

Supplemental Material for

Evolution of a Fluctuating Population in a Randomly Switching Environment

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In this Supplemental Material, we provide some technical details and supplementary information in support of the results discussed in the main text, as well as additional ones concerning the population's mean fixation time and its long-time distribution. We also comment the content of electronically available Videos [1] that illustrate the population dynamics in the pure resource competition and public good scenarios. In what follows, unless otherwise stated, the notation is the same as in the main text and the equations and figures refer to those therein. (As in the main text, unless stated otherwise, below we tacitly assume $x_0 = 1/2$.)

1 Derivation of Equations (1,2) and (4)

As explained in the main text, the population dynamics is governed by multivariate birth-death process in which at each time increment an individual of species $\alpha \in \{S, F\}$ is picked for reproduction, $N_\alpha \rightarrow N_\alpha + 1$, with transition rate $\mathcal{T}_\alpha^+ = T_\alpha^+ N_\alpha = g(x) f_\alpha N_\alpha / \bar{f}$ or death, $N_\alpha \rightarrow N_\alpha - 1$, with transition rate $\mathcal{T}_\alpha^- = T_\alpha^- N_\alpha = (N/K) N_\alpha$, or the carrying capacity is switched, $K_+ \leftrightarrow K_-$, with rate ν . When internal noise is neglected, N and x evolve according to the mean-field rate equations

$$\begin{aligned}\dot{N} &= \sum_{\alpha=S,F} (\mathcal{T}_\alpha^+ - \mathcal{T}_\alpha^-) = N \left(g(x) - \frac{N}{K} \right), \\ \dot{x} &= \frac{\mathcal{T}_S^+ - \mathcal{T}_S^-}{N} - x \frac{\dot{N}}{N} = -sg(x) \frac{x(1-x)}{1-sx},\end{aligned}$$

where we have used $f_F = 1$, $f_S = 1 - s$ and $\bar{f} = 1 - sx$. These equations coincide with (1) and (2) and, when the carrying capacity K is constant, they provide a suitable description of the ecological and evolutionary (composition). The deterministic description of the population dynamics in terms of (1) and (2) is valid only in the absence of internal and external noise.

When the carrying capacity randomly switches according to $K(t) = \frac{1}{2} [(K_+ + K_-) + \xi(t)(K_+ - K_-)]$, where $\xi \in \{-1, +1\}$ is the dichotomous noise defined in the main text, the equation for N becomes the following stochastic differential equation obtained by substituting $K(t)$ into (1) and using $\xi^2 = 1$:

$$\begin{aligned}\dot{N} &= N \left(g(x) - \frac{2N}{K_+ + K_- + \xi(t)(K_+ - K_-)} \right) = N \left(g(x) - \frac{N}{2K_+K_-} [K_+ + K_- - \xi(t)(K_+ - K_-)] \right) \\ &= N \left(g(x) - \frac{N}{\mathcal{K}} + \xi N \left\{ \frac{K_+ + K_-}{2K_+K_-} - \frac{2K_-}{2K_+K_-} \right\} \right) = N \left(g(x) - \frac{N}{\mathcal{K}} + \xi \frac{N(K_+ - \mathcal{K})}{\mathcal{K}K_+} \right),\end{aligned}$$

where $\mathcal{K} = 2K_+K_-/(K_+ + K_-)$. This stochastic differential equation coincides with (4) and, together with (2), defines a piecewise deterministic Markov process (PDMP) [2, 3, 4] describing the population dynamics when the sole form of randomness is the random switching of the carrying capacity (internal noise is neglected).

2 Fixation probability under random switching: Arguments underpinning formula (6) and (7) and their properties

We have studied the fixation probability ϕ that, starting with a fraction x_0 of individuals of the slow type S , the entire population eventually consists of $N(t)$ individuals of species S . The fixation of species F occurs with the complementary probability $\tilde{\phi} = 1 - \phi$. We have investigated the joint effect of external (dichotomous) and internal

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(demographic) noise on these fixation probabilities with help of Eqs. (6) and (7) when $K_- \gg 1, 0 < s \ll 1$ and $\nu > 0$, and by comparing the predictions of these formula with the results of stochastic simulations carried out using the Gillespie algorithm [5] which *exactly* simulates the master equation.

2.1 Physical arguments underpinning formula (6) and (7) and their corroboration

Formula (6) and (7) are assumed forms for the fixation probability ϕ of the slow species S when $0 < s \ll 1$ and $K_- \gg 1$. These expressions are based on a series of physical considerations that are fully corroborated by stochastic simulations of the underlying individual-based population dynamics. At its core, the rationale behind (6) is rooted in the timescale separation between N and x and on scaling arguments. For the sake of concreteness, here we first focus on the case of pure resource competition ($b = 0$) and present the physical arguments underpinning Eq. (6):

