N(t)$. This means that the expected coalescence time, and therefore the expected neutral heterozygosity $\pi_S$, are proportional to the time-harmonic mean of $N$, which thus corresponds to the long-term effective population size, $N_e$[1]. If fluctuations occur at a rate much higher than the median drift rate, $N_e$ is essentially independent of the history of the process and on current $N$ but solely determined by the stationary distribution of $N$[2], here controlled by the demographic parameters underlying the evolution of $N(t)$ ($r$, $K$… see below). If these demographic parameters evolved at a relatively slow rate, so would $N_e$ and $\pi_S$. Assuming fast enough population size fluctuations, we therefore predicts (i) a substantial amount of phylogenetic inertia on $\pi_S$ (because of the slowly evolving $N_e$) and (ii) a weak relationship between $\pi_S$ and current population size (because of the strongly fluctuating $N$), consistent with our findings.

We elaborate on these basic assumptions by considering two specific scenarios that might explain why *r*-strategist species exhibit a higher $\pi_S$ than *K*-strategists.

## Demographic scenarios

### *Scenario 1: deterministic environment driven fluctuations*

We first consider a simple scenario where environmental variations synchronously affect population size in a set of species with different demographic strategies – typically, climatic variations. For simplicity and mathematical tractability we consider a simple toy model, in which every $T_b$ time unit, an environmental event leads to a population bottleneck reducing the population size to $N_b = N(t)/b$, where $b > 1$ is the intensity of the bottleneck. Each bottleneck event is followed by a logistic growth with intrinsic growth rate, $r$, carrying capacity $K$, and generation time $g$. For a demographic cycle starting at $N(0) = N_b$ at $t = 0$ we have:

$$N(t) = \frac{KN_b e^{r\frac{t}{g}}}{K - N_b e^{r\frac{t}{g}}} \qquad (1)$$

Under the stationary regime $N_b = N(T_b)/b$, so that:

$$N_b = \frac{K\left(e^{rT_b/g} - b\right)}{b\left(e^{rT_b/g} - 1\right)} \qquad (2)$$

Inserting (2) in (1) and taking the harmonic mean we deduce:

$$N_e = \frac{1}{T_b}\int_0^{T_b} 1/N(t) = K\frac{rT_b/g\left(e^{rT_b/g} - b\right)}{1 - b - brT_b/g + be^{rT_b/g}\left(rT_b/g + b - 1\right)} \qquad (3)$$

Note that if $r\frac{T_b}{g} < b$, the population goes extinct. Assuming $r\frac{T_b}{g} >> b$ equation (3) simplifies to:

$$N_e = K\frac{rT_b/g}{b-1+rT_b/g} \qquad (4)$$

Equations (3) and (4) show that, for a given $K$, $N_e$ increases with $r$ simply because $r$-strategists recover more quickly after bottleneck events and spend less time at low population size, as illustrated in Figure S1.

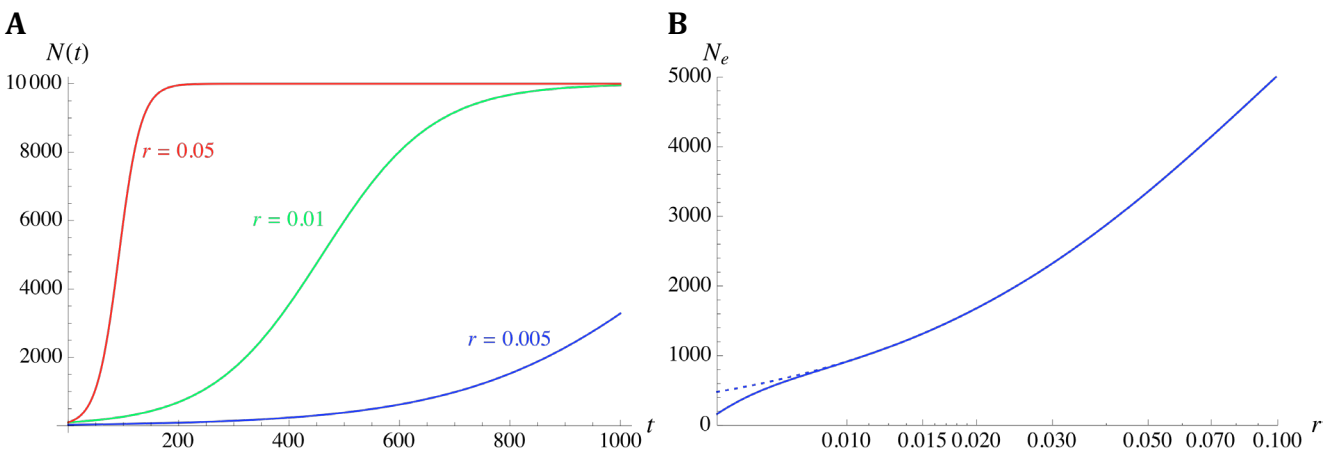


*Figure S1:* ***A) Evolution of population size, N(t), between two bottleneck events of intensity b = 100 and periodicity $T_b$ = 1,000; K = 10,000. B) $N_e$ as a function of r (log-scale) with the same parameters. Plain line corresponds to equation (3) and dotted line to the approximation given by equation (4). In A) and B), the generation time, g is fixed to 1.***

