Population Dynamics in a Changing Environment: Random versus Periodic Switching

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Environmental changes greatly influence the evolution of populations. Here, we study the dynamics of a population of two strains, one growing slightly faster than the other, competing for resources in a time-varying binary environment modeled by a carrying capacity that switches either randomly or periodically between states of abundance and scarcity. The population dynamics is characterized by demographic noise (birth and death events) coupled to the fluctuating population size. By combining analytical and simulation methods, we elucidate the similarities and differences of evolving subject to stochastic and periodic switching. We show that the population size distribution is broader under intermediate and fast random switching than under periodic variations, with periodic changes leading to an abrupt transition from slow to fast switching regimes. The fixation probability under intermediate/fast random and periodic switching can hence vary significantly, with markedly different asymptotic behaviors. We also determine the conditions under which the fixation probability of the slow strain is optimal when the dynamics is driven by asymmetric switching.

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The evolution of natural populations is influenced by varying environmental conditions. Here, the abundance of nutrients, toxins, or external factors like temperature are subject to random and seasonal variations, and have an important impact on population dynamics \cite{1,2}.

Several mechanisms have been suggested for a population to cope with changing environments by assuming that external factors vary either periodically or stochastically in time \cite{8,21}. A common choice to model external variations, both for its simplicity and experimental relevance, is to consider an environment that periodically or stochastically switches between two states \cite{22,41}. In finite populations, demographic noise (DN) is another important form of randomness that can lead to fixation (one species takes over the population \cite{42,43}). DN tends to be strong in small populations and negligible in large ones. Importantly, the evolution of a population composition is often coupled with the dynamics of its size \cite{14,49}. This can lead to DN being coupled to environmental variability (EV), with external factors affecting the population size, which in turn modulates the DN strength. The interplay between EV and DN is important in various fields, e.g., in gene regulatory networks, see \cite{13,17} and references therein. In particular, it is relevant to microbial communities, which are often volatile and subject to extreme environmental changes \cite{50,55}. These may lead to population bottlenecks where new colonies consisting of few individuals are prone to fluctuations.

In most studies, fluctuations stemming from EV and DN are considered to be independent, often by assuming that growth rates vary independently of the population \cite{5,6,10,13,20,22,24,26,81,83,86,88}. In this context, there is as yet no systematic comparison of the evolution under random and periodic switching: some works report that they lead to similar evolutionary processes while others find differences, see \textit{e.g.}, Refs. \cite{24,35}. Here, we systematically study the coupled influence of EV and DN on the evolution of a population where slow- and fast-growing strains compete for resources subject to a randomly and periodically switching carrying capacity.

A distinctive feature of this model is that it accounts for the stochastic or periodic depletion and recovery of resources via a binary environment that varies with a finite correlation time or period, see Fig. 1. This setting is motivated by realistic situations, but is simple enough to enable analytical progress. Indeed, while the cases of binary random and periodic switching are idealizations of real-world environments, they serve as baseline models to understand whether environmental perturbations of different nature lead to the same dynamics.

Using a combination of analytical and computational tools, we address the fundamental question of comparing the evolution subject to stochastic and deterministic changes by considering random versus periodic environmental switching. This is done by elucidating the influence of EV on the population size distribution (PSD) and its fixation properties. We analytically show that the PSD is broader under intermediate and fast random switching than under periodic switching, with the latter leading to a more abrupt transition from slow to fast switching regime. Consequently, the fixation probability under intermediate/fast random and periodic switching can vary significantly and exhibit markedly different asymptotic behaviors. We also determine the nontrivial asymmetric switching conditions under which the fixation probability of the slow strain is optimal.

We consider a well-mixed population of time-fluctuating size \(N(t) = N_S(t) + N_F(t)\) consisting of two strains. At time \(t\), \(N_S(t)\) individuals are of a slow-growing strain \(S\), corresponding to a fraction \(x = N_S/N\)
of the population, and $N_F$ are of a fast-growing species $F$. Individuals of strain $S$ and $F$ reproduce with respective per-capita growth rates $(1−s)$/$f$ and $1/f$, where $f=(1−s)x+1−x=1−sx$ is the population’s average fitness, and $0<s\ll1$ is the selection intensity denoting the small growth advantage of $F$ over $S$ [39 40 45 60]. The strains’ growth is limited by a logistic death rate $N/K$, where $K \gg 1$ is the carrying capacity. Population dynamics is often idealized by assuming a static environment (constant $K$) which yields a constant or logistically-varying population size [43 55 62]. Here, we instead consider a fluctuating population size subject to a time-varying environment, which evolves according to the birth-death process [40 62]:

$$N_{S/F} \xrightarrow{T_{S/F}^+} N_{S/F} + 1 \quad \text{and} \quad N_{S/F} \xrightarrow{T_{S/F}^-} N_{S/F} - 1, \quad (1)$$

with transition rates $T_{S/F}^+ = (1−s)N_S/f$ and $T_{S/F}^- = N_F/f$ and $T_{S/F}^+ = (N/K)N_{S/F}$. We model EV via a switching carrying capacity

$$K(t) = K_0[1 + \gamma \xi_\alpha(t)], \quad \text{with} \quad \xi_\alpha(t) \in (-1, +1), \quad (2)$$

$$K_0 = \frac{K_+ + K_-}{2} \quad \text{and} \quad \gamma = \frac{K_+ - K_-}{2K_0},$$

where $\alpha \in \{r, p\}$ and $\gamma = O(1)$. Here, resources vary either randomly ($\alpha = r$) or periodically ($\alpha = p$), between states of scarcity, $K = K_-$ ($\xi_\alpha = -1$), and abundance, $K = K_+$ ($\xi_\alpha = +1$), causing fluctuations of the population size and its composition, see Fig. 1.

When $K(t)$ switches randomly, $\xi_\alpha$ is a colored asymmetric dichotomous (telegraph) Markov noise (ADN) [60 61], with the transition $\xi_r \rightarrow -\xi_r$ occurring at rate $\nu_{\pm}$ when $\xi_r = \pm 1$. It is useful to introduce the average switching rate $\nu = (\nu_+ + \nu_-)/2$ and $\delta = (\nu_- - \nu_+)/2\nu$, measuring the switching asymmetry ($|\delta| < 1$) [62]. Clearly, $\delta = 0$ denotes symmetric dichotomous noise [39 40]. At stationarity, the ADN’s mean and autocorrelation functions are $\langle \xi_\alpha \rangle = \delta$ and $\langle \xi_\alpha(t)\xi_\alpha(t') \rangle = (1−\delta^2) e^{−2\nu(1−\delta^2) t}$ (where $\langle \cdot \rangle$ denotes ensemble averaging). When $K(t)$ switches periodically, $\xi_\alpha$ is a rectangular wave defined in terms of the rectangular function, $\text{rec}(\cdot)$ [63], of period $T$:

$$\xi_\alpha = \sum_{j=−\infty}^{\infty} \left\{ \text{rec} \left( t + \frac{1}{2\nu_+} + jT \right) / \nu_+ - \text{rec} \left( t - \frac{1}{2\nu_-} + jT \right) / \nu_- \right\},$$

where $T = (1/\nu_+) + (1/\nu_-) = 2/[(1−\delta^2)\nu]$. When $\delta = 0$, this reduces to the square wave $\xi_\alpha(t) = \text{sign} \left( \sin (\pi\nu t) \right)$.

At stationarity, $\xi_\alpha$ averaged over one period has the same mean and correlation function as $\xi_\alpha$. Henceforth we consider $\xi_\alpha$ and $\xi_\alpha$ at stationarity, and the mean and variance of $K(t)$ are thus the same for $\alpha \in \{r, p\}$ and given by $\langle K \rangle = K_0(1 + \gamma\delta)$ and $\text{var}(K) = (\gamma K_0^2)(1−\delta^2)$ [64], which increases with $\gamma$ and decreases with $|\delta|$.

Upon ignoring the eventual extinction of the population which occurs after an enormous time (unobservable when $K_0 \gg 1$) [39 59], the main features of this evolutionary model are the long-time population size distribution (PSD) and the fixation probability. These quantities, describing the system’s ecological and evolutionary dynamics, can be found by analyzing the underlying master equation [40 41 62 66 67].

Insight into the dynamics can be gained by ignoring fluctuations and considering the mean-field picture of a very large population subject to constant $K = K_0$. Here, the population size $N$ and $x$ evolve according to $dN/dt = N(1−N/K_0)$ and $\dot{x} = −sx(1−x)/(1−sx)$ [43 46 62 65], which predict that $x$ decays on a timescale $t \sim 1/s \gg 1$, while $N(t) = O(K_0)$ after $t = O(1)$. Thus, a timescale separation occurs when $s \ll 1$: the typical relaxation time of $x$ is much slower than that of $N$. Yet, a finite population is subject to DN (randomly occurring birth and death events), resulting in the eventual fixation of one of the species. Here, given a fixed population size $N$, the $S$ fixation probability starting from an initial fraction $x_0 = N_S/(N_0)$ is [43 58 67]

$$\phi(x_0) = \left[ e^{−Nx_0 \ln(1−s)} - 1 \right] / \left[ e^{−N \ln(1−s)} - 1 \right], \quad (3)$$

which exponentially decreases with $N$. For $s \ll N^{−1/2} \ll 1$ (“diffusion approximation”), this result simplifies to $\phi(x_0) = (e^{−Nsx(1−x_0)} - e^{−Nsx})/(1−e^{−Nsx})$ [39 49 67]. Eq. 3 also gives the approximate fixation probability when $N$ fluctuates about constant $K = K_0$.

This scenario significantly changes when in addition to DN, the population is subject to a time-varying carrying capacity, see Fig. 1. Inspired by the drastic changes in the environment of microbial communities at different frequencies [50 54], we study below the influence of the EV ($\nu$, $\gamma$, and $\delta$) on the PSD and fixation properties.

**Population size distribution.** Simulations show that the marginal quasi-stationary PSD, $P_N^\alpha(N)$ (unconditioned of $\xi_\alpha$), is characterized by different regimes depending on the switching rate $\nu$, with markedly different...
features in the case of random and periodic switching
when \( \nu = \mathcal{O}(1) \) and \( \nu \gg 1 \), see Fig. 2.

The case of random switching can be treated similarly to \( \delta = 0 \) (symmetric dichotomous noise) \([39, 40]\). Here, we ignore DN and assume that the population size is driven only by ADN according to the piecewise-deterministic Markov process (PDMP) \([62, 68, 69]\), defined by the stochastic differential equation \( \dot{N} = N\left[1 - (N/K)(1 - \gamma_{\alpha})/(1 - \gamma_{\beta})\right] \), where \( K \equiv K_0(1 - \gamma^2)/(1 - \gamma) \). When \( \nu \to \infty \), the ADN self-averages, \( \xi \xrightarrow{\nu \to \infty} (\xi) = \delta \), and \( N \xrightarrow{\nu \to \infty} K \). Therefore, the marginal PSD \([40, 60]\) of this PDMP satisfies

\[
P_{\nu}^{PDMP}(N) \propto \frac{1}{N^2} \left( \frac{K_0 - 1}{N} \right)^{\nu - 1} \left( 1 - \frac{K_0}{N} \right)^{-1},
\]

where the normalization constant has been omitted, and the dependence on \( \gamma, \delta \) and \( \nu \) is given by \( K_\pm = (1 \pm \gamma)K_0 \) and \( \nu_\pm = (1 \pm \delta)\nu \). Although \( P_{\nu}^{PDMP} \) has support \([K_-, K_+]\) and only accounts for EV, when \( K_0 \gg 1 \) and \( \gamma = \mathcal{O}(1) \), it captures the peaks of \( P_{\nu}^{PDMP} \) and the average population size, see Figs. 2 and S3(b) in \([62]\), which are the most relevant features for the population fixation properties. Clearly, \( P_{\nu}^{PDMP} \) ignores DN and cannot capture the width of \( P_{\nu}^{PDMP} \) about its peaks, see Fig. 2(a,c,d).