- The condition $0 < s \ll 1$ ensures that there is a timescale separation between the evolutionary and ecological dynamics. In fact, as shown in the Videos 1-3 [1], x evolves on a much slower timescale than N when $0 < s \ll 1$: x relaxes in a time of order $1/s$ while N is at quasi-stationarity after a time of order 1. The condition $K_- \gg 1$ ensures that the evolution of the population size is chiefly driven by random switching and is well described by the PDMP (4) that neglects the effects of demographic noise that are marginal when $K_- \gg 1$ (see also Sec. 3 below).
- Due to the timescale separation, when fixation occurs, typically after a time of order $1/s$ (see Fig. S3), N can be considered to be in the stationary state of the PDMP (4) whose probability density function (PDF) has support $[K_-, K_+]$.
- The evolution of x is much slower than the dynamics of N . The population size is therefore able to span much of its quasi-stationary distribution before fixation. This suggests to (approximately) compute ϕ by averaging $\phi|_N$, which is the S fixation probability in a fitness-dependent Moran model of constant population size N (see main text), over the stationary PDF of the underlying PDMP that captures the main features of long-time dynamics of N .
- Since x evolves on a timescale $1/s$ times slower than N , when $1/\nu$ (mean time between two switches) is much shorter than x 's relaxation time, the population composition changes by $1/N$ while N has already typically experienced many switches. Hence, when $\nu \gg s$, the external noise self averages on the timescale of the relaxation of x even if N experiences large excursions (e.g., from $N \approx K_{\pm}$ to $N \approx K_{\mp}$ as in the case of Fig. 3(c)): Hence, x changes by $1/N$ while the population size N appears to fluctuate about a characteristic value. It is therefore necessary to rescale the switching rate $\nu \rightarrow \nu/s$ in averaging $\phi|_N$ over the stationary PDF of Eq. (4) in order to compute the fixation probability ϕ . The rescaling $\nu \rightarrow \nu/s$ reflects the fact that $K(t)$ experiences on average ν/s switches prior to fixation (while x relaxes). In other words, this means that in this context the extent to which the environmental noise self-averages relative to the typical relaxation time of x determines whether the environment changes “fast” or “slowly”.
- With this rescaling, we obtain Eq. (6): $\phi \simeq \int_{K_-}^{K_+} \phi|_N p_{\nu/s}^*(N) dN$, where the integral over N spans $[K_-, K_+]$ which is the support of $p_{\nu/s}^*(N)$ given by Eq. (5). In Eq. (6), $\phi|_N$ accounts for internal noise in a population of size N while $p_{\nu/s}^*(N)$ captures the effect of the environmental noise on the (quasi-)stationarity distribution of N in terms of the PDMP (4).
- In the fast and slow switching regimes, the fixation probability ϕ can be computed directly from the properties of the fitness-dependent Moran model. In fact, when $\nu \rightarrow \infty$ (very fast switching), the dichotomous noise self-averages ($\xi \rightarrow \langle \xi \rangle = 0$ in Eq. (4)) and the population readily attains the effective size $N \simeq \mathcal{K} \gg 1$. The internal evolution thus mirrors that of a population of constant size \mathcal{K} obeying a fitness-dependent Moran process [6, 7, 8]. In this case, if the initial fraction of S individuals is x_0 , we have $\phi \xrightarrow{\nu \rightarrow \infty} \phi^{(\infty)} = \phi|_{\mathcal{K}} = (e^{-\mathcal{K}s(1-x_0)} - e^{-\mathcal{K}s}) / (1 - e^{-\mathcal{K}s})$ [7], see main text. Similarly, when $\nu \rightarrow 0$ (very slow switching), the population is equally likely to be locked in either of the environmental state $\xi = -1$ (where $N = K_-$) or $\xi = +1$ (where $N = K_+$) and from the properties of the fitness-dependent Moran model in this case the fixation probability is $\phi \xrightarrow{\nu \rightarrow 0} \phi^{(0)} = (\phi|_{K_-} + \phi|_{K_+})/2$.

- The stationary PDF $p_{\nu/s}^*(N)$ in Eq. (6) accounts for the fact that when $\nu > s$ there are typically many switches prior to fixation, and environmental noise essentially self-averages when $\nu \gg s$ and a large number of switches occur. In fact, Eq. (6) correctly reproduces the fixation probability under fast and slow switching: it predicts $\phi \simeq \phi^{(\infty)}$ when $\nu/s \gg 1$ and $\phi \simeq \phi^{(0)}$ when $\nu/s \ll 1$, see Figs. 2(a) and S1.
- The stationary PDF $p_{\nu/s}^*(N)$ is unimodal with a peak at $N \approx \mathcal{K}$ when $\nu > s$, and is bimodal with peaks about $N = K_{\pm}$ when $\nu < s$, see Fig. 3 and Videos 4 and 5. This suggests that in the regime of intermediate switching rate, shown as shaded areas in Fig. S1, the fixation probability interpolates between $\phi^{(0)}$ and $\phi^{(\infty)}$, and we expect that $\phi \approx \phi^{(\infty)}$ over a broad range of values of ν since $s \ll 1$ and $\nu/s \gg 1$ is always satisfied when ν is of order 1.