Note that because we consider periodic environmental events independent of species biology, species with longer generation time also recover more slowly by time unit (term $T_b/g$ in equations (3) and (4)) and are thus expected to have lower $N_e$. As $r$-strategists are expected to have lower generation time, this could reinforce the effect on $N_e$.

One limitation of this model is that we assume $r$- and $K$-strategists share a similar carrying capacity and experience similar environmental variations. However, $r$-strategy is supposed to be favored in case of environmental instability/unpredictability, whereas $K$-strategists tend to occupy more stable niches. $T_b$ could be thus lower for $r$- than for $K$-strategists. Equation (3) and (4) show that $N_e$ actually depends on $rT_b/g$. The net result will thus depend on the balance between $r$, $T_b$ and $g$. To take this into account we built another scenario where stochastic variations are explicitly taken into account and where $r$-strategists are supposed to fluctuate more than $K$-strategists.

### *Scenario 2: stochastic population size fluctuations*

General model

In this second scenario we simulated fluctuations in time of the logarithm of the effective population size of a panmictic population as a stochastic autoregressive process:

$$\log\left(N\left(t+1\right)\right) = (1-\phi)\mu + \phi\log\left(N\left(t\right)\right) + w\left(0,\sigma\right) \qquad (5)$$

where $w$ is a Gaussian random deviate of mean zero and variance $\sigma^2$ (white noise).
The process is determined by three parameters:
- $\mu$ is the arithmetic average log$N$;
- $\sigma$ measures the strength of the response to environmental noise;

- $\phi$ is the auto-correlation, or memory, of the process ($0 < \phi < 1$).
Population size fluctuations simulated under various parameter values is shown in figure S2.

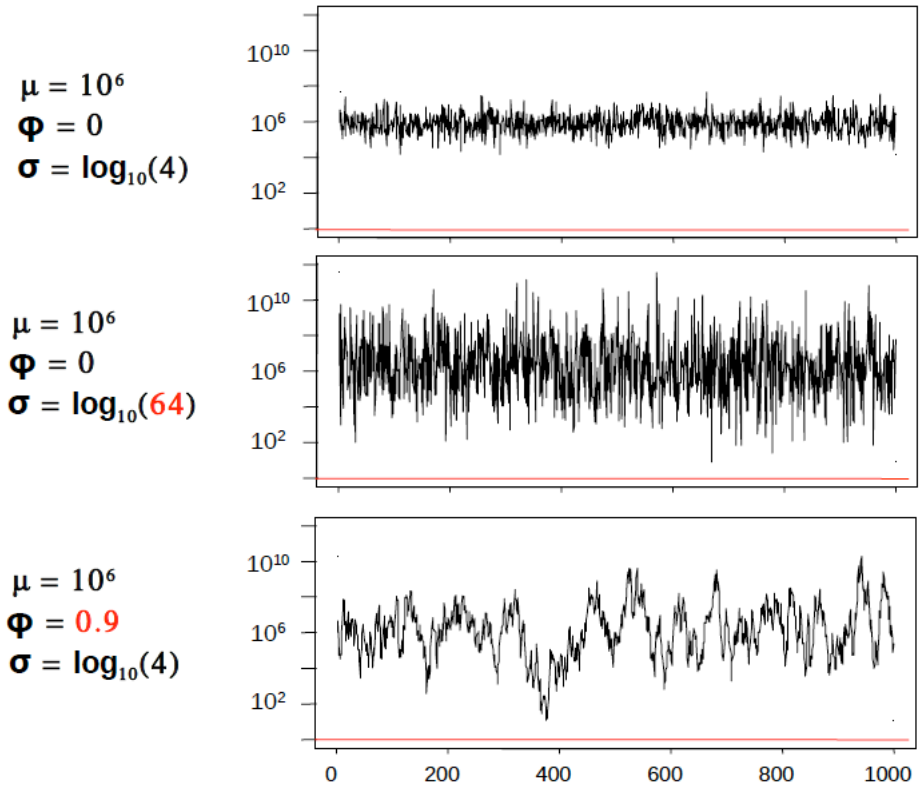


**Figure S2:** Examples of simulations for different values of $\mu$, $\sigma$ and $\phi$.

Noting $X_t = \log(N(t))$ and taking the continuous version of (5), $X_t$ satisfies the following stochastic differential equation:

