Invasion and fixation of microbial dormancy traits under competitive pressure

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Abstract

Microbial dormancy is an evolutionary trait that has emerged independently at various positions across the tree of life. It describes the ability of a microorganism to switch to a metabolically inactive state that can withstand unfavourable conditions. However, maintaining such a trait requires additional resources that could otherwise be used to increase e.g. reproductive rates. In this paper, we aim for gaining a basic understanding under which conditions maintaining a seed bank of dormant individuals provides a "fitness advantage" when facing resource limitations and competition for resources among individuals (in an otherwise stable environment). In particular, we wish to understand when an individual with a "dormancy trait" can invade a resident population lacking this trait despite having a lower reproduction rate than the residents. To this end, we follow a stochastic individual-based approach employing birth-and-death processes, where dormancy is triggered by competitive pressure for resources. In the large-population limit, we identify a necessary and sufficient condition under which a complete invasion of mutants has a positive probability. Further, we explicitly determine the limiting probability of invasion and the asymptotic time to fixation of mutants in the case of a successful invasion. In the proofs, we observe the three classical phases of invasion dynamics in the guise of Coron et al. (2017, 2019).
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1. Introduction

Dormancy is an evolutionary trait that has emerged independently at various positions across the tree of life. In the present article, we are in particular interested in microbial dormancy

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(cf. [27] and [30] for recent overviews of this subject). Microbial dormancy describes the ability of a microorganism to switch to a metabolically inactive state in order to withstand unfavourable conditions (such as resource scarcity and competitive pressure or extreme environmental fluctuations), and this seems to be a highly effective (yet costly) evolutionary strategy. In certain cases, for example in marine sediments, simulation studies indicate that under oligotrophic conditions, the fitness of an organism is determined to a large degree by its ability to simply stay alive, rather than to grow and reproduce (cf. [9]). Indeed, maintaining a dormancy trait requires additional resources in comparison to individuals lacking this trait, resulting in significant trade-offs such as e.g. a lower reproduction rate.

In this paper, we aim at gaining a basic rigorous understanding for the conditions under which maintaining a dormancy trait can be beneficial. We investigate the particular question whether an individual with a dormancy trait can invade a resident population lacking this trait, even if maintaining dormancy reduces its reproduction rate compared to the rate of the residents, under otherwise stable environmental conditions. To this end, we follow a stochastic individual-based approach employing birth-and-death processes (a classic set-up underlying much of adaptive dynamics, as outlined e.g. in [8]), where dormancy is triggered in response to competitive pressure for limited resources. In the large-population limit, we identify a necessary and sufficient condition under which the invasion of mutants, despite having a lower reproduction rate than the resident population, has a positive probability. Further, we explicitly determine the limiting probability of invasion and the asymptotic time of fixation of mutants in the case of a successful invasion.

To be more explicit, in our model the total population evolves according to a continuous time Markov chain. Initially, there is a fit resident population, which we assume to be close to its equilibrium population size, featuring (random) reproduction, natural death ("death by age"), and death by competition. This results in a stochastically evolving population with logistically regulated drift fluctuating around a constant carrying capacity (reflecting a stable yet limited supply of resources). We assume that environmental conditions are also stable and do not affect reproduction, death or competition rates. In this situation, we then assume that a single "mutant" (or "migrant") with "dormancy trait" appears in the population, who on the one hand is still fit enough to survive in absence of the residents (however with a strictly lower reproduction rate), but on the other hand is able to switch to a dormant state at a rate proportional to the "competitive pressure" exerted on her due to crowding and limited resource availability. That is, for some $0 < p < 1$, "competition events" that would normally cause death for an ordinary resident individual kill a mutant individual only with probability $1 - p$. Otherwise, with probability p, the mutant individual affected by competition will persist and switch to the dormant state. Finally, dormant mutant individuals neither reproduce nor are affected by competitive pressure for resources while they are still to some degree exposed to natural death (at a rate typically smaller than for active individuals). We assume that at a constant "resuscitation rate" , they switch back to the active state.