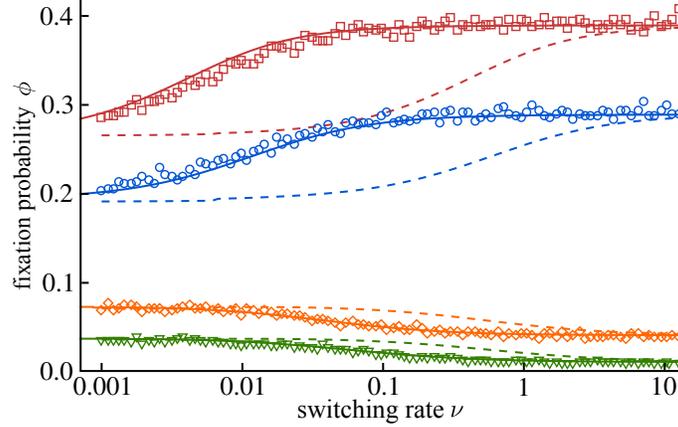


Figure S1: (*Color online*). Fixation probability ϕ as function of ν for different values of s in the pure competition case ($b = 0$). Here, $(K_+, K_-) = (450, 50)$. Symbols denote the results of stochastic simulations for different values of s : $s = 0.01$ (\square , red/dark gray), $s = 0.02$ (\circ , blue/black), $s = 0.07$ (\diamond , orange/gray) and $s = 0.1$ (∇ , green/light gray), from top to bottom. Solid lines denote the corresponding predictions of Eq. (6) and dashed lines represent the predictions of $\int_{K_-}^{K_+} \phi|_N p_{\nu}^*(N) dN$, obtained by averaging $\phi|_N$ over (5) *without* rescaling the switching rate ν , see text. The rescaling of the switching rate into ν/s in Eq. (6) reveals that ϕ is a scaling function of ν/s . In fact, without rescaling the switching rate, the predictions (dashed lines) agree with stochastic simulations only in the regimes of very large ν (fast switching) or very low ν (slow switching); whereas the predictions of Eq. (6) agree with simulations over four orders of magnitude. Hence, Eq. (6) with the average over the PDF (5) with rescaled switching rate $\nu \rightarrow \nu/s$ provides accurate predictions in the intermediate switching regime that separates the slow ($\nu/s \ll 1$) and fast ($\nu/s \gg 1$) switching regimes, see text.

At this point, it is worth emphasizing that the assumed form Eq.(6) has been proposed *without making any use of fitting parameters and does not rely on any input from stochastic simulations*, but only on the basis of the above physical considerations. Stochastic simulations have been used to validate the form of (6) by corroborating its predictions. In fact, a pragmatic and efficient way to assess the validity/accuracy of (6) is to systematically compare its predictions with results of extensive stochastic simulations of system's dynamics based on the Gillespie algorithm (typically sampling over 10^4 to 10^5 realizations). The form of Eq. (6) and the above considerations are thus supported by the following evidence:

- As shown in the supporting Videos 1-3 [1], stochastic simulations fully confirm that x always evolves much slower than N when $s \ll 1$, and that a timescale separation occurs when $b = 0$. Figs 2-4, as well as the supporting Videos 4-5 also confirm that about the time of fixation (and after fixation has occurred), the evolution of N is well described by the underlying PDMP when $K_- \gg 1$. In fact, except for the population collapse arising after an enormous, unobservable time, demographic noise has only a marginal effect on the (quasi-)stationary distribution of N .
- Stochastic simulations mirroring the predictions of the system's master equation fully confirm that Eq. (6) correctly predicts the expected behavior at fast and slow switching rate, with $\phi \simeq \phi^{(\infty)}$ when $\nu/s \gg 1$ and

$\phi \simeq \phi^{(0)}$ when $\nu/s \ll 1$. Furthermore, stochastic simulations show that the predictions of Eq. (6) correctly reproduces the nontrivial ν -dependence of ϕ , see Figs. 2(a) and S1, and agree remarkably well with simulation results also in the regime of intermediate switching rate.

The remarkable agreement between the predictions of Eq.(6) and stochastic simulations results has been confirmed for different values of s (namely $s = 0.01, 0.02, 0.07, 0.1$), and in all cases we have found an agreement within a few percent. More specifically, by a systematic comparison with simulations, we have estimated the mean square displacement of the predictions of Eq. (6) from the simulation results to be within 1.5% to 9% for the results of Fig. S1, with an accuracy that increases when s is lowered: In the tested datasets, the mean error ranges from about 1.5% when $s = 0.01$ to about 9% when $s = 0.1$ and $(K_-, K_+) = (50, 450)$ [11]. The fact that the accuracy of (6) improves when s is lowered stems from the fact that Eq. (6) is built on assuming a timescale separation between N and x , which is the more pronounced the lower s .

- Gillespie stochastic simulations confirm that rescaling $\nu \rightarrow \nu/s$ is necessary to correctly predict the fixation probability on a broad spectrum of ν/s values. This is illustrated in Fig. S1. When we compare the predictions of Eq. (6), obtained by averaging over the PDF (5) with the rescaled switching rate ν/s , against stochastic simulations for different values of s we find an excellent agreement over the entire range of ν values (spanning four orders of magnitude, from $\nu \sim 10^{-3}$ to $\nu \sim 10$) On the other hand, the predictions of $\int_{K_-}^{K_+} \phi|_N p_\nu^*(N) dN$, in which the switching rate has not been rescaled, are shown to be at odds with the results of stochastic simulations when $0.01 \lesssim \nu \lesssim 1$ which includes intermediate switching regime (the agreement is restricted to a limited range of very large/small values of ν/s corresponding to the very fast/slow switching regimes).

In summary, the results reported in Figs. 2(a) and S1 show that the predictions of Eq. (6) are in excellent agreement with the outcome of the system's Gillespie simulations (mirroring the dynamics described by the master equation) over a broad range of values of ν/s values. This confirms that Eq. (6) is indeed a good assumed expression (or, by a slight abuse of language, a suitable "Ansatz") for the actual fixation probability. The difference between the predictions of (6) and the corresponding simulation results can be estimated numerically, but for the purpose of our discussion here, it suffices to notice that an agreement within a few percent is found over the broad range of ν/s values tested. Further technical details about the accuracy of (6) will be investigated elsewhere [11].