For periodic switching, \( P_{\nu}^{(p)} \) can be found analytically in the limits of very slow \( \nu \to 0 \) and fast \( \nu \gg 1 \) switching. For \( \nu \to 0 \) the carrying capacity is initially randomly allocated and is almost constant, i.e. \( K(t) \approx K(0) \). The PSD is thus the same in the periodic and random switching: \( P_{\nu}^{(p)} = P_{\nu}^{(r)} \equiv P_0 \), and can be computed from the master equation. Assuming \( K_0 \gg 1 \) and \( \gamma = \mathcal{O}(1) \), the PSD turns out to be bimodal with peaks about \( N = K_\pm \), whose intensity depends on \( \delta \) \([62]\): \( P_0(N) \approx \left[(1 + \delta) \frac{1}{2} + e^{-K_+ - (1 - \delta) K_\pm } / [2(N + 1)]\right] \). This result excellently agrees with simulations, see Fig. 2(a).

Under fast periodic switching, \( P_{\nu}^{(p)} \) differs markedly from its random counterpart, see Fig. 2(b). An approximate expression of \( P_{\nu}^{(p)} \) to leading order in \( 1/\nu \) can be obtained from the master equation using the WKB approximation \([20, 71]\) and Kapitza method \([11, 20, 71]\). The latter involves separating the dynamics into fast and slow variables, and averaging the fast variables. As shown in Sec. 2.2 of \([62]\), this yields (up to a normalization factor)

\[
P_{\nu}^{Kap} \sim \mathcal{P}(N) \exp \left[ -\frac{K_0}{2\nu^2} \left( \gamma - \frac{1}{1 - \gamma^2} \right)^2 \frac{2(N - K_\pm )^3}{K_0} \right],
\]

where \( \mathcal{P}(N) \approx \exp[N(1 - \ln(N/K))] \) is the PSD at \( \nu \to \infty \), peaked at \( N = K_\pm \). We notice that both \( P_{\nu}^{(p)} \approx P_{\nu}^{Kap} \) and \( P_{\nu}^{(r)} \approx P_{\nu}^{PDMP} \) are unimodal and peaked about \( N \approx K \) when \( \nu \gg 1 \), but \( P_{\nu}^{Kap} \) is significantly sharper and narrower than \( P_{\nu}^{PDMP} \). In fact, the variance of \( P_{\nu}^{PDMP} \) scales as \( K_0/\nu \) when \( \nu \ll K_0 \), and is much larger than the variance of \( P_{\nu}^{Kap} \) which is of order \( K_0 \), see Sec. 4.3 in \([62]\).

Note that while \( P_0 \) and \( P_{\nu}^{(p)} \) [Eq. (5)] account for DN and EV, \( P_{\nu}^{PDMP} \) [Eq. (6)] only accounts for EV. Yet, in the regime \( 1 \lesssim \nu \ll K_0 \), DN is negligible compared to EV \([62]\), and \( P_{\nu}^{PDMP} \) provides a suitable description of \( P_{\nu}^{(r)} \) in this regime. In particular, \( P_{\nu}^{PDMP} \) allows us to characterize interesting phenomena arising in the intermediate asymmetric switching regime where \( \nu \gtrsim 1 \) with \( \nu_- \gg 1 \) and \( \nu_+ < 1 \) (longer sojourn in state \( K = K_\pm \)), or \( \nu_- < 1 \) and \( \nu_+ > 1 \), i.e. when \( 1/(1 + \delta) < \nu < 1/(1 - \delta) \).

In the former case \( \delta > 0 \), \( P_{\nu}^{(r)} \) has a peak at \( N \approx K_\pm \) and, under sufficiently strong EV, exhibits also a peak \( N^* \) between \( K_\pm \) (i.e. \( K_\pm < N^* < K_\pm \)), whose position is aptly captured by Eq. (4), see Fig. 2(c) and Sec. 3.1 in \([62]\). In Fig. 2(c), one can see that \( P_{\nu}^{(p)} \) also has two peaks, but it is narrower than \( P_{\nu}^{(r)} \). When \( \nu \gtrsim 1 \), with a peak \( N \approx K_\pm \) and \( \nu_+ > 1 \) (\( \delta < 0 \)), \( P_{\nu}^{(r)} \) exhibits a single peak at \( N \approx K_\pm \), again well predicted by Eq. (4), see Fig. 2(d).

Probability fixation. When \( s \ll 1 \), at \( t \gtrsim \mathcal{O}(1) \), once the system has settled in its long-lived PSD, given an initial fraction \( x_0 \) of \( S \) individuals, the \( S \)-species fixation probability subject to \( \alpha \)-switching \((\alpha \in \{r, p\})\), \( \phi_\alpha \), can be approximated by averaging \( \phi(x_0)N \) over \( P_{\nu_\mu}^{(r)}(N) \), upon rescaling \( \nu \to \nu/s \) \([39, 40]\):

\[
\phi_\alpha(\nu) \simeq \int_0^\infty P_{\nu_\mu}^{(r)}(N) \phi(x_0)N \, dN, \quad \alpha \in \{r, p\}.
\]

This result is valid under weak selection, \( 1/K_0 \ll s \ll 1 \), when there are \( \mathcal{O}(\nu/s) \) switches prior to fixation \([39, 40, 62]\). The difference between \( \phi_r \) and \( \phi_p \) stems from the different \( \nu \)-dependence of \( P_{\nu}^{(r)} \) and \( P_{\nu}^{(p)} \) see Figs. 2. In the case of random switching \( \phi_\alpha(\nu) \) can be approximated by substituting Eq. (4) into (6), yielding Eq. (S33) of \([62]\), which is valid over a broad range of \( \nu \) \([39, 62]\), as confirmed by simulations, see Fig. 3 and S2(c,d) of \([62]\).
When \( \nu \to 0 \) (slow switching), there are no switches prior to fixation and the population density is peaked at \( N = K_+ \) under random and periodic switching. Hence, with \( \lambda = \lambda^*(s) \), we approximate \( \lim_{\nu \to 0} \phi_\alpha(\nu) \approx \phi(0) = [(1 - \delta)\phi(x_0)|_{\Sigma_+} + (1 + \delta)\phi(x_0)|_{\Sigma_-}]/2 \). In Fig. 3(d) we confirm that, when \( \nu/s \ll 1 \), \( \phi(0) \) coincides with \( \phi_0(\nu) \) and \( \phi_\alpha(\nu) \).

When \( \nu/s \gg 1 \) (fast switching), \( P^{(\alpha)}_{\nu/s} \) is sharply peaked at \( N \approx K_0 \), see Fig. 2(b), and to leading order \( \lim_{\nu \to \infty} \phi_\alpha(\nu) \approx \phi(\infty) = \phi(x_0)|_{\Sigma_+} \). Simulation results of Fig. 3 confirm that at \( \nu \gg s \), \( \phi_0(\nu) \) and \( \phi_\alpha(\nu) \) converge to \( \phi(\infty) \). Thus, the fixation probability under fast random/periodic switching is the same to lowest order in \( 1/\nu \). Yet, the rate of convergence to \( \phi(\infty) \) is different in the random and periodic case, see Fig. 3(a). This is explained by computing the next-to-leading order of \( \phi_\alpha \) in \( \nu/s \gg 1 \). For this, along with (5), we use Eq. (S33) of \( \phi(\infty) = e^{n/2} \), \( m = 2\mathcal{K}(1 - x_0)\ln(1 - s) \), and \( \mathcal{A}_r = m(4 + m)(1 - \delta^2)(\gamma/(1 - \gamma)) \). Then, when \( K \nu_s \gg 1 \), \( \phi_\alpha(\nu) \) converges to \( \phi(\infty) \) much faster for \( \alpha = p \) than when \( \alpha = r \), see Fig. 3(a)-(c); i.e., the fixation probability exhibits markedly different behaviors under periodic and random switching. Also, the ratio \( \phi_\alpha(\nu)/\phi_\alpha(\nu) \) [see inset of Fig. 3(a)] has a sharp peak at a nontrivial intermediate \( \nu \).

Under intermediate switching, \( \phi_\alpha \) exhibits a rich behavior as \( \nu \) increases and \( \phi_\alpha \) interpolates between \( \phi(0) \) and \( \phi(\infty) \), see Fig. 3(d). Under large enough switching asymmetry, \( \phi_\alpha \) is a non-monotonic function of \( \nu \) in a nontrivial region \( \gamma > \gamma_0(s) \). For intermediate \( \nu \), there are no switches to \( \phi_\alpha \) in this regime, and that it has a clear maximum at \( \nu^*_c \sim \nu \). This optimal switching rate for the \( S \) species fixation at given \( \gamma \), \( \delta \) and \( s \) corresponds to \( \mathcal{O}(1) \) switches prior to fixation, while \( \phi_\alpha(\nu)/\max(\phi(0), \phi(\infty)) \) – 1 reaches up to \( 30\% \), see Fig. 3(d,e). Similar results are found for periodic switching with an optimal switching rate \( \nu^*_p \approx \nu^*_c \) and a sharper/narrower peak \( \phi_\alpha(\nu) \). The existence of a maximum \( \phi_\alpha(\nu^*_p) \) is thus a signature of asymmetric switching. For intermediate switching rate and not too large asymmetry \( |\alpha| < \delta \), \( \phi_\alpha(\nu) \) is a monotonic function: it increases/decreases with \( \nu \) above/below a critical selection intensity \( s_c \) (with \( \gamma, \delta \) fixed), that we have determined, see Fig. S2(b) and Sec. 5.2 in [62]. A similar qualitative behavior is observed for \( \phi_\alpha(\nu) \).

Remarkably, similar qualitative results are obtained in the more intricate case of eco-evolutionary dynamics, arising when the slow strain produces public goods benefitting the entire population, see Sec. 7 and Fig. S4 in [62].

Inspired by the evolution of microbial communities in fluctuating environments, we have studied the dynamics of a population of two strains, one growing slightly faster than the other, competing for resources in a binary environment. Importantly, our model accounts for coupling between demographic noise and environmental variability, where the latter has been modeled by a carrying capacity that switches between states of scarcity/abundance randomly or periodically in time. Here, we have systematically compared the effects of random and periodic switching on the population size and its fixation properties. Our findings hence highlight the effect of evolving subject to a stochastically- versus deterministically-varying environment. We have shown that the population size distribution is broader under intermediate and fast random switching than under periodic change, with a more abrupt transition from the slow to fast switching regime in the periodic case. As a consequence we have found markedly different asym-
to frequent environmental changes.

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[62] See Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevLett.000.00000 for information about the simulations, the approximations of the PSD and (7), further details about Fig. 3, the mean fixation time results, and the generalization to a public good scenario.

[63] A rectangular function is defined as follows: \( \text{rec}(x) = 1 \) if \( |x| < 1/2 \), \( \text{rec}(x) = 0 \) if \( |x| > 1/2 \), while \( \text{rec}(\pm 1/2) = 0 \).

[64] Here, \( \langle \cdot \rangle \) is the ensemble average in the case of random switching \( (\alpha = r) \), and the average obtained by integrating over one period \( T \), i.e. \( \langle K(t) \rangle = (1/T) \int_{t}^{t+T} K(\tau) d\tau \), in the case of periodic switching \( (\alpha = p) \).