Our main results show that the mutants will invade the resident population with positive probability under a suitable condition on the parameters of the model. This condition has the following interpretation: the advantage of the resident population caused by its higher reproduction rate needs to be over-compensated by the advantage of the mutant population resulting from being able to escape competitive deaths due to overcrowding by switching into dormancy. This condition can be made entirely transparent in terms of the parameters of the model, see (5) resp. Section 3. Under this condition, we characterize the probability of invasion (that is, the mutants completely replace the residents and reach their own equilibrium carrying

capacity), and we identify the expected time of invasion on a logarithmic scale in the large-population limit. With high probability, a successful mutation follows the three classical phases exhibited in basic adaptive dynamics models (which were introduced in [11, Section 3]; see e.g. [8, Section 4.1] for a slightly more general picture, but in particular [15,16] for work in a closely related context that inspired our analysis and provides many of the necessary tools): (1) mutant growth until reaching a population size comparable to the carrying capacity, while during the same time period the resident population stays close to its equilibrium size, (2) a phase where all sub-populations are large and the dynamics of the frequency process can be approximated by a deterministic dynamical system, (3) extinction of the resident population, while the mutant population remains close to its equilibrium size.

Note that for our results it is essential that switching into dormancy is induced by competitive pressure. Indeed, if instead this switching happens at a constant rate ("spontaneous" or "stochastic switching", cf. e.g. [27]), the mutants will *never* be able to invade the resident population unless their birth rate is higher than that of the residents (in which case their invasion would also be possible without a dormancy trait, and the assumption that dormancy is a costly trait would be violated). Further, mutants cannot make the residents go extinct unless they are fit enough to survive on their own; thus, evolutionary suicide, as observed e.g. in [4], does not occur in our model. Long-term coexistence of residents and mutants is also excluded in our modelling set-up.

Let us note that while dormancy was recently investigated in several mathematical works in the area of population genetics and coalescent theory (see e.g. [5–7,24,26]), in the field of adaptive dynamics we are not aware of prior work involving dormancy. The present paper takes a first step in this direction, analysing the invasion dynamics in a simple toy model. In order to make this model more realistic, one could e.g. incorporate further mutations in the spirit of adaptive dynamics. In the regime of very rare mutations introduced by Champagnat (cf. [3,11,13]), we expect that the model behaves similarly to the case of no further mutation. Recently, in [14], a regime of still rare but more frequent mutations was considered, with the additional effect of horizontal gene transfer. Here, mutation rates are large enough so that small sub-populations can have macroscopic effects on the whole population. It should be interesting to study the additional effects of dormancy traits in this regime. As a further step, one could also introduce spatiality in the model, which is relevant in modelling the trait space (see e.g. [2]) or the environment of the populations (see e.g. [12,20]). Finally, the resuscitation rate, which is assumed constant in the present paper, could also be made dependent on the strength of competition.

Note that related scenarios involving "phenotypic switches", arising e.g. in cancer modelling, have been analysed recently by [2,23]. For dormancy and switching models in *fluctuating environments*, dynamical systems and branching process models have been investigated in [17,29]. Here, as in the *competition* setup of the present paper, the basis of a rigorous understanding for the evolutionary advantages of seed banks seems to be emerging. It seems fair to say that dormancy in its many forms, and its interplay with other evolutionary and ecological forces, will provide many interesting future research challenges in mathematical biology.

The remainder of this paper is organized as follows. In Section 2 we introduce our model and state our main results. Next, in Section 3 we discuss some strongly related questions. Finally, in Section 4 we prove the main results. Each of these sections starts with a description about its internal organization.

2. Model definition and main results

The structure of this section is the following. In Section 2.1 we define our stochastic population model. Next, the goal of Section 2.2 is to introduce necessary and sufficient conditions for mutant invasion with positive probability, to present the formulas for the probability and time of invasion in the large-population limit, and to provide a heuristic justification for these. In particular, we comment on the probability and time of the invasion. The introduced quantities and conditions are then used in Section 2.3 in order to state our main results, Theorems 2.1, 2.2, and 2.3, the proof of which will make our heuristic arguments rigorous.