The physical considerations leading to Eq. (6) when $b = 0$ also lead to Eq. (7) in the public good scenario with $b > 0$. However, since Eqs. (2) and (4) for N and x are coupled in this case, we use a constant effective parameter $q \geq 0$ in our analysis. As explained in the main text (see also below), this parameter is determined by matching simulation results. In fact, when $b > 0$, the effective parameter q is introduced by considering the auxiliary stochastic differential equation obtained by substituting $g = 1 + q$ in Eq. (4), see Sec. 1, which yields

$$\frac{\dot{N}}{N} = 1 + q - \frac{N}{K} = 1 + q - \frac{N}{\mathcal{K}} + \xi \frac{N(K_+ - \mathcal{K})}{\mathcal{K}K_+}. \quad (\text{S1})$$

This equation is decoupled from the rate equation (2) for x and corresponds to a PDMP [2, 4], describing how the size of an *effective* population evolves under the sole effect of the environmental noise. This PDMP is characterized by a probability $p_{\nu,q}^\pm(N, t) = p_{\nu,q}(N, \xi = \pm 1, t)$ to be in state $\{N, \xi\}$ at time t for q given, where

$$\frac{\partial}{\partial t} p_{\nu,q}^\pm(N, t) = -\frac{\partial}{\partial N} \left[N \left(1 + q - \frac{N}{\mathcal{K}} \right) p_{\nu,q}^\pm(N, t) \right] - \nu [p_{\nu,q}^\mp(N, t) - p_{\nu,q}^\pm(N, t)].$$

By assuming that the probability current is zero at $N = (1 + q)K_\pm$ (natural boundary conditions [4]) and $\nu > 0$, the stationary marginal probability density function $p_{\nu,q}^*(N) = \lim_{t \rightarrow \infty} (p_{\nu,q}^+(N, t) + p_{\nu,q}^-(N, t))$ of (S1) is given by [2, 4, 9]

$$p_{\nu,q}^*(N) = \frac{\mathcal{Z}_{\nu,q}}{N^2} \left[\frac{\{(1 + q)K_+ - N\} \{N - (1 + q)K_-\}}{N^2} \right]^{\frac{\nu}{1+q}-1}, \quad (\text{S2})$$

where $\mathcal{Z}_{\nu,q}$ is the normalization constant, $(1 + q)K_\pm$ are the effective carrying capacities, whose harmonic mean is $(1 + q)\mathcal{K}$, and $[(1 + q)K_-, (1 + q)K_+]$ is the support of $p_{\nu,q}^*$.

To determine the parameter $0 \leq q \leq b$, we consider the limit $\nu \rightarrow \infty$. In such a regime, the environmental noise switches very rapidly and self-averages, and Eq. (S1) is thus characterized by an effective population size $N =$

$(1+q)\mathcal{K}$. The corresponding fixation probability of species S is thus $\phi|_{(1+q)\mathcal{K}}$. We then vary q in order to match $\phi|_{(1+q)\mathcal{K}}$ with the fixation probability obtained in our simulations for $\nu \gg 1$ [10].

In the realm of this effective theory, we can use this q to determine $p_{\nu,q}^*(N)$ given by (S2). Then, as we did to obtain Eq.(6), an expression ϕ_q fixation probability of S is obtained by averaging $\phi|_N$ over (S2) with a rescaled switching rate $\nu \rightarrow \nu/s$. This yields Eq. (7) for ϕ_q whose expression has been used in Figs. 4(b)-4(d) in lieu of ϕ , see also Sec. 4 below. It is worth noting that in the realm of this effective theory, the parameter q accounts for the correlations of the dynamics of x and N .

By setting $q = b > 0$ in (S2), we can obtain the (marginal) PDF $p_{\nu,b}^*(N)$ conditioned to the fixation of species S (but unconditioned of whether $\xi = \pm 1$) in the public good scenario. Similarly, by setting $q = 0$ in (S2), we obtain $p_{\nu,0}^*(N) = p_{\nu}^*(N)$ which coincides with (5) and is the marginal PDF conditioned to the fixation of F (but unconditioned of $\xi = \pm 1$) in the public good scenario and the marginal PDF in the pure resource scenario. In the latter case, $p_{\nu}^*(N)$ is used to obtain the expression (6) for the fixation probability ϕ .

2.2 Properties of formula (6) and (7)

It is worth noting that formula (6) and (7) explicitly reflect the coupling between internal and external noise.

As discussed above, Eq. (6) provides an excellent approximation of the fixation probability of S for all the values of $\nu > 0$, when $K_- \gg 1$. Moreover, it captures the fact that external and internal noise can jointly significantly enhance the fixation probability of the slow type with the respect to its counterpart in a population of constant size $\langle K \rangle = (K_+ + K_-)/2 \gg 1$ subject to non-random environment, where this probability is exponentially small ($\phi|_{\langle K \rangle} \approx e^{-\langle K \rangle s/2}$ when $x_0 = 1/2$ and $\langle K \rangle s \gg 1$). This is also true in the limit $\nu \rightarrow 0$ where the population is as likely to be subject to a carrying capacity smaller or larger than $\langle K \rangle$, which generally greatly increases the fixation probability of S with respect to the case where $N = \langle K \rangle$ even if there may be no switches prior to fixation. For instance, in Fig. 2(a) we find that $\phi \approx 0.20 - 0.30$ when $s = 0.02$ while $\phi|_{\langle K \rangle=250} \approx 0.08$, and for $s = 0.07$ we have obtained $\phi \approx 0.05 - 0.07$ while $\phi|_{\langle K \rangle=250} \approx 0.002$.

Fig. 4(a) shows that expression (7) of ϕ_q is very close to ϕ when $\nu/s \gg 1$ (high switching rate) and $K_- \gg 1$, but slightly deviates from it when $\nu/s \ll 1$. This stems from the fact that the effective theory underpinning (7) builds on the value of q inferred at high switching rate.