$$dX_t = (1-\phi)(\mu - X_t)dt + \sigma dW_t \qquad (6)$$

where $W_t$ is the Wiener process. $X_t$ is thus a Ornstein–Uhlenbeck process and admits a stationary distribution which is a normal distribution with mean $\mu$ and variance $\sigma^2/(1-\phi)$ [3]. The stationary distribution of $N$ is thus a log-normal distribution with parameters $\mu$ and $\sigma^2/(1-\phi)$. Noting $f(\mu,\sigma,\phi,z)$, the density function of the log-normal distribution, the harmonic mean of $N$ under the stationary regime can thus be computed as:

$$N_e = 1\Big/\int_0^\infty \frac{1}{z} f(\mu,\sigma,\phi,z)\,dz = \exp\left(\mu - \frac{\sigma}{4(1-\phi)}\right) \qquad (7)$$

Equation (7) clearly shows that demographic stochasticity decreases $N_e$, all the more so auto-correlation, $\phi$, is strong. Considering that the median of $N$, $\exp(\mu)$, is roughly equivalent to $K$, for a given $K$, species with higher fluctuation rates should have lower $N_e$. This model would thus predict that lower $N_e$ for $r$-strategists, which is the opposite prediction of scenario 1.

<u>Conditioning on non extinction</u>

However, only species that have escaped extinction are observable. The risk of extinction obviously increases as $\mu$ decreases and $\sigma$ and $\phi$ increase. A high level of autocorrelation increases the risk of extinction because the effects of successive drops in $N$ cumulate to some extent, increasing the variance of the process. When conditioning on non-extinction, increasing $\sigma$ and/or

$\phi$ should thus result in higher $\mu$.

We assume that a species goes extinct when its population size $N$ reaches a value below some threshold $N_{\min}$. First, we can determine the minimal value of $\mu$ required to avoid extinction, for a given $\sigma$ and $\phi$. We assume that extinction is avoided when the probability of $N$ being lower than $N_{\min}$ is lower than a threshold $\alpha$. $\mu_{\min}$ is thus solution of:

$$\int_0^{N_{\min}} f(\mu_{\min},\sigma,\phi,z) = \alpha \qquad (8)$$

which is

$$\mu_{\min} = \sqrt{\frac{\sigma}{1-\phi}} erfc^{-1}(2\alpha) + \log(N_{\min}) \qquad (9)$$

where $erfc^{-1}$ is the inverse complementary error function[4]. Inserting (9) in (7), we then have the minimum $N_e$ observable for given $\sigma$ and $\phi$ conditioning on non-extinction:

$$N_e^{\min} = N_{\min} \exp\left( \sqrt{\frac{\sigma}{1-\phi}} erfc^{-1}(2\alpha) - \frac{\sigma}{4(1-\phi)} \right) \qquad (10)$$

Equation (10) shows that $N_e^{\min}$ (i) increases linearly with $N_{\min}$, and (ii) increases with $\frac{\sigma}{1-\phi}$ as far as $\frac{\sigma}{1-\phi} < \left(4erfc^{-1}(2\alpha)\right)^2$. For low values of $\alpha$, the threshold is very high (21.64 for $\alpha$= 0.05 and 43.30 for $\alpha$= 0.01) and distribution with such high variances are not realistic. For instance the median of the distribution would be of the order of $10^9$ for $\alpha$= 0.05 and $10^{18}$ for $\alpha$= 0.01, but the mode would be lower than one. Under realistic biological conditions, $N_e^{\min}$ is thus expected to increase with the rate of demographic fluctuations.

We qualitatively verified these predictions by simulations. Here we arbitrarily assumed that extinction is avoided when the probability of extinction in $10^5$ generations is below 0.05, $N_{\min}$ being set to 1 in this first analysis. The minimal sustainable $\mu$ was obtained by simulations for various ($\phi$, $\sigma$) pairs (Figure S3).