2.1. The model

We have two traits, the resident one (1) and the mutant one (2). Mutant individuals can have an active (2a) and a dormant (2d) state. As an interpretation, we will sometimes say that the dormant individuals are in the *seed bank*. Informally speaking, the model is defined as follows.

- A resident individual gives birth to another such individual at rate $\lambda_1 > 0$.
- An active mutant individual gives birth to another such individual at rate $\lambda_2 \in (0, \lambda_1)$.
- Any active individual has a natural death rate $\mu \in (0, \lambda_2)$.
- $K > 0$ is the carrying capacity of the population.
- The competitive pressure felt by an active individual from another active individual is $\alpha/K > 0$, where $\alpha > 0$. For any ordered pair (x_i, x_j) of active individuals, at rate $\alpha/K > 0$ a competitive event affecting x_i happens. We fix $p \in (0, 1)$. At a competitive event, in case x_i is a resident individual, it dies. If x_i is a mutant individual, it dies with probability $1 - p$ and becomes a dormant (mutant) individual with probability p.
  In other words, writing $\mathbb{N}_0 = \{0, 1, 2, \ldots\}$ and $\mathbb{N} = \{1, 2, \ldots\}$, in a population with $n_1 \in \mathbb{N}_0$ (active) resident individuals and $n_{2a} \in \mathbb{N}_0$ active mutant individuals, writing $n_a = n_1 + n_{2a}$ for the total number of active individuals, a resident individual dies by competition at rate $\alpha n_a/K$, an active mutant dies by competition at rate $(1 - p)\alpha n_a/K$ and switches to dormant mutant at rate $p\alpha n_a/K$.
- For some $\kappa \geq 0$, a dormant (mutant) individual dies at rate $\kappa\mu$.
- A dormant (mutant) individual becomes an active (mutant) individual at rate $\sigma > 0$.

Further necessary conditions on the parameters will be specified later in the sequel.

To be more precise, we consider, for $t \geq 0$, a finite number $N_t \in \mathbb{N}_0$ of individuals $\{x_i : i \in [N_t]\}$, where for all $i \in [N_t]$ we have $x_i \in \{1, 2a, 2d\}$. Here we wrote $[n] = \{1, 2, \ldots, n\}$ for $n \in \mathbb{N}_0$, in particular, $[0] = \varnothing$. We define the triple of rescaled frequency processes

$$(\mathbf{N}_t^K)_{t\geq0} = ((N_{1,t}^K, N_{2a,t}^K, N_{2d,t}^K))_{t\geq0},$$

where for $x \in \{1, 2a, 2d\}$,

$$N_{x,t}^K = \frac{1}{K}\#\{x_i : i \in [N_t], x_i = x\}$$

is the number of individuals of type x rescaled by K. We also write

$$N_{2,t}^K = N_{2a,t}^K + N_{2d,t}^K$$

for $1/K$ times the total population size of mutant individuals and

$$N_t^K = N_{1,t}^K + N_{2,t}^K = \frac{N_t}{K}.$$

for $1/K$ times the total population size. Hence, $\mathbf{N}_t^K$ is a $\left(\frac{1}{K}\mathbb{N}\right)^3$-valued Markov process with transitions

$$(n_1, n_{2a}, n_{2d}) \rightarrow \begin{cases} (n_1 + \frac{1}{K}, n_{2a}, n_{2d}) \text{ at rate } K n_1 \lambda_1, \\ (n_1, n_{2a} + \frac{1}{K}, n_{2d}) \text{ at rate } K n_{2a} \lambda_2, \\ (n_1 - \frac{1}{K}, n_{2a}, n_{2d}) \text{ at rate } K n_1 (\mu + \alpha(n_1 + n_{2a})), \\ (n_1, n_{2a} - \frac{1}{K}, n_{2d}) \text{ at rate } K n_{2a} (\mu + (1-p)\alpha(n_1 + n_{2a})), \\ (n_1, n_{2a} - \frac{1}{K}, n_{2d} + \frac{1}{K}) \text{ at rate } K n_{2a} p \alpha(n_1 + n_{2a}), \\ (n_1, n_{2a}, n_{2d} - \frac{1}{K}) \text{ at rate } K n_{2d} \kappa \mu, \\ (n_1, n_{2a} + \frac{1}{K}, n_{2d} - \frac{1}{K}) \text{ at rate } K n_{2d} \sigma. \end{cases}$$