[65] When \( N \) and \( x \) are not coupled and \( s \ll 1 \), the initial condition \( N(0) \) is irrelevant for our analysis. In our simulations we have considered either \( N(0) = K_0 \) or \( N(0) = K_0(1 - \gamma^2)/(1 - \gamma \delta) = K \), and have confirmed that our results are independent of the choice of \( N(0) \).

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Appendix: Supplementary Material to

Population Dynamics in a Changing Environment: Random versus Periodic Switching

In this Supplemental Material, we provide some further technical details and supplementary information in support of the results discussed in the main text. We also provide additional information concerning the population’s mean fixation time (MFT), and the generalization of the model in a scenario where the slow strain is a public goods producer.

In what follows, unless stated otherwise, the notation is the same as in the main text and the equations and figures refer to those therein.

S1. MASTER EQUATION AND SIMULATION METHODS

In this section, we give the master equation (ME) of the birth-death process according to which the system evolves and describe the methods used to simulate the population dynamics in the case of random and periodic switching.

S1.1. Master equation of the underlying birth-death process

As explained in the main text, the population evolves according to a multivariate birth-death process where reproduction of S/F individuals, \( N_{S/F} \to N_{S/F} + 1 \), occurs at a rate \( T_{S/F}^+ \), and death \( N_{S/F} \to N_{S/F} - 1 \), occurs at a rate \( T_{S/F}^- \), with the transition rates \[39, 40\]

\[ T_{S}^+ = \left( \frac{1 - s}{f} \right) N_S, \quad T_F^+ = \frac{1}{f} N_F \quad \text{and} \quad T_{S}^- = \frac{N}{K(t)} N_S, \quad T_F^- = \frac{N}{K(t)} N_F, \quad (S1) \]

where \( f = 1 - s(N_S/N) \) is the population’s average fitness. Here, the carrying capacity \( K(t) \) varies in time either randomly or periodically. In the former case, at each time increment either an individual is picked for reproduction/death or the carrying capacity is switched with rates \( \nu_\pm \) according to \( K_+ \to K_- \) with rate \( \nu_+ \) and \( K_- \to K_+ \) with rate \( \nu_- \) [see Eq. (2) in the main text, with \( \alpha = r \)]. This results in a birth-death process obeying the ME which, with \( \bar{N} = (N_S, N_F) \) and \( \pm \) as a shorthand notation for \( \xi_r = \pm 1 \), reads

\[
\frac{dP_r^{(r)}(\bar{N},+,t)}{dt} = (\mathbb{E}_{\bar{S}} - 1)[T_{S}^+ P_r^{(r)}(\bar{N},+,t)] + (\mathbb{E}_{\bar{F}} - 1)[T_F^+ P_r^{(r)}(\bar{N},+,t)]
+ (\mathbb{E}_{\bar{S}} - 1)[T_{S}^- P_r^{(r)}(\bar{N},-,t)] + (\mathbb{E}_{\bar{F}} - 1)[T_F^- P_r^{(r)}(\bar{N},-,t)]
+ \nu_+ P_r^{(r)}(\bar{N},-,t) - \nu_- P_r^{(r)}(\bar{N},+,t),
\]

\[
\frac{dP_r^{(r)}(\bar{N},-,t)}{dt} = (\mathbb{E}_{\bar{S}} - 1)[T_{S}^+ P_r^{(r)}(\bar{N},-,t)] + (\mathbb{E}_{\bar{F}} - 1)[T_F^+ P_r^{(r)}(\bar{N},-,t)]
+ (\mathbb{E}_{\bar{S}} - 1)[T_{S}^- P_r^{(r)}(\bar{N},+,t)] + (\mathbb{E}_{\bar{F}} - 1)[T_F^- P_r^{(r)}(\bar{N},+,t)]
+ \nu_+ P_r^{(r)}(\bar{N},+,t) - \nu_- P_r^{(r)}(\bar{N},-,t),
\]

where \( \mathbb{E}_{\bar{S/F}} \) are shift operators such that \( \mathbb{E}_{\bar{S}} f(N_S, N_F, \xi, t) = f(N_S \pm 1, N_F, \xi, t) \) and similarly for any \( \mathbb{E}_{\bar{F}} \). Clearly, Eqs. \( S2a \) and \( S2b \) are coupled and the last lines on their right-hand-side account for the stochastic switching of \( K \).

For periodic switching, the carrying capacity \( K(t) = K_0[1 + \gamma \xi_\rho(t)] \), varies deterministically with \( \xi_\rho(t) \equiv \xi_\rho(t + T) \), where the shape of \( \xi_\rho(t) \) is taken to be a rectangular wave of period \( T = (1/\nu_+) + (1/\nu_-) \) \[76\]. In this case, the ME reads

\[
\frac{dP_r^{(r)}(\bar{N},t)}{dt} = (\mathbb{E}_{\bar{S}} - 1)[T_{S}^+ P_r^{(r)}(\bar{N},-,t)] + (\mathbb{E}_{\bar{F}} - 1)[T_F^+ P_r^{(r)}(\bar{N},-,t)]
+ (\mathbb{E}_{\bar{S}} - 1)[T_{S}^- P_r^{(r)}(\bar{N},+,t)] + (\mathbb{E}_{\bar{F}} - 1)[T_F^- P_r^{(r)}(\bar{N},+,t)],
\]

where \( T_{S/F}^{(r)}(\xi_\rho) \) are now the time-dependent transition rates given by \( S1 \) that vary periodically with \( \xi_\rho \). Note, that in both MEs \( S2a-S3 \), \( P_r^{(r)}(\bar{N},t) = 0 \) whenever \( N_S < 0 \) or \( N_F < 0 \).
Ignoring demographic and environmental fluctuations, the mean-field description, i.e., the dynamics of the average number of individuals of species \(i \in \{S,F\}\), denoted by \(\langle N_i \rangle\), can be obtained from MEs \(\mathbf{S2-3}\) by assuming \(K(t) = K_0 \gg 1\): \((d/dt)\langle N_i \rangle \equiv \langle \dot{N}_i \rangle = \sum \dot{N}_s \xi_s N_i (d/dt)P^{(s)}_\nu\). From these, the mean-field description of \(N\) and \(x = N_S/N\) yields: \(\dot{N} = N(1-N/K_0)\) and \(\dot{x} = sx(1-x)/(1-sx)\) \(\mathbf{39-41}\). Similarly, the stochastic differential equation \(\dot{N} = [1 - (N/K_0)(1 - \gamma \xi_s)1/1 - \gamma \delta]\) with \(K \equiv K_0(1 - \gamma)^2(1 - \gamma\delta)\), defining the underlying piecewise deterministic Markov process (PDMP), can be obtained by ignoring demographic fluctuations in \(\langle \dot{N}(\xi_s) \rangle = \sum \dot{N}_s N_i (d/dt)P^{(s)}_\nu\).

### S1. Simulation methods

While the MEs \(\mathbf{S2}\) and \(\mathbf{S3}\) fully describe the population dynamics in the case of random and periodic switching, respectively, in general, they cannot be solved analytically. However, to gain insight into the stochastic dynamics, one can employ efficient numerical simulations. In the case of random switching, the birth-death process \(\mathbf{S2}\) defined by the six reactions \(\mathbf{S1}\) can be exactly simulated using the standard Gillespie algorithm \(\mathbf{78}\). In the case of periodic switching, it is convenient to simulate the birth-death process \(\mathbf{S3}\) with time-dependent (periodic) transition rates \(\mathbf{S1}\) using the simulation method outlined below.

#### S1.2.1. Simulation of the periodic switching case with the modified next reaction method

In the periodic case we used the modified next reaction method \(\mathbf{79}\), which is a suitable algorithm for system with explicit time dependent rates. Unlike the classic Gillespie Algorithm, this version considers all possible birth/death processes as independent reactions. We can calculate the time step \(\Delta t_i\) in which the next reaction occurs by generating a random number from a uniform distribution \(r_i \in U(0,1)\) for the probability that reaction \(i\) did not occur after time interval of \(\Delta t_i\). In the case of periodic switching, we deal with four stochastic reactions \(i \in \{1,\ldots,4\}\) (birth/death of \(S\) and \(F\)) each with a propensity function \(a_i \in \{T^+_S, T^-_S(\xi_\nu(t)), T^+_F, T^-_F(\xi_\nu(t))\}\). Hence, we have

\[
\dot{r}_i = \exp \left[- \int_{t}^{t+\Delta t_i} a_i(t') \, dt' \right]. \tag{S4}
\]

We start the simulation with time \(t = 0\), and for each reaction we set the “internal time” \(T_i = 0\) and the quantity \(P_i = \ln(1/r_i)\). We also set the initial number of each species, the environmental state (such that the ensemble is stationary), and the initial time to next switch \(\Delta t_{\text{switch}}\). We find the time step \(\Delta t_i\) by a different version of Eq. \(\mathbf{4}\), \(\int_{t}^{t+\Delta t_i} a_i(t') \, dt' = P_i - T_i\), which can be solved easily, since for discrete \(K\) the time-dependence in each iteration is in fact constant. At this point we find the reaction that has the minimal time step \(\Delta t_\mu = \min_i \{\Delta t_i\}\), then propagate the time \(t \rightarrow t + \Delta t_\mu\), update the population size, the internal times \(T_i \rightarrow T_i + \int_{t}^{t+\Delta t_\mu} a_i(t') \, dt'\), and also \(P_i \rightarrow P_i + \delta_i, \mu \ln(1/r_i)\). Then we recalculate the rates \(a_i\), generate another random number \(r_i \in U(0,1)\), and repeat these steps iteratively until one of the species has undergone extinction. We treat the switches \(\xi \rightarrow -\xi\), that occurred during a period of \(1/\nu\), in a different way than in the case of random switching. Since the switches are deterministic, we can simply calculate the switching times from the initial conditions, without any stochastic calculation. If \(\Delta t_{\text{switch}} < \Delta t_\mu\), we switch \(\xi \rightarrow -\xi\) and propagate the time \(t \rightarrow t + \Delta t_{\text{switch}}\).

### S2. Approximations of the quasi-stationary population density in the slow and fast switching regimes

In this section we compute the quasi-stationary population size distribution (PSD), \(P_N\), in the slow switching regime and under fast periodic switching. To do so, we first compute the PSD in the case of constant carrying capacity. That is, we assume a static environment \(\xi_a(t) = \xi\) and carrying capacity \(K(t) = K\).

To compute the PSD we start with the ME for \(P(N)|_K\) – the probability to find the total population size \(N\) subject to a constant carrying capacity \(K\)

\[
\frac{dP(N)|_K}{dt} = (N - 1)P(N - 1)|_K + \frac{(N + 1)^2}{K}P(N + 1)|_K - \left(N + \frac{N^2}{K}\right)P(N)|_K. \tag{S5}
\]

The PSD can be found by putting \(\dot{P}(N)|_K = 0\) and demanding a reflecting boundary condition at \(N = 1\). The latter assumes that the probability flux to the extinction state \(P(N = 0)\) is negligibly small, which is legitimate since the
mean time to extinction is assumed to be much larger than the time scales we are interested in here, see main text.
The normalized solution of the resulting recursion equation reads

\[ P(N)_{|K} = \frac{1}{\text{Ei}(K) - \gamma - \ln(K)} \frac{K^N}{N!} \approx \frac{K^{N+1} e^{-K}}{(N+1)!}, \tag{S6} \]

where \( \text{Ei}(x) = - \int_{-x}^{\infty} \frac{e^{-t}}{t} \, dt \) is the exponential integral function, \( \gamma = 0.577... \) is the Euler–Mascheroni constant, and the last approximation holds when \( K \gg 1 \).