Remarkably, both (6) and (7) are able to capture the nontrivial dependence of ϕ on the switching rate ν , see Figs. 2(a), S1 and 4(a): ϕ increases with ν when $\phi^{(\infty)} > \phi^{(0)}$ and decreases when $\phi^{(\infty)} < \phi^{(0)}$. The former situation arises under sufficiently low selection pressure, whereas the latter scenario occurs above a certain selection intensity. The intuitive explanation for this is that $\nu \approx 0$ corresponds to a high-volatility-high-reward setting, in which S is equally likely to end up in an environment with relatively high demographic noise ($K = K_-$), where its fixation probability is high, or in one ($K = K_+$) with low noise and lower fixation probability. When $\nu \gg 1$, on the other hand, the species S is in a low-volatility-low-reward setting: it faces an almost constant population size ($N \approx \mathcal{K}$). When the selection intensity s is increased, it becomes increasingly less favorable for S to be in the low-volatility-low-reward setting, and thus $\phi^{(\infty)} < \phi^{(0)}$ and thus ϕ decreases with ν . In the case of Fig. 2(a), we can explicitly determine the critical selection pressure s_c below which $\phi^{(\infty)} > \phi^{(0)}$. When $K_+ \gg K_- \gg 1$, we have $\mathcal{K} = 2K_-(1 + \mathcal{O}(K_-/K_+))$ and therefore $\phi^{(\infty)} \simeq (e^{-K-s} - e^{-2K-s})/(1 - e^{-2K-s})$ while $\phi^{(0)} \simeq (e^{-K-s/2} - e^{-K-s})/[2(1 - e^{-K-s})]$. Hence, the condition $\phi^{(\infty)} > \phi^{(0)}$ for ϕ to increase with ν leads to $2y^2/(1+y^2) > y/(1+y)$, where $y = e^{-K-s/2}$. Therefore, ϕ is an increasing function of ν/s when $y^2 + 2y - 1 > 0$, i.e. if $y = e^{-K-s/2} > \sqrt{2} - 1$, while ϕ decreases with ν if $e^{-K-s/2} < \sqrt{2} - 1$. The critical selection pressure is thus defined by $e^{-K-s_c/2} = \sqrt{2} - 1$. For $(K_+, K_-, s) = (450, 50, 0.02)$, we find $s_c \approx 0.035$. Hence, $s = 0.02 < s_c$ and $s = 0.07 > s_c$. Therefore, ϕ increases with ν when $s = 0.02$, and it decreases with ν when $s = 0.07$, as reported in Figs. 2(a) and S1.

Finally, we note that while (7) is useful to obtain an approximation of ϕ and its dependence on ν and s , it is unable to capture its dependence on the public good parameter $b > 0$. However, we know that the typical population size increases with b when $x \approx 1$ and S is close to fixation, and therefore the intensity of the demographic fluctuations is reduced by increasing b . Based on the properties of the Moran process, we thus expect ϕ to decay exponentially with b [11], which is confirmed by Fig. S2.

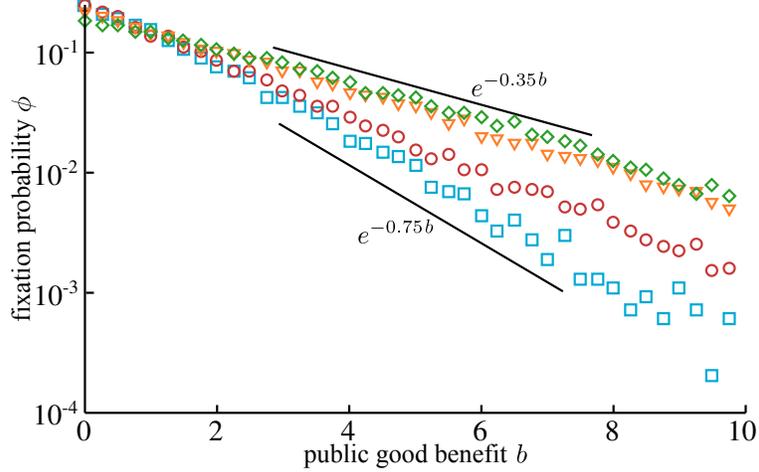


Figure S2: (*Color online*). ϕ as function of b for $\nu = (0.002, 0.02, 0.2, 2)$ (top to bottom) and $(s, K_+, K_-) = (0.025, 450, 50)$ in log scale. Straight lines show $0.3e^{-0.35b}$ and $0.175e^{-0.75b}$ as eyeguides.

3 Mean fixation time

We have also investigated the mean fixation time $T(x_0)$, which is 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 in the population.

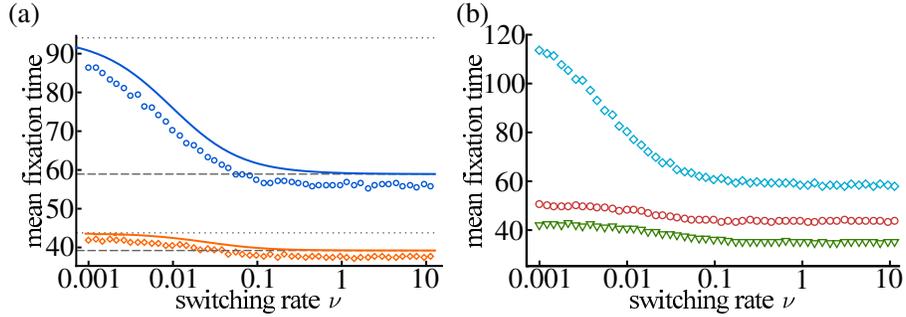


Figure S3: (*Color online*). (a) $T(x_0) = T$ vs. ν in the pure competition case $b = 0$ with $s = 0.02$ (\circ , blue/black) and $s = 0.07$ (\diamond , orange/gray). Symbols are simulation results for T , solid lines are from (S3), dashed and dotted lines show $T|_{K_-}$ and $(T|_{K_-} + T|_{K_+})/2$, respectively. (b) T vs. ν in the public good scenario with $b = 0.2$ (\diamond , blue/gray for $s = 0.01$; \circ , red/black for $s = 0.05$) and $b = 2$, $s = 0.05$ (∇ , green/dark gray). $(K_+, K_-, x_0) = (450, 50, 1/2)$ in both panels.