2.2. Assumptions and heuristics

The Markov process $(\mathbf{N}_t^K)_{t \geq 0}$ is well-defined for any $K > 0$, given the initial condition. Relevant initial conditions satisfy $\bar{N}_0^K \approx (\bar{n}_1, \frac{1}{K}, 0)$ where $\bar{n}_1$ is the equilibrium population size of the resident population in absence of the mutant population. That is, at time 0, resident individuals are close to equilibrium, and there is precisely one active mutant and there are no dormant mutants.

Now, we want to find necessary and sufficient conditions under which the probability of mutant invasion is nonvanishing in the large-population limit. Further, conditional on a successful invasion, we want to identify the time of invasion for large K on the logarithmic scale. To this aim, we have to choose the parameters in such a way that, roughly speaking, the following assertions hold.

1. The resident population is able to survive on its own, i.e., $\bar{n}_1 > 0$.
2. Mutants are also fit: their equilibrium population size $(\bar{n}_{2a}, \bar{n}_{2d})$ is coordinatewise positive.
3. *Phase I of the invasion*: For large K, starting from $\bar{N}_0^K \approx (\bar{n}_1, \frac{1}{K}, 0)$, the probability that $N_{2,t}^K = 0$ eventually is not close to one for large K.
4. *Phase II*: Given that the total mutant population has reached size εK, for $\varepsilon > 0$ small, with high probability $\bar{N}_t^K$ will get close to $(K\varepsilon, K\bar{n}_{2a}, K\bar{n}_{2d})$ for arbitrarily small $\varepsilon > 0$.
5. *Phase III*: Given that the process reached the state $(K\varepsilon, K\bar{n}_{2a}, K\bar{n}_{2d})$, the resident population will die out with high probability.

Let us now heuristically identify the conditions corresponding to (1)–(5). The conditions that are necessary and sufficient for (3) will turn out also to be sufficient for (4) and (5). These heuristics will be made precise during the proof of the main results of the paper.

1. In absence of mutants, for large K, the rescaled resident population $N_{1,t}^K$ can be approximated by $n_1(t)$, where $n_1(\cdot)$ solves the quadratic ODE

   $$\dot{n}_1(t) = n_1(t)(\lambda_1 - \mu - \alpha n_1(t)).$$

   If $\lambda_1 > \mu$, this system has a unique positive equilibrium, given as

   $$\bar{n}_1 = \frac{\lambda_1 - \mu}{\alpha},$$

   which is also asymptotically stable. Else, there is no stable positive equilibrium.

2. Similarly, in absence of residents, for large K, the rescaled mutant population size $(N_{2a,t}^K, N_{2d,t}^K)$ can be approximated by $(n_{2a}(t), n_{2d}(t))$, where $(n_{2a}(\cdot), n_{2d}(\cdot))$ solves the two-dimensional system of ODEs

$$\begin{aligned}\dot{n}_{2a}(t) &= n_{2a}(t)(\lambda_2 - \mu - \alpha n_{2a}(t)) + \sigma n_{2d}(t), \\ \dot{n}_{2d}(t) &= p\alpha n_{2a}(t)^2 - (\kappa\mu + \sigma)n_{2d}(t).\end{aligned} \tag{1}$$

Linearizing this system, we obtain the Jacobian matrix

$$A(n_{2a}, n_{2d}) = \begin{pmatrix} \lambda_2 - \mu - 2\alpha n_{2a} & \sigma \\ 2p\alpha n_{2a} & -\kappa\mu - \sigma \end{pmatrix}. \tag{2}$$