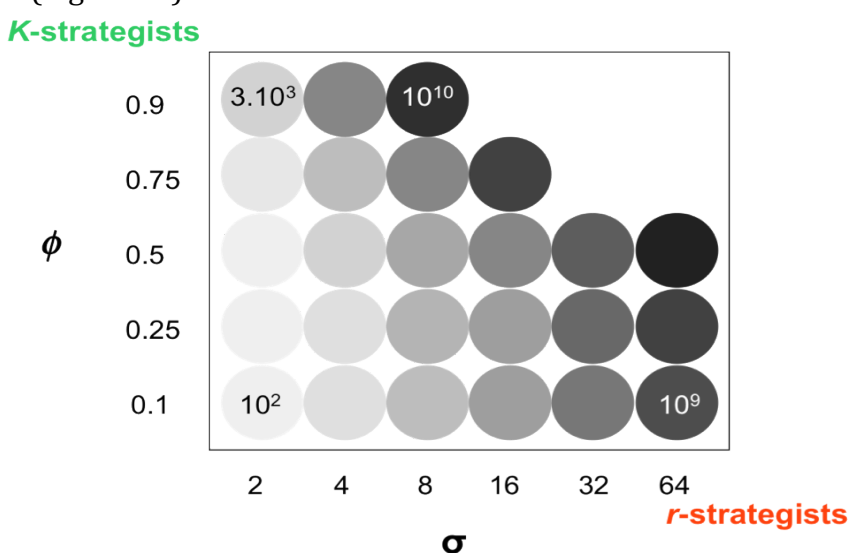


**Figure S3:** Minimal population size required to avoid extinction in $10^5$ generations as a function of $\sigma$ and $\phi$.

Figure S4 shows that, for any given value of $\phi$, the minimal sustainable $N_e$, and therefore the minimal $\pi_S$ conditional on non-extinction, increases with $\sigma$. According to this model, species experiencing a high rate of demographic fluctuation can only carry relatively large amounts of genetic diversity – or quickly reach extinction. When fixing $\sigma$ and $\phi$ increase, we found that the minimal sustainable $N_e$ increases more or less linearly with $N_{min}$ (not shown), as predicted by equation (10). This result indicates that, for a given intensity of demographic fluctuation, species strongly affected by the Allee effect would tend to be genetically more diverse than species weakly affected by the Allee effect, conditional on non-extinction.

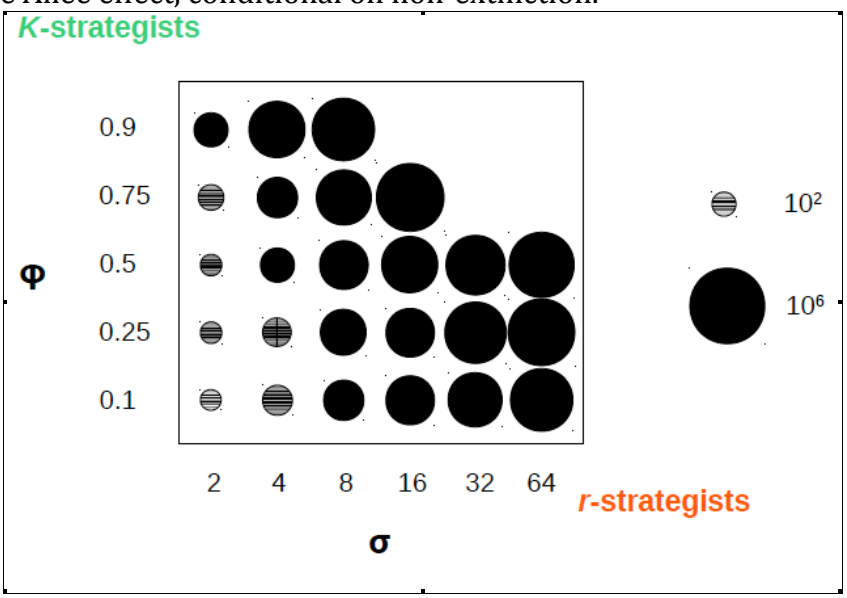


**Figure S4:** Minimal harmonic mean, $N_e$, conditional on non extinction as a function of $\sigma$ and $\phi$.

## The *r*/*K* effect on genetic diversity

Though making different assumptions, these two models predict higher long-term $N_e$ in *r*-strategists than in *K*-strategists.

According to scenario 1, *r*-strategists would respond more quickly than *K*-strategists to environmental perturbations, which here are assumed to be of common intensity across species and strategies. This is plausible if we consider that large-scale environmental variations (typically climatic events) may have stronger demographic consequences at the species level than local stochastic variations.

According to scenario 2, assuming that the population size tends to fluctuate more widely in *r*-strategists than in *K*-strategists is sufficient to predict a higher average level of genetic diversity (conditional on non-extinction) in the former than in the latter. Alternatively, a higher average genetic diversity in *r*-strategists than in *K*-strategists could also be explained by a higher prevalence of the Allee effect in the former. The connection between *r*-strategy and Allee effect is not so obvious, but this hypothesis might account for at least some of the highly polymorphic *r*-species we identified, such as marine sessile species (mussels, oysters, slipper snails, sea squirts). These animals, in which immobile adults release gametes in the water column, can only reproduce at high population density, and therefore presumably suffer from the Allee effect. A connection between the Allee effect and genetic diversity was recently made in the context of expanding populations and colonization[5].

These potential explanations are non-mutually exclusive and would deserve additional empirical support.

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