3.1 Mean fixation time when $b = 0$

In the case $b = 0$, N evolves independently of which species has fixated the population, see Videos 1-3 [1]. This allows us to proceed just as we did with (6) for the fixation probability, and estimate the mean fixation time by $T_{\nu/s}$. This quantity is obtained by averaging the unconditional mean fixation time $T(x_0)|_N$ [7, 8] obtained in a Moran process for a population of constant size N over $p_{\nu/s}^*(N)$ given by (5) with a rescaled switching rate $\nu \rightarrow \nu/s$. This yields

$$T_{\nu/s} = \int_{K_-}^{K_+} T(x_0)|_N p_{\nu/s}^*(N) dN, \quad (\text{S3})$$

where $T(x_0)|_N \sim \mathcal{O}(1/s)$ when $e^{1/s} \gg K_-$. As Figure S3(a) shows, this expression agrees well with the leading contribution $T(x_0) \simeq T_{\nu/s} \sim \mathcal{O}(1/s)$ when x_0 is well separated from the absorbing boundaries. The scaling of the mean fixation time in the presence of EN is therefore the same as $T(x_0)|_N = T|_N$ [7, 8]. The main effect of the EN is to affect the subleading prefactor of T [11]: as shown in Fig. S3 (a) and captured by (S3), the mean fixation time decreases when ν increases. This stems from the fact that $\langle N \rangle^*$ decreases with ν , see Fig. 2(b). In the case of pure resource competition, our theory is therefore able to correctly predict that the mean fixation time always scales as $1/s$ but is shortened when the switching rate is increased.

3.2 Mean fixation time when $b > 0$

In the public good scenario ($b > 0$), the mean fixation time still scales as $T(x_0) \sim \mathcal{O}(1/s)$ and decreases with the environmental switching rate ν , as shown in S3(b). This is because the average population size also decreases with ν (see Fig. 3). In this case, however the fixation of the S type happens in larger populations (and, hence, after longer times) than the fixation of F , see Videos 6-7 [1]. As a result, to accurately compute $T(x_0)$, it is necessary to determine the two conditional mean fixation times (which are equal only when $b = 0$) [11]. Clearly, this cannot be achieved by assuming a timescale separation between N and x , and is beyond the reach of our effective theory.

4 Population size quasi-stationary distribution: additional discussion and results

In this section, we provide additional discussion and results about the population size distribution after the occurrence of fixation. An important common feature of the $b = 0$ and $b > 0$ scenarios is that long-time population size distribution is well described by p_ν^* (5) when $b = 0$, and by combining the conditional PDFs p_ν^* and $p_{\nu,b}^*$ (S2) with ϕ when $b > 0$, as explained in the main text.

4.1 Noise-induced transitions

The quasi-stationary population size distributions are thus characterized by different regimes in which they are unimodal, bimodal, or even multimodal, see Figs. 3, 4 and S4. The transitions between these various regimes are called “noise-induced transitions” because they are solely caused by the environmental noise [4, 9]. In fact, if the carrying capacity in (S1) was oscillating periodically (deterministically), the corresponding PDF would *always* be bimodal: the transition to the unimodal regime is only possible for randomly fluctuating K [9].

4.2 Simulation and prediction of the population size steady state distribution

To assess the theoretical predictions for the long-time population size distribution inferred from (5) and (S2), we have generated 10^5 replicas that we let run until 99% of them reached fixation. The outcome has then been binned to generate the histograms shown as solid lines in Figs. 3, 4(c,d) and in Fig.S4.

In the pure competition case ($b = 0$), see Fig. 3, these simulation results are compared with $p_\nu^*(N)$ (5) multiplied by the number of replicas. (In this case, N evolves independently of x , therefore it is not necessary to wait until 99% of fixation has occurred, see Videos 4-5 [1]. We have proceeded in this way for consistency with the case $b > 0$).

In the public good scenario ($b > 0$), see Figs. 4(c,d) and S4, we have waited until fixation had occurred in almost all replicas (99% of them) to collect the data to build the histograms that correctly reflect the quasi-stationary state distributions of the population size (now depending on x), see Videos 8-10 [1]. Via our effective theory, we have computed the fixation probability of the strain S and F . Multiplying these values by 10^5 (number of samples), we have obtained the expected number of replicas to fixate to S and to F . By multiplying these numbers by p_ν^* (5) and $p_{\nu,b}^*$ (S2) we obtain the histograms associated with the conditional probability distributions (unconditioned of $\xi = \pm 1$). These are shown by dotted lines in Fig. S4 and their sum gives the histogram of the marginal distribution (orange dashed lines in Fig S4), which can be directly compared with the histogram from the simulations.