Clearly, there is no equilibrium of the form $(0, \cdot)$ or $(\cdot, 0)$ apart from $(0, 0)$. Further, we have

$$A(0, 0) = \begin{pmatrix} \lambda_2 - \mu & \sigma \\ 0 & -\kappa\mu - \sigma \end{pmatrix}.$$

For $\lambda_2 > \mu$, it is easy show that $A(0, 0)$ has one negative and one positive eigenvalue and hence $(0, 0)$ is unstable. Let us now show that for $\lambda_2 > \mu$ we have a unique (coordinatewise) positive equilibrium, which is asymptotically stable. For an equilibrium (n_{2a}, n_{2d}) with $n_{2a} \neq 0$, dividing both equations in (1) by n_{2a}, we obtain

$$\frac{n_{2d}}{n_{2a}} = -\frac{\lambda_2 - \mu - \alpha n_{2a}}{\sigma} = \frac{p\alpha n_{2a}}{\kappa\mu + \sigma}. \tag{3}$$

From (3) we obtain that there is precisely one such equilibrium, with coordinates

$$\bar{n}_{2a} = \frac{(\lambda_2 - \mu)(\kappa\mu + \sigma)}{\alpha(\kappa\mu + (1 - p)\sigma)} > 0, \qquad \bar{n}_{2d} = \frac{(\lambda_2 - \mu)^2 p(\kappa\mu + \sigma)}{\alpha(\kappa\mu + (1 - p)\sigma)^2} > 0.$$

were we used that $\lambda_2 > \mu$, $\kappa\mu \geq 0$, $\sigma > 0$ and $p \in (0, 1)$. Comparing this to (2), we obtain

$$\det A(\bar{n}_{2a}, \bar{n}_{2d}) = (\kappa\mu + \sigma)(\lambda_2 - \mu).$$

If $\lambda_2 > \mu$, then the right-hand side is positive. In this case there are two strictly negative eigenvalues. This is true because the trace $\operatorname{Tr} A(\bar{n}_{2a}, \bar{n}_{2d})$ is negative, which follows from the fact that $\bar{n}_{2a} > \lambda_2 - \mu$ and $\kappa\mu + \sigma > 0$. Hence, $(\bar{n}_{2a}, \bar{n}_{2d})$ is asymptotically stable.

3. As long as the mutant population size $KN_{2,t}^K$ is negligible compared to K, the resident population can be approximated by its equilibrium population size, and the competition pressure felt by a mutant individual comes essentially only from the resident population. This implies that the dynamics of the mutant population size process $(KN_{2a,t}^K, KN_{2d,t}^K)$ can be approximated by a bi-type linear branching process $(\widehat{Z}_{2a}(t), \widehat{Z}_{2d}(t))$ with rates

$$(n_{2a}, n_{2d}) \rightarrow \begin{cases} (n_{2a} + 1, n_{2d}) & \text{at rate } n_{2a}\lambda_2, \\ (n_{2a} - 1, n_{2d}) & \text{at rate } n_{2a}(\mu + \alpha\bar{n}_1(1 - p)), \\ (n_{2a} - 1, n_{2d} + 1) & \text{at rate } n_{2a}\bar{n}_1\alpha p, \\ (n_{2a} + 1, n_{2d} - 1) & \text{at rate } \sigma n_{2d}, \\ (n_{2a}, n_{2d} - 1) & \text{at rate } \kappa\mu n_{2d}. \end{cases}$$

By classical results on multitype branching processes [1, Section 7.2], the process is supercritical, i.e., there is no almost sure convergence to $(0, 0)$, if and only if the following *mean matrix* has a positive eigenvalue

$$J = \begin{pmatrix} \lambda_2 - \mu - \alpha\bar{n}_1 & p\alpha\bar{n}_1 \\ \sigma & -\kappa\mu - \sigma \end{pmatrix} = \begin{pmatrix} \lambda_2 - \lambda_1 & p(\lambda_1 - \mu) \\ \sigma & -\kappa\mu - \sigma \end{pmatrix}. \tag{4}$$