**S2.1. Quasi-stationary population density under slow switching**

When \( \nu \to 0 \) and there are no switches prior to fixation, the population evolves in a static environment \( \xi_{\alpha} = \pm 1 \), with \( \xi_{\alpha} \) that is distributed with a probability \( p(\xi_{\alpha}) = (1 \pm \delta)/2 \). If \( \xi_{\alpha} = +1 \), the population is subject to a constant carrying capacity \( K = K_+ \), whereas if \( \xi_{\alpha} = -1 \) it is subject to \( K = K_- \). Hence, from Eq. (S5) we have \( P(N|\xi_{\alpha} = \pm 1) \equiv (K_{\pm}^{N+1} e^{-K_{\pm}})/(N+1)! \), yielding the PSD under slow switching

\[ P_0(N) = \sum_{\xi_{\alpha} = \pm 1} P(N|\xi_{\alpha}) \, p(\xi_{\alpha}) \approx \left( \frac{1+\delta}{2} \right) \frac{K_+^{N+1} e^{-K_+}}{(N+1)!} + \left( \frac{1-\delta}{2} \right) \frac{K_-^{N+1} e^{-K_-}}{(N+1)!}. \tag{S7} \]

As explained in the main text, this result is valid both for periodic and random switching.

**S2.2. Kapitza method for the quasi-stationary population density under fast periodic switching**

In the opposite limit \( \nu \gg 1 \), the carrying capacity \( K \) rapidly oscillates around \( K_0 \). To find the PSD in the case of fast periodic switching, we employ the Kapitza method \[11\], valid for a general periodic \( \xi_{\alpha}(t) \), which involves separating the dynamics into fast and slow variables, and averaging the fast variables over the period of variation.

Our starting point is again the ME (S5), but now with \( K = K_0[1 + \gamma \xi(t)] \) and hence explicitly time-dependent rates. In order to treat this master equation semi-classically, we define the probability generating function \( G(p, t) = \sum_{m=0}^{\infty} P(m, t) p^m \), where \( p \) is an auxiliary variable that serves as the momentum coordinate, see below. Conservation of probability yields \( G(1, t) = 1 \). The definition of \( G \) is useful since

\[ P(N, t) = \frac{1}{N!} \frac{\partial^N G(p, t)}{\partial p^N} |_{p=0}. \tag{S8} \]

Multiplying Eq. (S5) by \( p^N \) and summing over all \( N \)'s, we obtain a second-order partial differential equation for \( G \)

\[ \frac{\partial G}{\partial t} = (1 - p) \left( \frac{-p}{K(t)} \frac{\partial G}{\partial p} + \frac{1}{K(t)} \frac{\partial G}{\partial p} + \frac{p}{K(t)} \frac{\partial^2 G}{\partial p^2} \right). \tag{S9} \]

This differential equation cannot be solved in general. To find its approximate solution, we exploit the fact that the typical carrying capacity is large, \( K_0 \gg 1 \), and employ the WKB ansatz \( G = G_0 \exp[-K_0 S(p, t)] \) in Eq. (S9) \[19\]. Keeping leading- and subleading-order terms with respect to \( O(K) \), we arrive at the following Hamilton-Jacobi equation

\[ -\frac{\partial S}{\partial t} = q (1 - p) \left( -p + \frac{1}{K(t)} + \frac{K_0}{K(t)} pq \right) \equiv H(p, q). \tag{S10} \]

Here \( H \) is the Hamiltonian, \( S \) is the action associated with the Hamiltonian, and we have defined \( q = -\frac{\partial S}{\partial p} \) as the coordinate conjugate to the momentum \[74\].

Let us separate the fast and slow time scales by denoting \( q(t) = X(t) + \zeta(t) \) and \( p(t) = Y(t) + \eta(t) \). Here \( X \) and \( Y \) are slow variables, while \( \zeta \) and \( \eta \) are small corrections (to be shown a-posteriori) that rapidly oscillate around 0 \[1]. Expanding the Hamiltonian (S10) up to second order around \( q = X \) and \( p = Y \) we find

\[ H(q, p, t) \approx H(X, Y, t) + \frac{\zeta}{2} \frac{\partial^2 H}{\partial X^2} + \frac{\eta}{2} \frac{\partial^2 H}{\partial Y^2} + \frac{\eta^2}{2} \frac{\partial^2 H}{\partial Y^2} \approx \tilde{H}(X, Y, t). \]
Using the Hamilton equations \( \dot{q} = \dot{X} + \zeta \simeq \partial_Y \tilde{H}(X,Y,t) \) and \( \dot{p} = \dot{Y} + \dot{\eta} \simeq -\partial_X \tilde{H}(X,Y,t) \), and equating the rapidly oscillating terms yields in the leading order in \( K_0 \gg 1 \): 
\[
\zeta \simeq (X^2 - 2XY^2) (B/\nu) \quad \text{and} \quad \eta \simeq - (2XY - 2XY^2) (B/\nu).
\]
Here \( B(t) = \mathcal{O}(1) \) is defined in Eq. (S13), and in the calculation \( X \) and \( Y \) were considered as constants during the period of rapid oscillations, and we have neglected terms of order \( \zeta \) and \( \eta \), but kept their time derivatives (proportional to \( \nu \gg 1 \)).

Following this result, we define a canonical transformation from the old \((q,p)\) to the new \((X,Y)\) variable
\[
q \simeq X + X^2 (1 - 2Y) \frac{B}{\nu} + 2X^3 (1 - 2Y)^2 \frac{B^2}{\nu^2}, \quad p \simeq Y - 2 \left( Y - Y^2 \right) X \frac{B}{\nu} - 2X^2 \left( Y - 3Y^2 + 2Y^3 \right) \frac{B^2}{\nu^2},
\]
which can be obtained using the generating function \( F_2(q,Y,t) = qY - q^2 (Y - Y^2) (B/\nu) \). This transformation is canonical up to second order in the small parameter \( 1/\nu \) since the Poisson brackets satisfy \( \{ q,p \}_{(X,Y)} = 1 + O \left( \frac{1}{\nu} \right) \).

Using Eqs. (S10) and (S11) and defining \( H' = H + \frac{\partial C}{\partial t} \), by averaging over a period of a rapid oscillation, we find after some algebra
\[
\mathcal{H}(X,Y) = XY (1 - Y) \left[ AX - 1 + X^2C (2 - 4Y + 4Y^2 - XA) \right] \frac{1}{\nu^2},
\]
where we have defined the following \( O(1) \) variables
\[
A'(\gamma) = \frac{K_0}{K(t)} = \frac{1}{T} \int_{t_0}^{t_{0} + T} K_0 \frac{1}{K(t)} dt; \quad C'(\gamma) = B' = \frac{1}{T} \int_{t_0}^{t_{0} + T} B(t) dt; \quad B(t) = K_0 \nu \int dt \left[ \frac{1}{K(t)} - \frac{1}{K_0} \right],
\]
and used the fact that \( B(t) \) is periodic. It can be shown that the \( \mathcal{O}(\nu^0) \) terms in Hamiltonian (S12) yield the PSD in the constant environment case [Eq. (S6)].

Having found the time-independent Hamiltonian, Eq. (S12), which effectively takes into account the rapid environmental oscillations, we can compute the PSD by finding the nontrivial zero-energy trajectory of \( \mathcal{H}(X,Y) \). Up to second order in \( \frac{1}{\nu} \), this trajectory is given by \( X(Y) = 1/A - C/(4A^3\nu^2) (2Y - 1)^2 + O (\nu^{-3}) \). Thus, recalling that \( q = -\frac{\partial S}{\partial \eta} \), and using the fact that the transformation \( (q,p) \rightarrow (X,Y) \) is canonical, we find \( S(Y) = -\int X dY = -Y/A + C/(6A^3\nu^2)(2Y - 1)^3 \). As a result, the generating function becomes
\[
G(Y) \simeq G_0 \exp \left[ -K_0 S(Y) \right] = G_0 \exp \left[ K_0 \frac{Y}{A} - K_0 \frac{C}{6A^3\nu^2} (2Y - 1)^3 \right],
\]
where \( G_0 \) is a constant, see below.

At this point, the PSD can be found by employing the Cauchy theorem to Eq. (S8), which yields
\[
P(N) = \frac{1}{2\pi i} \oint \frac{G(Y)}{Y^{N+1}} dY = \frac{G_0}{2\pi i} \oint \frac{1}{Y} \exp \left[ K_0 g(Y) \right] dY,
\]
where the integration has to be performed over a closed contour in the complex \( Y \) plane around the singular point \( Y = 0 \) and we have defined \( g(Y) = -S(Y) - \frac{Y}{2} \ln Y \). This integral can be calculated using the saddle point approximation [K6]. The saddle point, up to second order in \( 1/\nu \), is found at \( Y^* = AN/K_0 + [CN/(AK_0)] (2AN/K_0 - 1)^2 \nu^{-2} \).

Furthermore, since \( g''(Y^*) > 0 \) the integration contour in the vicinity of the saddle point must be chosen perpendicular to the real axis. This adds an additional phase of \( e^{i\pi/2} \) to the solution, which cancels the \( i \) factor in the denominator. As a result, the Gaussian integration yields \( P(N) \simeq \left[ G_0 / \left( Y^* \sqrt{2\pi K_0 |g''(Y^*)|} \right) \right] e^{K_0 g(Y^*)} \). Note, however, that only the leading-order result can be taken into account here; accounting for the prefactor would be an excess of accuracy since we have ignored the \( p \)-dependent prefactors in both \( G \) and in \( P \). Putting it all together, we finally obtain
\[
P(N) \simeq P_0 \exp \left[ N - N \ln (AN/K_0) - K_0 \frac{C}{6A^3\nu^2} (2AN/K_0 - 1)^3 \right],
\]
where \( P_0 \) is a normalization constant which can be found by demanding \( \int P(N) dN = 1 \).

S2.2.1. Rectangular and square wave

Our derivation above for \( \nu \gg 1 \) has been carried out for a general periodic function \( \xi_p(t) \). Let us now compute the PSD in the particular case of a rectangular wave. Using the expression of \( \xi_p(t) \) given in the main text and the
definition of a square wave, we find
\[
B(t) = \frac{\gamma}{1 - \gamma^2} \times \begin{cases} 
(\delta - 1)\nu t - 1/2 - \frac{1}{\nu_r} & 0 \leq t \leq 0 \\
(\delta + 1)\nu t - 1/2 & 0 \leq t \leq \frac{1}{\nu_u}
\end{cases}, \tag{S15}
\]
where the constant of integration was determined by the demand that \(B = 0\). Plugging this into Eq. (S13) yields \(K(t)^{-1} = A/K_0 = (1 - \gamma\delta)/[K_0 (1 - \gamma^2)]\) and \(C = (1/12)\gamma^2 / (1 - \gamma^2)^2\). Using these results, Eq. (S14) becomes
\[
P_{\nu}^{\text{Kap}} \sim P(N) \exp \left[ -\frac{K_0}{72\nu^2} \left(\frac{\gamma}{1 - \gamma^2}\right)^2 \left(\frac{2N - K_0}{K_0}\right)^3 \right], \tag{S16}
\]
which coincides with Eq. (5) in the main text, with \(P(N) \sim \exp\{N(1 - \ln(N/K))\}\), and \(K = K_0(1 - \gamma^2)/(1 - \gamma\delta)\).

S3. PDMP APPROXIMATION: INTERMEDIATE SWITCHING REGIME & LINEAR NOISE APPROXIMATION

When demographic noise is neglected, by assuming that the fluctuating population size is always large, and the only source of noise stems from the randomly switching carrying capacity, we have seen that the PSD, \(P_{\nu}(N)\), can be described in terms of the marginal stationary probability density of the underlying PDMP. Upon omitting the normalization constant, this PSD reads [see Eq. (4) in the main text]
\[
P_{\nu}^{\text{PDMP}}(N) \propto \frac{1}{N^2} \left[ \left(\frac{K}{N} - 1\right)^{\nu_u - 1} \left(1 - \frac{K}{N}\right)^{\nu_d - 1} \right], \tag{S17}
\]
with \(\nu_d = (1 + \delta)\nu\). This expression gives a suitable description of \(P_{\nu}(N)\) in the intermediate switching regime where interesting phenomena arise.