4.3 Long-time population size distribution in the public good scenario ($b > 0$)

To understand the properties of the quasi-stationary marginal population size distribution when $b > 0$, it is useful to notice that when S fixates ($x = 1$), the relevant conditional PDF (unconditioned of $\xi = \pm 1$) is $p_{\nu,b}^*$ which is unimodal and peaked at $N = (1+b)\mathcal{K}$ when $\nu > 1+b$, while it is bimodal with peaks at $N = (1+b)K_\pm$ if $\nu < 1+b$. Similarly, p_ν^* is the PDF conditioned to fixation of F (but unconditioned of $\xi = \pm 1$): it is unimodal and peaked at $N \approx \mathcal{K}$ if

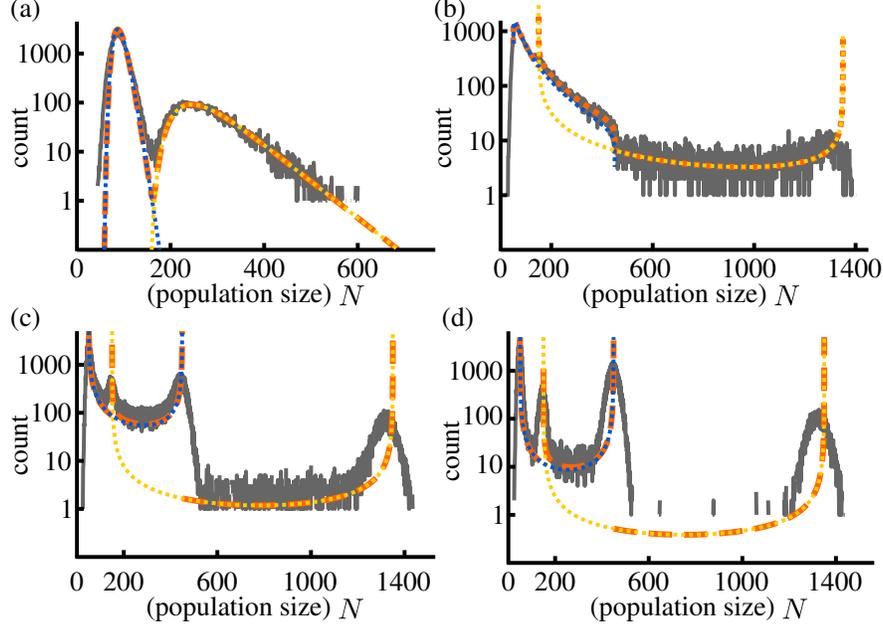


Figure S4: (*Color online*). Long-time population size distributions for $\nu = 20$ (a), $\nu = 1.2$ (b), $\nu = 0.2$ (c), and $\nu = 0.02$ (d) with $(K_+, K_-, x_0, s, b) = (450, 50, 0.5, 0.02, 2)$ similar to Fig. 4(c,d) but now showing also the results obtained from the S -conditional (dotted, yellow/light gray) and F -conditional (dotted, blue/dark gray) PDFs. The histogram of the marginal PDF (dashed) is the sum of the S/F -conditional histograms weighted by ϕ_q (7), see text.

$\nu > 1$, whereas it is bimodal with peaks at $N \approx K_{\pm}$ when $\nu < 1$. The sum of the conditional PDFs weighted by ϕ_q yields the marginal PDF (unconditioned of $\xi = \pm 1$ and of whether S or F fixates) that, depending on ν and b , is either bimodal or multimodal. Therefore, as shown in Figs. 4(c,d) and S4 as well as in Videos 8-10 [1], the marginal quasi-stationary population size distribution is characterized by

- two peaks at about $N = \mathcal{K}$ and $N = (1 + b)\mathcal{K}$ when $\nu > 1 + p$, see Video 8.
- three peaks located about $N = \mathcal{K}$ and $N = (1 + b)K_{\pm}$ when $1 < \nu < 1 + p$, see Video 9.
- four peaks located around $N = (1 + b)K_{\pm}$ and $N = K_{\pm}$ when $\nu < 1$, see Video 10.

The peaks at $N = (1 + b)K_{\pm}$ and $N = (1 + b)\mathcal{K}$ stem from the fixation of S and thus are less marked than those at $N \approx K_{\pm}$ and $N \approx \mathcal{K}$ which result from the more likely fixation of F .

4.4 Figure 4(c, d) revisited

In Fig. 4(c,d), we report the histograms of the stationary marginal population distribution at $\nu = 20$ and $\nu = 0.02$ with $b = 2$. For the sake of completeness, in Fig. S4 we also consider the intermediate switching rates $\nu = 1.2$ and $\nu = 0.2$, and show the conditional PDFs p_{ν}^* and $p_{\nu,b}^*$. The marginal PDF is obtained as the sum of p_{ν}^* and $p_{\nu,b}^*$ weighted by ϕ_q and $1 - \phi_q$ given by (7).

4.5 Deviations from the PDF predictions

We have seen that coupled internal and environmental noise greatly influences the population fixation probability (aptly described by Eqs.(6) and (7)), and therefore significantly influences the population internal composition (evolutionary dynamics), and in turn also its ecological dynamics when $b > 0$ (internal and ecological dynamics being then explicitly coupled). We have also seen that once fixation has occurred, the population size quasi-stationary distribution is well described by the stationary (conditional) PDFs (5) and (S2) of underlying PDMP that are able to predict when the long-time population size distributions are unimodal, bimodal or multimodal and the location of the peaks, as shown

by Figs. 3, 4 and S4.

However, Eqs. (5) and (S2) ignore the effects of demographic fluctuations on the population size distribution. In fact, demographic fluctuations are responsible for the population size quasi-stationary distributions obtained from the simulations not to be strictly confined within the support of the PDFs (5) and (S2), especially at low ν , as can be seen in Figs. 3, 4 and S4. As clearly visible in the supporting Videos [1], these deviations appear because, due to demographic noise, the population fluctuates around the fixed points $N = K_{\pm}$ and $N = (1 + b)K_{\pm}$, see Video 10. The small deviations from the PDMP predictions have limited influence on quantity such as the average population size $\langle N \rangle^*$, see main text, and their intensity depends on the values of K_{\pm} (high values of K_{\pm} typically yield broader peaks) [11].