In the interesting case $\lambda_2 < \lambda_1$, it is impossible that we have two positive eigenvalues because $\operatorname{Tr} J < 0$ follows from the definition of $\bar{n}_1$. Hence, J has a positive eigenvalue if and only its determinant is negative, which is equivalent to

$$\lambda_1 - \lambda_2 < p(\lambda_1 - \mu)\frac{\sigma}{\kappa\mu + \sigma} = p\alpha\bar{n}_1\frac{\sigma}{\kappa\mu + \sigma}. \tag{5}$$

The condition (5) turns out to be necessary and sufficient for the invasion probability to be asymptotically positive. We will interpret it and discuss the related notion of invasion fitness in Section 3.1.

4. Now we argue that under condition (5), given that the total mutant population has reached a population size of order K, the second phase of invasion also takes place, which ends with $\mathbf{N}_t^K \approx (0, \bar{n}_{2a}, \bar{n}_{2d})$. In that phase, as long as all sub-populations are of order K, the process $\mathbf{N}_t^K$ can be approximated, for K large, by the (deterministic) Lotka–Volterra type system

$$\begin{aligned}
\dot{n}_1(t) &= n_1(t)(\lambda_1 - \mu) - \alpha(n_1(t) + n_{2a}(t)), \\
\dot{n}_{2a}(t) &= n_{2a}(t)(\lambda_2 - \mu) - \alpha(n_1(t) + n_{2a}(t)) + \sigma n_{2d}(t), \\
\dot{n}_{2d}(t) &= p\alpha n_{2a}(t)(n_1(t) + n_{2a}(t)) - (\kappa\mu + \sigma)n_{2d}(t).
\end{aligned} \tag{6}$$

We will show below (see Proposition 4.5) that (5) with $\lambda_1 > \lambda_2 > \mu$ is also sufficient to guarantee that this system has only one stable nonnegative equilibrium, which is equal to $(0, \bar{n}_{2a}, \bar{n}_{2d})$ and asymptotically stable. Moreover, there is a set of initial conditions that $\mathbf{N}_t^K$ reaches with high probability given that the mutants survived the first phase, such that starting from this set, the solution of (6) tends to $(0, \bar{n}_{2a}, \bar{n}_{2d})$ as $t \to \infty$.

5. After the second phase of invasion, the population rescaled by $1/K$ is close to the equilibrium $(0, \bar{n}_{2a}, \bar{n}_{2d})$. To be more precise, the resident population size is of order εK for some $\varepsilon > 0$ small. It remains to show that for large K, with probability tending to one, the resident population dies out within $O(\log K)$ time, while the mutant population stays close to equilibrium. Now, as long as $(KN_{2a,t}^K, KN_{2d,t}^K)$ is near $(K\bar{n}_{2a}, K\bar{n}_{2d})$ and the resident population is small compared to K, the competitive pressure that the resident individuals feel comes essentially only from the mutant population. This implies that $KN_{1,t}^K$ can be approximated by a branching process $\widehat{Z}_1(t)$ with rates

$$n \to \begin{cases} n+1 & \text{at rate } n_1\lambda_1, \\ n-1 & \text{at rate } n_1(\mu + \alpha\bar{n}_{2a}). \end{cases}$$

In order to show that this branching process goes extinct almost surely, we have to verify that it is subcritical, i.e., the rate $n \to n+1$ is smaller than the rate $n \to n-1$. But this assertion is equivalent to the inequality (5).

6. Using our multitype branching process approach, now we can compute the extinction probabilities under condition (5) with $\lambda_1 > \lambda_2 > \mu$. Define

$$q = \mathbb{P}\big(\exists t < \infty \colon \widehat{Z}_{2a}(t) + \widehat{Z}_{2d}(t) = 0 \big| (\widehat{Z}_{2a}(0), \widehat{Z}_{2d}(0)) = (1, 0)\big). \tag{7}$$

By [1, Section 7], q is the first coordinate of the unique solution of the system of equations

$$\begin{aligned}
\lambda_2(s_a^2 - s_a) + p(\lambda_1 - \mu)(s_d - s_a) + (\mu + (1 - p)(\lambda_1 - \mu))(1 - s_a) &= 0, \\
\sigma(s_a - s_d) + \kappa\mu(1 - s_d) &= 0,
\end{aligned} \tag{8}$$

in $[0, 1]^2 \setminus \{(1, 1)\}$, while the second coordinate of the same solution is the extinction probability given that the branching process is started from $(0, 1)$. We will discuss the

dynamics of the process started with one dormant individual and interpret the relation between s_a and s_d in Section 3.3.