S3.1. \(P_{\nu}^{\text{PDMP}}\) and \(P_{\nu}(r)\) dependence on \(\gamma\) and \(\delta\) in the intermediate switching regime

The PSD, \(P_{\nu}(N)\), and its PDMP approximation \(P_{\nu}^{\text{PDMP}}\) are bimodal, with peaks about \(K_{\pm}\), when \(\nu < 1\), and unimodal when \(\nu > 1\) with a peak \(N^*\) that is the smaller solution to
\[
N^2 - (\nu(1 - \gamma\delta) + 1) K_0 N + (1 - \gamma^2) K_0^2 \nu = 0, \tag{S18}
\]
with \(N^* \to K\) as \(\nu \to \infty\). In addition, two other regimes can arise under asymmetric switching at intermediate rate when \(1/(1 + |\delta|) < \nu < 1/(1 - |\delta|)\). Here, the PSD has a different form not found when \(\delta = 0\): When \(\delta < 0\) and \(1/(1 - \delta) < \nu < 1/(1 + \delta)\), \(P_{\nu}^{\text{PDMP}}\) and \(P_{\nu}(r)\) have a peak at \(N \simeq K_+\). When \(\delta > 0\) and \(1/(1 + \delta) < \nu < 1/(1 - \delta)\), \(P_{\nu}^{\text{PDMP}}\) and \(P_{\nu}(r)\) have a peak at \(N \simeq K_-\) and, depending on \(\delta, \gamma\), and \(\nu\), also a peak at \(N^*\). The condition for the existence of such a peak at \(K_- < N^* < K_+\) can be inferred from the PDMP approximation [S17] by noting that (S18) has real roots when
\[
(1 - \gamma\delta)^2 \nu^2 - 2(1 + \gamma(\delta - 2\gamma))\nu + 1 > 0. \tag{S19}
\]
We thus distinguish four regions, I-IV, in the \((\delta, \gamma)\) - space, see Fig. S1.

I: \(\delta < \gamma\), where \(N^*\) exists for all intermediate \(\nu\).

II: \(\gamma < \delta < \frac{2\gamma}{1 + \gamma}\), where \(N^*\) exists for all intermediate \(\nu\) that lie outside the interval between the two solutions of (S19), here denoted by \(\nu_{1,2}\) (with \(\nu_2 \geq \nu_1\)).

III: \(\frac{2\gamma}{1 + \gamma} < \delta < \frac{2\gamma}{1 - \gamma}\), where \(N^*\) only exists if \(\frac{1}{1 + \delta} < \nu < \nu_1\).

IV: \(\delta > \frac{2\gamma}{1 - \gamma}\) - where \(N^*\) does not exist.

Simulation results of Figs. 2 and S1 confirm that the above analysis correctly reflects the properties of \(P_{\nu}(r)\). The above PDMP-based predictions also capture the features of the PSD, \(P_{\nu}(p)\), under periodic switching, even if \(P_{\nu}^{\text{PDMP}}\) describes only qualitatively the properties of \(P_{\nu}(p)\) under intermediate/fast periodic switching, see Fig. 2 (c).
FIG. 1: Phase diagram for the PSD, $P^{(r)}(N)$, and its approximations $P_{\nu}^{PDMP}$ and $P_{\nu}^{LNA}$ (insets), see Eq. (S21). We distinguish four regions described in the text: In addition to a peak about $K_+\bar{N}$, the PSD has always a local maximum $K_- < N^* < K_+$ in the intermediate switching regime in I; in regime II and III, the PSD and $P_{\nu}^{PDMP}$ have a peak about $K_+$ and, depending on $\nu$, possibly another peak at some values $K_- < N^* < K_+$, see insets; the PSD and $P_{\nu}^{PDMP}$ have one single peak about $K_+$ in IV. Insets illustrate the form of $P^{(r)}(N)$, $P_{\nu}^{PDMP}$ and $P_{\nu}^{LNA}$ in regions I-III. In the insets, solid lines are from the $P_{\nu}^{PDMP}$, given by Eq. (S17), dashed lines are from $P_{\nu}^{LNA}$, given by Eq. (S21), solid areas are from computer simulations, and the vertical dashed lines are eyeguides showing $N = K_{\pm}$. Parameters are: $(K_0, \gamma, s, x_0) = (250, 0.8, 0.05, 0.5)$ and (inset I) $\delta = 0.7$, $\nu = (0.05, 1.4, 1.75)$ (pink, orange, blue); (inset II) $\delta = 0.85$, $\nu = (1.3, 6.5)$ (purple, blue, green); (inset III) $\delta = 0.92$, $\nu = (1.3, 12)$ (purple, blue, green). In inset I, $N^*$ is in the intermediate regime for $\nu = 1.4$ (orange). In inset II, $N^*$ is in the intermediate regime for $\nu = 1$ (purple) and $\nu = 6.5$ (green). In inset III, $N^*$ is in the intermediate regime for $\nu = 1$ (purple).

We notice that the LNA excellently agrees with simulation results for the PSD: $P_{\nu}^{(r)}(N)$ and $P_{\nu}^{LNA}$ are almost indistinguishable in each inset.

S3.2. Linear noise approximation about $P_{\nu}^{PDMP}$

While $P_{\nu}^{PDMP}$ [S17] captures well the position of the peaks of the PSD and some of its main features, the PDMP approximation fails to capture the width of $P_{\nu}^{(r)}(N)$. In order to account for the demographic noise responsible for the shape of $P_{\nu}^{(r)}(N)$ near its peaks, we can perform a linear noise approximation (LNA) about the PDMP [40]

$$\frac{d}{dt} N = N \left[ 1 - \frac{N}{K} \left( \frac{1 - \gamma \xi_r}{1 - \gamma \delta} \right) \right], \quad \text{(S20)}$$

whose probability density $P_{\nu}^{PDMP}(N, \xi_r)$ in the environmental state $\xi_r = \pm 1$, is given by [60]

$$P_{\nu}^{PDMP}(N, \xi_r) \propto \left\{ \begin{array}{ll}
\frac{1 + \delta}{N^2} [\frac{K_+}{N} - 1]^{\nu_+ - 1} [1 - \frac{N}{\bar{N}}]^{-\nu_-}, & (\xi_r = +1) \\
\frac{1 - \delta}{N^2} [\frac{K_+}{N} - 1]^{\nu_+} [1 - \frac{N}{\bar{N}}]^{\nu_- - 1}, & (\xi_r = -1),
\end{array} \right.$$  

where $K_{\pm} = (1 \pm \gamma)K_0$ and $\nu_{\pm} = (1 \mp \delta)\nu$. As in Refs. [38, 40], we also make the simplifying assumption that demographic noise is approximately the same in each environmental state, yielding the Gaussian distribution $\propto \exp \left( -\frac{(N - \bar{N})^2}{2\bar{N}} \right) / \sqrt{\bar{N}}$ for the demographic fluctuations $N - \bar{N}$ about the PDMP (S20). Proceeding as in the case of symmetric switching ($\delta = 0$), see Ref. [40] where full details are provided, and omitting the normalization
constant, we obtain the LNA of the marginal stationary probability density about the PDMP \( P_{\nu}^{\text{LNA}}(N) \) \( \propto \int_{K_{\nu}}^{K_{\nu}^+} e^{-(N-\bar{N})^2 / N^{5/2}} \left\{ (1+\delta) \left[ K_{\nu}^+ - 1 \right]^{-\nu_+ - 1} \right. \left. + (1-\delta) \left[ K_{\nu}^+ - 1 \right]^{-\nu_- - 1} \right\} d\bar{N}. \) (S21)

The results shown in the insets of Fig. S1 illustrate that \( P_{\nu}^{\text{LNA}}(N) \) is an excellent approximation of the PSD: it accurately predicts all the details of the population probability density \( P_{\nu}^{(r)}(N) \) obtained from stochastic simulations. While \( P_{\nu}^{\text{LNA}} \) significantly improves over \( P_{\nu}^{\text{PDMP}} \) to describe the PSD, we have verified that computing \( \phi_r \) in the realm of the PDMP-based approximation (i.e. with \( \langle S33 \rangle \)) or by averaging \( \phi(x_0) \) over \( P_{\nu}^{\text{LNA}} \), as an approximation of \( P_{\nu}^{(r)} \), according to Eq. (6), yields essentially the same results: As shown in Fig. S2(c), the fixation probability calculated using \( P_{\nu}^{\text{LNA}} \) gives only a minute improvement over the results obtained with \( P_{\nu}^{\text{PDMP}} \). The LNA approximation \( P_{\nu}^{\text{LNA}} \) is thus useful to describe the PSD, but the PDMP approximation is sufficient to compute the fixation probability.

S4. SADDLE-POINT CALCULATION OF THE FIXATION PROBABILITY UNDER FAST SWITCHING

In this section we perform a saddle-point approximation to find the fixation probability, \( \phi_\alpha \), in the fast switching regime \( \nu/s \gg 1 \). Rewriting Eq. (6) of the main text in terms of the total population density \( y = N/K_\nu \), and accounting for the normalizaton of the probability distribution, the fixation probability can be written as

\[
\phi_\alpha(\nu) = \frac{\int_0^\infty \nu^{(\nu/s)}(y) \exp \left\{ K_\nu \left[ 1 - x_0 \right] \ln (1 - s) y \right\} dy}{\int_0^\infty \nu^{(\nu/s)}(y) dy} \equiv \frac{\int_0^\infty \exp \left\{ f^{(\nu)}_{\text{num}}(y) \right\} dy}{\int_0^\infty \exp \left\{ f^{(\nu)}_{\text{den}}(y) \right\} dy},
\]

(S22)

where we have defined \( f^{(\nu)}_{\text{den}}(y) = \ln \nu^{(\nu/s)}(y) \), and \( f^{(\nu)}_{\text{num}}(y) = f^{(\nu)}_{\text{den}}(y) + K_\nu \left[ 1 - x_0 \right] \ln (1 - s) y \), and \( \alpha \) denotes either \( r \) (random) or \( p \) (periodic). Evaluating both integrals separately via the saddle point approximation, we obtain

\[
\phi_\alpha(\nu) \approx \sqrt{\frac{\kappa^{(\nu)}_1}{\kappa^{(\nu)}_2}} e^{f^{(\nu)}_{\text{num}}\left( y^{(\nu)}_1 \right) - f^{(\nu)}_{\text{den}}\left( y^{(\nu)}_2 \right)}.
\]

(S23)

Here \( y^{(\nu)}_1 \) and \( y^{(\nu)}_2 \) are the positions of the saddle points of the denominator and numerator, respectively, and satisfy \( (d/dy)f^{(\nu)}_{\text{den}}\left( y^{(\nu)}_1 \right) = 0 \) and \( (d/dy)f^{(\nu)}_{\text{num}}\left( y^{(\nu)}_2 \right) = 0 \). In addition, \( \kappa^{(\nu)}_1 = (d^2/dy^2)f^{(\nu)}_{\text{den}}\left( y^{(\nu)}_1 \right) \) and \( \kappa^{(\nu)}_2 = (d^2/dy^2)f^{(\nu)}_{\text{num}}\left( y^{(\nu)}_2 \right) \) represent the curvatures at the saddle point of the denominator and numerator, respectively.