5 Supporting videos

The dynamics of the models and our findings are illustrated by a series of videos available electronically [1].

5.1 Videos 1-5: $b = 0$

Videos 1-5 illustrate the population dynamics in the pure resource competition scenario for the parameters $(s, K_+, K_-, x_0) = (0.02, 450, 50, 0.5)$ and different switching rates.

- Video 1 shows the sample paths $N(t)$ (left) and $x(t)$ (right) of five replicas for $\nu = 20$. We clearly notice a timescale separation: the population size quickly starts to endlessly fluctuate about $N \approx \mathcal{K} = 90$ while $x(t)$ evolves much more slowly, with fixation occurring in time $t \sim \mathcal{O}(1/s)$.
- Video 2 shows similar paths for $\nu = 0.01$ (and a sped-up animation). We again see the timescale separation between $N(t)$ and $x(t)$. However, in the long run $N(t)$ endlessly jumps between $N \approx K_-$ and $N \approx K_+$. Moreover, the video shows how the behavior of the population size is unaffected by changes in x : N relaxes at a faster timescale and maintains the same behavior also after fixation (of either species).
- Video 3: $N(t)$ and $x(t)$ sample paths as in Videos 1 and 2 but for very slow switching rate $\nu = 0.0001 \ll s = 0.02$. In all but one replicas, the population evolves subject to the carrying capacity K_- or K_+ , randomly allocated initially with same probability, without experiencing any switches and $N(t)$ fluctuates about K_+ or K_- . In only one realization, after a long time (at $t \approx 750$), the carrying capacity switches and the population jumps from K_+ to K_- . The video also illustrates that S fixation is more likely when the population is subject to $K = K_-$ than to $K = K_+$: both the purple and pink samples ending at $x = 1$ correspond to a population of size $N(t) \approx K_-$.
- Video 4 shows the histograms of the population size (left) and of the fraction of S individuals (right) for a slow-switching environment ($\nu = 0.2$). We notice that the population size distribution readily attains a right-tailed, bimodal shape with peaks about $N = K_{\pm}$, and is independent of the distribution of x (internal dynamics). On the other hand, the histogram of x evolves slowly and is eventually characterized by asymmetric peaks at $x = 0$ and $x = 1$ corresponding to the fixation probability of F and S , respectively.
- Video 5: as in Video 3, but for a fast-switching environment ($\nu = 20$). The population size histogram rapidly becomes bell-shaped and centered about $N = \mathcal{K}$. It reaches this form much before fixation typically occurs, and is independent of the distribution of x (internal dynamics). The histogram of x has the same properties as in Video 3.

5.2 Videos 6-10: $b > 0$

Movies 6-8 illustrate the internal and ecological dynamics in the public good scenario, $b > 0$, for the parameters $(s, K_+, K_-, b, x_0) = (0.02, 450, 50, 2, 0.5)$ and different switching rates. In this scenario, the fast N dynamics is enslaved to the slower evolution of x . The population size distribution is characterized by peaks that slowly emerge as occurrences of S and F fixation accumulate (right panels).

- Video 6 shows sample paths of N and x for five realizations with $\nu = 20$, as in Video 1. The population size and composition are correlated: the population size attains large values when x dwells about 1, while N is

much smaller when $x \ll 1$ (for example, the green replica is almost always larger than the purple one). As the species fixate, the sample paths for N separate into two distinct sets: those associated with the fixation of S ($x = 1$) fluctuate about $N \approx \mathcal{K} = 90$, while the paths associated to $x = 0$ (fixation of F) fluctuate around $N \approx (1 + b)\mathcal{K} = 270$.

- Video 7 shows similar sample paths for $\nu = 2$. In addition to showing the correlation between N and x , the video illustrates how populations with a high fraction of S ($x \approx 1$) experience random switching with an effectively reduced switching rate. For example, in the purple sample paths, which readily attains $x \approx 1$, N evolves by large abrupt jumps, in agreement with the properties of the S -conditional PDF $p_{\nu,2}^*$, see (S2).
- Video 8 shows the histograms of N and x for fast switching ($\nu = 20$). The histogram of the population size (left) has first a right-tailed bell shape. As fixation occurrences build up, the distribution gradually splits into asymmetric peaks about $\mathcal{K} = 90$ and $(1 + b)\mathcal{K} = 270$. The histogram of x is characterized by slowly-developing asymmetric peaks at $x = 0$ and $x = 1$.
- Video 9 shows the histograms of N and x for intermediate switching ($\nu = 1.2$). Similarly to Video 7, the histogram of N changes from having first a right-tailed bell shape to its eventual quasi-stationary form. In this case, the quasi-stationary state is characterized by three asymmetric peaks, located at about $\mathcal{K} = 90$ and $(1 + b)K_- = 150$, and about $(1 + b)K_+ = 1350$, that slowly develop as fixation occurrences pile up (right panel).
- Video 10 shows the histograms of N and x for slow switching $\nu = 0.2$. Initially, the histogram of N develops as in Videos 7 and 8, but now the quasi-stationary state is characterized by four slowly-developing asymmetric peaks, located at about $K_- = 50$, $(1 + b)K_- = 150$, and about $K_+ = 450$ and $(1 + b)K_+ = 1350$.

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