S4.1. Fast random switching

Here we compute Eq. (S25) in the case of randomly switching environment in the realm of the PDMP approximation, with \( \nu^{(r)} \approx \nu^{\text{PDMP}} \). To compute the denominator of Eq. (S25), with Eq. (S19), we define

\[
f^{(\nu)}_{\text{den}}(y) = \ln \nu^{\text{PDMP}}(y) = -2\nu y + \left[ (1-\delta) \nu - 1 \right] \ln (1 + \gamma - y) + \left[ (1+\delta) \nu - 1 \right] \ln (y - 1 + \gamma).
\]

(S24)

Thus, the saddle point is found at

\[
y^{(r)}_1 \approx \frac{1 - \gamma^2}{1 - \delta^2} \left[ 1 + \frac{\gamma (\delta - \gamma)}{(1 - \delta^2)^2 \nu/s} \left[ 1 + \frac{2\nu \gamma (1 - \gamma) - \delta \gamma}{(1 - \delta^2)^2 \nu/s} \right] \right].
\]

As a result, we find

\[
f^{(\nu)}_{\text{den}}\left( y^{(r)}_1 \right) \approx \frac{(\nu/s)}{\left( 1 + \delta \right) \ln \left[ \frac{\gamma (1+\delta) (1-\gamma)}{(1-\delta^2)^2 \nu/s} \right] + (1 - \delta) \ln \left[ \frac{\gamma (1-\delta) (1+\gamma)}{(1-\delta^2)^2 \nu/s} \right] - 2 \ln \left[ \frac{1 - \gamma^2}{1 - \delta^2} \right]}
\]

\[
+ \ln \left[ \frac{(1 - \delta \gamma)^2}{(1 - \delta \gamma)^2 (1 - \delta^2)^2 \nu/s} \right] + \frac{(\delta - \gamma)^2 (1 - \delta^2)^2 (1 - \delta)^2 \nu/s}{(1 - \delta^2)^2 (1 - \delta)^2 \nu/s},
\]

\[
\kappa^{(\nu)}_1 = \frac{d^2}{dy^2} f^{(\nu)}_{\text{den}}\left( y^{(r)}_1 \right) \approx -2 \frac{(1 - \delta \gamma)^2 \nu/s}{(1 - \delta^2)^2 (1 - \delta)^2 \gamma^2} + \frac{2 (1 - \delta \gamma)^2 (1 + 6\delta \gamma - 2\delta^3 \gamma - 5\gamma^2 - 3\delta^2 (1 - \gamma^2))}{(1 - \delta^2)^2 (1 - \delta)^2 \gamma^2}.\]

(S25)
To compute the numerator of (S23) we define \( f_{\text{num}}^{(r)}(y) = f_{\text{den}}^{(r)}(y) + K_0 \ln(1-s)(1-x_0) \), and find the saddle point at

\[
y_2^{(r)} \simeq \left( \frac{1 - \gamma^2}{1 - \delta \gamma} \right) \left\{ 1 + \frac{\gamma \left[ 2 (1 - \delta \gamma) (\delta - \gamma) + b_\gamma (1 - \gamma^2) (1 - \delta^2) \right]}{2 (1 - \delta \gamma)^3 \nu/s} \right. \\
\left. + \frac{2 - 2 \gamma^2 (2 + \delta^2 - 2 \delta \gamma) - b_\gamma (1 - \gamma^2) (2 \delta - 3 \gamma + \delta^2 \gamma)}{2 (1 - \delta \gamma)^3 \nu/s} \right\},
\]

where \( b = K_0 (1 - x_0) \ln(1-s) \). As a result, we find

\[
f^{(r)}_{\text{num}} \left( y_2^{(r)} \right) \simeq (\nu/s) \left\{ (1 + \delta) \ln \left[ \frac{\gamma (1 + \delta) (1 - \gamma)}{(1 - \delta \gamma)} \right] + (1 - \delta) \ln \left[ \frac{\gamma (1 - \delta) (1 + \gamma)}{(1 - \delta \gamma)} \right] - 2 \ln \left[ \frac{1 - \gamma^2}{1 - \delta \gamma} \right] \right. \\
+ \ln \left[ \frac{(1 - \delta \gamma)^2}{\gamma^2 (1 - \delta^2) (1 - \gamma^2)} \right] + b_\gamma \frac{(1 - \gamma^2)}{1 - \delta \gamma} + \left. \frac{2 (\delta - \gamma) (1 - \delta \gamma) + b_\gamma (1 - \gamma^2) (1 - \delta^2)^2}{4 (1 - \delta^2) (1 - \delta \gamma)^4 \nu/s} \right],
\]

\[
\kappa_2^{(r)} = \frac{d^2}{dy^2} f^{(r)}_{\text{num}} \left( y_2^{(r)} \right) \simeq -\frac{2 (1 - \delta \gamma)^4 \nu/s}{(1 - \delta^2) \gamma^2 (1 - \gamma^2)} - \frac{2 (1 - \delta \gamma) \nu/s}{(1 - \delta^2)^2 (1 - \gamma^2)^2 \gamma^2} \\
\left[ 5 - 3b \right] \gamma^2 + 3b \gamma^4 + \delta^2 (3 + (3 + 4b) \gamma^2 - 4b \gamma^4) - \delta \gamma^2 (2 + b (1 - \gamma^2)) + \delta^3 \gamma (-1 + 3 \gamma^2 - 2b (1 - \gamma^2)) + \delta \gamma (2b (1 - \gamma^2) - 5 (1 + \gamma^2)) - 1. \tag{S26}
\]

### S4.2. Fast periodic switching

Here we compute Eq. (S23) in the case of periodically switching environment using \( P^\nu_s \simeq P^\nu_s^{Kap} \) with Eq. (S16). To compute the denominator of Eq. (S23) we define

\[
f^{(p)}_{\text{den}}(y) = \ln P^\nu_s^{Kap}(y) = K_0 \left[ y - y \ln \left( \frac{K_0}{K} \right) y - \frac{1}{72 \nu^2 s^2} \left( \frac{\gamma}{1 - \gamma^2} \right)^2 \left( 2y - \frac{K}{K_0} \right)^3 \right]. \tag{S27}
\]

Thus, using Eq. (S13), the saddle point is found at \( y_1^{(p)} \simeq A^{-1} \left[ 1 - C/(A^2 \nu^2) \right] \), where \( A \) and \( C \) are given in Sec. 2.2.1. As a result, we find

\[
f^{(p)}_{\text{den}} \left( y_1^{(p)} \right) \simeq \frac{1}{A} \left( 1 - \frac{C}{6A^2 \nu^2} \right), \quad \kappa_1^{(p)} = \frac{d^2}{dy^2} f^{(p)}_{\text{den}} \left( y_1^{(p)} \right) \simeq -A - \frac{5C}{A^2 \nu^2}. \tag{S28}
\]

To compute the numerator of (S23) we define \( f^{(p)}_{\text{num}}(y) = f^{(p)}_{\text{den}}(y) + K_0 \ln(1-s)(1-x_0) \), and find the saddle point at

\[
y_2^{(p)} \simeq A^{-1} (1-s)^{1-x_0} \left[ 1 - C/(A^2 \nu^2) \right] \left[ 2 (1-s)^{1-x_0} - 1 \right]^2.
\]

As a result, we find

\[
f^{(p)}_{\text{num}} \left( y_2^{(p)} \right) \simeq \frac{(1-s)^{1-x_0}}{A} - \frac{C}{6A^2 \nu^2} \left[ 2 (1-s)^{1-x_0} - 1 \right]^3, \]

\[
\kappa_2^{(p)} = \frac{d^2}{dy^2} f^{(p)}_{\text{num}} \left( y_2^{(p)} \right) \simeq -\frac{A}{(1-s)^{1-x_0}} \left[ 1 + \frac{C}{A^2 \nu^2} \left[ 2 (1-s)^{1-x_0} - 1 \right] \left[ 6 (1-s)^{1-x_0} - 1 \right] \right]. \tag{S29}
\]

Thus, for both random and periodic switching (S23) predicts the same fixation probability \( \phi_r = \phi_p \simeq \phi^{(\infty)} = \phi(x_0)|_\nu \), for \( \nu \to \infty \). Yet, the asymptotic convergence to \( \phi^{(\infty)} \) is markedly different [see Eq. (7) in the main text]:

\[
\ln \left( \frac{\phi_\alpha}{\phi^{(\infty)}} \right) = \begin{cases} A_r(\nu/s)^{-1} & \text{for randomly switching environment} \\ A_p(\nu/s)^{-2} & \text{for periodically switching environment, with} \end{cases}
\]
$$A_r = (1 - x_0) \ln (1 - s) K \frac{(1 - \delta^2)^{\gamma^2}}{2(1 - \delta \gamma)^2} \left( 1 + \frac{(1 - x_0) \ln (1 - s) K_0}{2} \right),$$

$$A_p = \frac{K}{72} \left[ 1 - [1 + 2(1 - x_0) \ln (1 - s)]^3 \right] \left( \frac{\gamma}{1 - \gamma \delta} \right)^2. \quad (S30)$$

These show that $\phi_p(\nu)$ approaches $\phi(\infty)$ much faster than $\phi_r(\nu)$ as $\nu$ increases: the convergence towards the fast switching limit is attained much quicker with periodic than random switching, see Figs. 4(a) and S2(c).

### S4.3. Validity of the PDMP approximation to $P_{\nu}^{(r)}(N)$ in the intermediate/fast switching regime

Simulation results show that $P_{\nu}^{PDMP}$ is generally a good approximation of $P_{\nu}^{(r)}$ for a broad range of $\nu$. We now combine the results of Sections S3.2 and S4.1 to assess the theoretical validity of the PDMP approximation, $P_{\nu}^{PDMP}(N)$ given by Eq. (S17), under intermediate/fast switching. This can be done by computing the variance of $P_{\nu}^{PDMP}$, i.e., var($P_{\nu}^{PDMP}(N)$), and by comparing it with $K$, which is the variance of the population size distribution when, in the limit $\nu \to \infty$, it is solely governed by demographic noise. Indeed, when $\nu \to \infty$, the LNA [Eq. (S21)] reduces to a Gaussian of mean and variance $K$, i.e., $P_{\nu \to \infty}^{LNA}(N) \propto e^{-(N-K)^2/(2K)}/\sqrt{2\pi}$. Proceeding as in Sec. S4.1, we compute var($P_{\nu}^{PDMP}(N)$) by performing a saddle-point calculation and find

$$\text{var}(P_{\nu}^{PDMP}(N)) = \int_{K-}^{K+} (N - \langle N \rangle)^2 P_{\nu}^{PDMP}(N) dN = \left( \frac{\gamma K_0}{1 - \gamma \delta} \right)^2 \left( 1 - \delta^2 \right) \frac{1}{2\nu} \text{ when } \nu \gg 1, \quad (S31)$$

with Eq. (S17) and $\langle N \rangle = \int_{K-}^{K+} N P_{\nu}^{PDMP}(N) dN$. This result has been obtained by performing the integral using the saddle-point approximation, as in Sec. S4.1, with $f^{(r)}_{\text{den}}(y) = \ln P_{\nu}^{PDMP}(y)$ as in (S24), $f^{(N\langle N \rangle,r)}_{\text{num}}(y) = f^{(r)}_{\text{den}}(y) + 2 \ln y$ for calculating the mean, and $f^{(N\langle N \rangle,r)}_{\text{num}}(y) = f^{(r)}_{\text{den}}(y) + 2 \ln y$ for calculating the expectation of $N^2$.

According to Eq. (S31), var($P_{\nu}^{PDMP}(N)$) $\gg K$ when $1 \ll \nu \ll K_0$, and in this case the variance stemming from random switching is much larger than the variance caused by demographic fluctuations. However, when $\nu \gg K_0$, the variance of the population size is determined mainly by demographic noise. Hence, $P_{\nu}^{PDMP}$ is an accurate approximation of $P_{\nu}^{(r)}$ in the fast switching regime where $1 \ll \nu \ll K_0$. Yet, environmental noise also dominates over demographic fluctuations when $\nu \gg 1$, see Fig. 2. Therefore, the PDMP approximation gives an accurate description of $P_{\nu}^{(r)}$ in the entire intermediate/fast switching regime $1 \ll \nu \ll K_0$, and is thus broadly applicable when $K_0$ is large.

It is also useful to compute the variance in the case of fast periodic switching, using $P_{\nu}^{Kap}(N)$ given by Eq. (S16). Proceeding as above, we obtain

$$\text{var}(P_{\nu}^{Kap}(N)) = \int_0^\infty (N - \langle N \rangle)^2 P_{\nu}^{Kap}(N) dN = K \left[ 1 + O\left( \frac{1}{\nu^2} \right) \right]. \quad (S32)$$

This means that the variance in the case of fast periodic switching is dominated by demographic noise and scales as $K_0$. Hence, the width of $P_{\nu}^{(p)}$ and $P_{\nu}^{Kap}$ in the fast switching regime is $O(\sqrt{K_0})$. The comparison of Eqs. (S32) and (S31) shows that, under fast switching, in the regime $1 \ll \nu \ll K_0$, the width of $P_{\nu}^{(r)}$ and $P_{\nu}^{PDMP}$, scaling as $K_0/\sqrt{\nu}$, is significantly larger than the width of $P_{\nu}^{(p)}$ and $P_{\nu}^{Kap}$ that scales as $\sqrt{K_0}$. These results also show that, when $1 \ll \nu \ll K_0$, the variance of $P_{\nu}^{(r)}$ and $P_{\nu}^{PDMP}$ decreases as $1/\nu$, whereas that of $P_{\nu}^{(p)}$ and $P_{\nu}^{Kap}$ is almost constant for $\nu \gg 1$. The fact that the variance of $P_{\nu}^{(r)}$ is much larger than that of $P_{\nu}^{(p)}$ explains that the fixation probability varies more steeply (as $\nu$ increases) under periodic switching than in the random case, see main text.

### S5. Further details about Figure 3(d,e): Effect of $s$ and $\delta$ on the Fixation Probability

In the main text, we have seen that under certain conditions, the fixation probability of the $S$ species, $\phi_{\alpha}$, at given $s, \gamma, \delta, K_0, x_0$ is optimal for a nontrivial switching rate $\nu_*^{(s)}$, see Fig. 3(d,e). We also discuss the critical selection intensity below/above which $\phi_{\alpha}(\nu)$ is an increasing/decreasing function under weak switching asymmetry.
S5.1. Region of the parameter space in which $\phi_0(\nu)$ is nonmonotonic

Our starting point is Eq. (6) in the main text which, when plugging the PDMP approximation, reads

$$
\phi_r(\nu) \simeq \int_{K_-}^{K_+} P^{PDMP}_{\nu/s}(N) \phi(x_0)|_N \, dN,
$$

(S33)

FIG. S2: (a) Triangular-like region in the parameter space in which $\phi_0(\nu)$ has a nontrivial maximum at $\nu = \nu^*$ for $s = 0.04, 0.05, 0.06, 0.07, 0.08, 0.09$ (red to blue, left to right) obtained from Eq. (S33). This region, defined by $\gamma > \gamma_c$, $\delta > \delta_c(\gamma, s)$ is delimited by the solid and dashed lines, see text and compare with Fig. 3(e) in the main text. (b) Critical selection intensity $s_c$ as a function of $\delta$ for $\gamma = 0.6, 0.7, 0.8, 0.9$ (red to blue, bottom to top) for $K_0 = 250$ and $x_0 = 0.6$, see text. (c) $\phi_r$ (circles) and $\phi_\nu$ (squares) versus $\nu$ with $(s, K_0, \gamma, x_0) = (0.05, 250, 0.8, 0.6)$, $\delta = 0.7$ (purple) and $\delta = 0.8$ (blue). Symbols are from simulations; coloured solid lines are from Eq. (S33) and dashed lines are based on formula (6) by averaging over Eq. (S21), see text. (d) $\phi_r$ (coloured symbols) and $\phi_\nu$ (black squares) versus $\nu$ for $(s, K_0, x_0) = (0.05, 250, 0.6)$ and $(\gamma, \delta) = (0.9, 0.5)$ (purple/black), $(\gamma, \delta) = (0.8, 0.6)$ (blue/dark gray). Solid lines are from Eq. (S33); dashed lines show $\phi(0,\infty)$ for $\nu \to 0, \infty$.

We now give further details on how to determine from this equation the region of the parameter space of Fig. 3(e) in which $\phi_0(\nu)$ is non-monotonic, and how this region changes when $s$ is increased. Using the diffusion approximation $\phi(x_0)|_N \simeq (e^{-Ns_0} - e^{-Ns_0})/(1 - e^{-Ns_0})$, and Eq. (S17), we compare the PDMP-based approximation of $\phi_r(\nu)$ [Eq. (S33)] for different switching rates (slow, intermediate and fast switching) for a given set ($K_0, s, \gamma, \delta, x_0$), and determine for which of these values $\phi_r$ is maximum.

If $\phi_r(\nu \ll s) > \phi_r(\nu \gg s)$, $\phi_r(\nu \sim s)$, we say that the optimal fixation probability is $\phi_r(0) = \phi(0)$ at slow switching, i.e., $\nu_s^* = 0$. Similarly, if $\phi_r(\nu \gg s) > \phi_r(\nu \ll s)$, $\phi_r(\nu \sim s)$, the optimal fixation probability is $\phi_r(\infty) = \phi(\infty)$, i.e., $\nu_s^* = \infty$, see Fig. 3(a). Otherwise, the $S$ fixation probability is maximum at a non-trivial switching rate $\nu_s^* \sim s$ that Eq. (S33) captures reasonably well. In this case, $\phi_r$ varies non-monotonically with $\nu$, see Fig. 3(d,e). We have performed extensive stochastic simulations of the model’s dynamics and found that this behavior arises in a triangular-like region in the subset of the parameter space where $\gamma$ and $\delta$ exceed some critical values $\gamma_c(s)$ and $\delta_c(\gamma, s)$, see Fig. 3(e). In order to determine the boundary ($\gamma_c(s), \delta_c(\gamma, s)$) of this triangular-like region at fixed $s$ and $K_0$, we have systematically calculated the fixation probability as $\nu$ varies from $10^{-3}$ (proxy for $\nu \ll s$) to 1 (proxy for $\nu \gg s$) for fixed $(\gamma, \delta)$, with $\gamma \gtrsim 0.7$, and $\delta \gtrsim 0.2$. For each pair ($\gamma, \delta$) we have then found the value of $\nu$ for which it attains its maximum and store it in a matrix. In practice, the diagonal part of the boundary is then found by keeping $\gamma$ fixed and increasing $\delta$ until we find the first entry of the matrix for which $10^{-3} < \nu_s^* < 1$. This determines $\delta_c(\gamma, s)$. The left hand side of the boundary, $\gamma_c(s)$ is found by finding the largest value of $\gamma$ such that $\nu_s^* = 1$ or $\nu_s^* = 10^{-3}$ for all $\delta$. Predictions of Eq. (S33) are in good agreement with simulation results which confirm that $\phi_0(\nu)$ has a nontrivial maximum at
As explained in the main text, it is useful to determine the critical selection intensity \( s_c \), which is reported in Fig. S2(b), where we find that \( s_c \) decreases with \( \delta \) and increases with \( \gamma \). When \( s < s_c \), \( \phi(0) < \phi(\infty) \) and \( \phi(0) > \phi(\infty) \) if \( s > s_c \). This allows us to determine the monotonic behavior of \( \phi_\alpha(\nu) \) under weak switching asymmetry \( (|\delta| < \delta_c) \): When \( s < s_c \), \( \phi_\alpha(\nu) \) is an increasing function of \( \nu \), while it decreases with \( \nu \) if \( s > s_c \) (at \( s, \gamma, \delta \) given). In the examples of Fig. S2(d) that \( s_c \approx 0.06 \) for \( (\gamma, \delta) = (0.9, 0.5) \), \( s_c \approx 0.03 \) for \( (\gamma, \delta) = (0.8, 0.6) \), and \( s_c \approx 0.095 \) for \( (\gamma, \delta) = (0.9, -0.5) \). When \( s = 0.05 \), this corresponds to \( \phi_\alpha(\nu) \) being an increasing function of \( \nu \) for \( (\gamma, \delta) = (0.9, 0.5) \) and \( (\gamma, \delta) = (0.9, -0.5) \), and decreasing with \( \nu \) in the case \( (\gamma, \delta) = (0.8, 0.6) \), which is in accord with simulation results of Fig. S2(d). In the regime \( \gamma > \gamma_c(s) \) and \( \delta > \delta_c(\gamma, s) \) where \( \phi_\alpha(\nu) \) is non-monotonic, we can determine that \( \phi_\alpha(\nu) \) increases steeper at slow/intermediate switching if \( s < s_c \) while it is the opposite when \( s > s_c \). These results hold for both random and periodic switching since \( \phi_\alpha(\nu) \) essentially coincides with \( \phi(0) \) and \( \phi(\infty) \) in slow/fast switching, respectively, both for random and periodic switching.

S5.3. Effective selection intensity under fast switching

As discussed in the main text, see also Sec. S4, under fast random and periodic switching \( \phi_\alpha(\nu) \approx \phi(\infty) = \phi(\infty)|_K \), with \( \phi(\infty) = e^{\gamma t/2} \) and \( m = 2K(1-x_0)\ln(1-s) = 2(1-\gamma^2)/(1-\gamma\delta)K_0(1-x_0)\ln(1-s) \), to leading order in \( 1/\nu \). When \( 1/K_0 \ll s \ll 1/\sqrt{K_0} \) and \( \gamma = O(1) \), the above expression simplifies: \( \phi(\infty) \approx e^{-K_0(1-x_0)} = e^{-s(1-\gamma^2)/(1-\gamma\delta)K_0(1-x_0)} \). Hence, in this regime, under fast random and periodic switching, the \( S \) fixation probability is the same as in a population subject to a constant carrying capacity \( K_0 \) under a rescaled selection intensity \( s \rightarrow s' = s(1-\gamma^2)/(1-\gamma\delta) \). This result yields the following remarkably simple and enlightening interpretation: In the above regime, the effect of environmental variability, when \( \delta < \gamma \), is to effectively reduce the selection intensity with respect to the static environment, yielding \( \phi_\alpha > \phi(x_0)|_{K_0} \) under a selection intensity \( s \). Similarly, there is an effective increase of selection intensity \( (s' > s) \) when \( \delta > \gamma \) resulting in \( \phi_\alpha < \phi(x_0)|_{K_0} \).

S5.4. Duty cycle and general effect of \( \delta \) on \( \phi_\alpha \)

The parameter \( \delta \) measures the asymmetry in the switching rate, and can be used to define the “duty cycle” as \((1+\delta)/2\) in the case of periodic switching between \( K_+ \) and \( K_- \) with period \( T = (1/\nu_-) + (1/\nu_+) \). The duty cycle gives the fraction \((1/\nu_+)/T\) of one period spent in the environmental state \( \xi = 1 \). Clearly, when \( \delta > 0 \), the population spends more time in the environmental state \( \xi = +1 \) (with \( K = K_+ \)) than in the state \( \xi = -1 \) (with \( K = K_- \)). Since \( s > 0 \), species \( S \) has a selective disadvantage with respect to strain \( F \) and \( \phi_\alpha \) is therefore a decreasing function of \( \delta \) when all the other parameters are fixed, see Fig. S2(c,d).

S6. MEAN FIXATION TIME AND AVERAGE NUMBER OF SWITCHES

In addition to the fixation probability, we have also computed the MFT, \( T^{(\alpha)}(x_0) \) – the unconditional mean time until the fixation of either species \( S \) or \( F \), starting from a initial fraction \( x_0 \) of individuals of type \( S \). As in the
case $\delta = 0$, $T^{(\alpha)}(x_0)$ is obtained by averaging the unconditional MFT, $T(x_0)|_N$, obtained in a population of constant size $N$ over $P^{(\alpha)}_{\nu/s}(N)$ with a rescaled switching rate $\nu \rightarrow \nu/s$ \cite{39, 40}. In the limits of slow and fast switching, we have $T^{(\alpha)}(x_0) = [(1 + \delta)T(x_0)|_{K^+} + (1 - \delta)T(x_0)|_{K^-}]2$ when $\nu/s \ll 1$ and $T^{(\alpha)}(x_0) = T(x_0)|_K$ when $\nu/s \gg 1$, see Fig. S3(a). When $1/K_0 \ll s \ll 1$, $T(x_0)|_N \sim O(1/s)$ \cite{43, 57}, and the MFT under random switching also scales as $1/s$, i.e., $T^{(\alpha)}(x_0) = O(1/s)$; this result is evident since $x$ deterministically relaxes on a time scale $O(1/s)$. As the average population size $\langle N \rangle$ decreases with $\nu$, see Fig. S3(b), environmental variability reduces the subleading prefactor of $T^{(\alpha)}(x_0)$ \cite{40}. As a consequence, on average the population experiences $O(\nu/s)$ switches prior to fixation when $1/K_0 \ll s \ll 1$. Fig. S3(c) confirms that in this regime the average number of switches prior to fixation scales as $1/s$ and increases linearly with $\nu$ to leading order. Since the PSD greatly varies when $\nu$ and $\delta$ change, see Figs. (2) and (S1), the fact that the average number of switches increases linearly with $\nu$ shows that it is essentially independent of the population size and supports the rescaling $\nu \rightarrow \nu/s$ in the approximations of Eqs. (6) and (S33).

S7. ECO-EVOLUTIONARY DYNAMICS & FIXATION PROBABILITY IN A PUBLIC GOOD SCENARIO

The model introduced in the main text describes the competition for resources of the slow and fast growing strains $S$ and $F$ without assuming any explicit interactions between them. Yet, the population size growth often depends on its composition; e.g. one strain may produce public goods, which generate feedback eco-evolutionary loops yielding rich complex behaviors. As an example, we now show that when the slow species is a public good (PG) producer, the fixation probability under random switching exhibits complex behavior reported in Fig. S4(b,c) characterized by a very different dependence on $\nu$. Below, we explain these results by extending the analysis carried out in the main text.

A simple way to describe a PG scenario is to consider that the slow strain produces PG that benefits the entire population \cite{20, 45, 55}. This can be modeled by a birth-death process in which the birth rates of both strains are multiplied by a global growth rate $g(x) = 1 + bx$, with $b \geq 0$ \cite{20, 45, 55}. Here, population size and composition change according to the continuous-time birth-death process, as in Eq. (1): $N_{S/F} \xrightarrow{T_{S/F}} N_{S/F} - 1$, and $N_{S/F} \xrightarrow{T_{S/F}} N_{S/F} + 1$, with modified transition rates $T^S = g(x)((1-s)/f)N_S$, $T^F = 2(x)N_F$, $T^S = \frac{N_s}{K(t)}N_S$, $T^F = \frac{N_f}{K(t)}N_F$, where $b = O(1)$ and $K(t)$ is given by Eq. (2) in the main text. MEs (S2) and (S3), with the above rates, fully describe the population’s eco-evolutionary dynamics for random and periodic switching, respectively.

Proceeding as in Sec. S1.1 (see also \cite{40, 41}), when demographic noise is neglected and the only source of randomness stems from the randomly switching carrying capacity, the population dynamics is described by \cite{39, 40}

$$\frac{dx}{dt} = -sg(x)x(1-x) \quad \text{and} \quad \frac{dN}{dt} = N \left[ g(x) - \frac{N}{K} \left( \frac{1 - \gamma \xi(t)}{1 - \gamma \delta} \right) \right].$$

(S34)
FIG. S4: (a) Effective parameter $q$ versus $s$ for $\delta = -0.5, 0.5$ (black, red) and $s = 0.02, 0.05$ (squares, circles). Dependence of $q$ on $b$ is approximately linear while $q$ depends weakly on $\delta$ and $s$ (solid lines are eyeguides). (b,c,d,e) $\phi$ versus $\nu$ for $(K_0, \gamma, s, \delta, x_0) = (250, 0.9, 0.04, 0.6, 0.6)$ in (b,d) and $(250, 0.9, 0.05, 0.7, 0.6)$ in (c,e). Here (b,c) and (d,e) show results for random and periodic switching, respectively, with the same parameters. In (b,c,d,e) $b \approx (0, 0.1, 0.3, 0.5, 1)$ from red to blue (top to bottom), open circles are simulation results and solid lines are from (S36). In (b,d), $\phi_{\text{PDMP}}(\nu)$ is an increasing function of $\nu$ at low values of $b$, and varies nonmonotonically with $\nu$ for intermediate $b$'s. In (c,e), $\phi_{\text{PDMP}}(\nu)$ is a nonmonotonic function of $\nu$ at low $b$'s and becomes a decreasing function of $\nu$ as $b$ increases.

with $K \equiv K_0(1 - \gamma^2)/(1 - \gamma \delta)$. In this PG scenario, $N$ and $x$ are explicitly coupled and their interplay yields a form of eco-evolutionary dynamics. Thus, further analytical progress can be made by using an effective theory [39, 40]. Guided by the fact that dynamics of the model subject to a constant carrying capacity is well described in terms of a population of an effective size, as in the case $\delta = 0$ [39, 40], we introduce a suitable parameter $q$ (with $0 \leq q \leq b$) and replace $g(x)$ by $1 + q$ in Eq. (S34). This decouples $N$ and $x$, and one can perform a similar PDMP-based approximation as before, yielding

$$P_{\nu, q}^{\text{PDMP}}(N) \propto \frac{1}{N^2} \left[ \left( \frac{(1 + q)K_+}{N} - 1 \right)^{\nu/(1+q) - 1} \left( 1 - \frac{(1 + q)K_+}{N} - 1 \right)^{\nu/(1+q) - 1} \right],$$  

(S35)

where we have omitted the normalization constant. As in Refs. [39, 40], the parameter $q$ is obtained by matching the simulation results for the $S$ fixation probability in the fast switching limit (i.e., when $\nu/s \gg 1$) with $\phi(x_0)(1 + q)K_+$. Results reported in Fig. S4(a), obtained using the diffusion approximation $\phi(x_0)(1 + q)K_+ \simeq (e^{-(1+q)K_+x_0} - e^{-(1+q)K_+})/(1 - e^{-(1+q)K_+})$, show that $q = q(b)$ increases almost linearly with $b$, and depends only weakly on $s$ and $\delta$, with $q(0) = 0$ when $b = 0$. From $P_{\nu, q}^{\text{PDMP}}$ it is clear that the effect of increasing $b$, and therefore the effective parameter $g(x)$, results in effectively increasing the carrying capacity $K_+ \to (1 + q(b))K_+$ and reducing the switching rates $\nu_+ \to \nu_+/(1 + q) = \nu/(1 + \delta)/(1 + q)$. Proceeding as in the case $b = q = 0$ and $\delta = 0$ [39, 40], the fixation probability in the realm of this effective theory is obtained by averaging $\phi(s, x_0)|_N$ over the distribution in Eq. (S35) with rescaled average switching rate $\nu \to \nu/s$ [72]. Furthermore, by changing the variable of integration to $N' = N/(1 + q)$ we find that this is equivalent to rescaling the selection strength to $s_{\text{eff}} = (1 + q) s$ in the model without a public good

$$\phi_{\text{PDMP}}(\nu, q) = \int_{(1+q)K_+}^{(1+q)K_-} \phi(s, x_0)|_N P_{\nu, q}^{\text{PDMP}}(N) \, dN = \int_{K_-}^{K_+} \phi(s_{\text{eff}}, x_0)|_{N'} P_{\nu, q_{\text{eff}}}^{\text{PDMP}}(N') \, dN',$$

(S36)

where we have used $\phi(s, x_0)|_N \simeq (e^{-(N'+(1-x_0)} - e^{-N'd})/(1 - e^{-N'})$, and from the first to the second integral, we have made the change of variable $N \to N' = N/(1 + q)$. This transforms the expression of $\phi_{\text{PDMP}}(\nu, q)$ to the fixation
probability in the absence of PG but under an effective selection intensity $s_{\text{eff}} = (1 + q)s$. According to Eq. \( \text{(S36)} \) and the behaviour of $\phi_r^{PG}(\nu, q)$ when $\nu/s \ll 1$ and $\nu/s \gg 1$, the effect of increasing $b$ results in raising the value of the corresponding value of $q$, see Fig. \( \text{S2(a)} \), which in turn results in a carrying capacity switching between $(1 + q(b))K_\pm$. As in the case $\delta = 0$, the effect of raising $b$ on the $S$ fixation probability is hence equivalent to increasing the selection intensity as $s \rightarrow s_{\text{eff}} = (1 + q(b))s$ with respect to the model without PG production. This results in $\phi_r^{PG}$ decaying approximately exponentially with $b$.\cite{40}.

Since Eq. \( \text{(S36)} \) is an approximation valid over a broad range of frequencies $\nu$, we can understand qualitatively the effect of PG production on the fixation probability by considering that raising $b$ at fixed $s$ results in an effective selection intensity $s_{\text{eff}} = (1 + q(b))s$. With this and Fig. \( \text{S2(a)} \) in mind, we can understand how raising $b$ changes the diagram of Fig. \( \text{S2(a)} \): As $b$ is increased, the triangular-like region is squashed since $\gamma_c$ increases under the effect of $s \rightarrow s_{\text{eff}} = (1 + q(b))s$. This allows us to qualitatively explain how the fixation probability $\phi_r^{PG}$ varies with $\nu$ under intermediate switching at $\gamma, \delta, s$ fixed. In the case of Fig. \( \text{S4(b)} \), $\delta < \delta_c$ at low $b$ and therefore $\phi_r^{PG}(\nu)$ increases monotonically; then as $\gamma_c$ increases together with $b$, $(\gamma, \delta)$ enter the triangular-shaped region (i.e., $\gamma > \gamma_c, \delta > \delta_c$) of Fig. \( \text{S2(a)} \) where $\phi_r^{PG}(\nu)$ varies non-monotonically with $\nu$. In the example of Fig. \( \text{S4(c)} \), $\gamma > \gamma_c$ and $\delta > \delta_c$ at low $b$ implying that $\phi_r^{PG}(\nu)$ is a nonmonotonic function of $\nu$; then $\gamma_c$ increases along with $b$ and attains a value such that $\gamma < \gamma_c$ with $\delta > \delta_c$, and in this case $\phi_r^{PG}(\nu)$ decreases monotonically with $\nu$. These are examples of the rich and complex behavior that eco-evolutionary loops can generate. The results discussed in this section have focused on the case of random switching but, as in the scenario without PG production, we have obtained a similar qualitative behavior also with periodic switching, as can be seen in Fig. \( \text{S4(d,e)} \).