Summarizing, our heuristics indicates that under condition (5), for large K, given that the mutants survive the first phase of invasion, the second and the third phase of the invasion are also successful with high probability.

2.3. Statement of results

Recall that we have assumed $\lambda_1 > \lambda_2 > \mu > 0$, and recall also the stable equilibrium $(\bar{n}_{2a}, \bar{n}_{2d})$, which is the unique solution of the system of Eqs. (3) under the assumption $\lambda_2 > \mu$. For $\beta > 0$ define

$$S_\beta = \{0\} \times [\bar{n}_{2a} - \beta, \bar{n}_{2a} + \beta] \times [\bar{n}_{2d} - \beta, \bar{n}_{2d} + \beta], \tag{9}$$

a stopping time at which $\mathbf{N}_t^K$ reaches this set:

$$T_{S_\beta} := \inf\{t > 0 \colon \mathbf{N}_t^K \in S_\beta\}, \tag{10}$$

and the first time when the rescaled mutant population size reaches a threshold $x \geq 0$ (from below or above):

$$T_x^2 := \inf\{t > 0 \colon K N_{2,t}^K = \lfloor xK \rfloor\}. \tag{11}$$

We further note that the largest eigenvalue of the matrix J defined in (4) is given as follows.

$$\widetilde{\lambda} = \frac{1}{2} \Big((\lambda_2 - \lambda_1 - \kappa\mu - \sigma) + \sqrt{(\lambda_1 - \lambda_2 + \kappa\mu + \sigma)^2 - 4\big((\lambda_1 - \lambda_2)(\kappa\mu + \sigma) - p(\lambda_1 - \mu)\sigma\big)} \Big). \tag{12}$$

Our first main result characterizes the probability of mutant invasion in the large-population limit.

Theorem 2.1. *Assume that* (5) *holds. Assume further that*

$$N_1^K(0) \underset{K\to\infty}{\to} \bar{n}_1$$

and

$$(N_{2a}^K(0), N_{2d}^K(0)) = (\tfrac{1}{K}, 0).$$

Then for any $0 < \beta < \min\{\bar{n}_{2a}, \bar{n}_{2d}\}$, we have

$$\lim_{K\to\infty} \mathbb{P}\Big(T_{S_\beta} < T_0^2\Big) = 1 - q.$$

Next, we identify the time of fixation of mutants in the case of a successful invasion.

Theorem 2.2. *Under the assumptions of Theorem 2.1, we have that on the event $\{T_{S_\beta} < T_0^2\}$,*

$$\lim_{K\to\infty} \frac{T_{S_\beta}}{\log K} = \frac{1}{\widetilde{\lambda}} + \frac{1}{\mu + \alpha\bar{n}_{2a} - \lambda_1} \tag{13}$$

in probability.

Finally, we show that in case of an unsuccessful mutation, with high probability, the extinction takes a sub-logarithmic time (in particular, the extinction happens during the first

phase of the invasion), and at the time of extinction the resident population is close to its equilibrium population size.

Theorem 2.3. *Under the assumptions of Theorem 2.1, we have that on the event $\{T_0^2 < T_{S_\beta}\}$,*

$$\lim_{K \to \infty} \frac{T_0^2}{\log K} = 0 \tag{14}$$

and

$$\mathbb{1}\{T_{S_\beta} > T_0^2\} \Big| \mathbf{N}_{T_0^2}^K - (\bar{n}_1, 0, 0) \Big| \xrightarrow[K \to \infty]{} 0, \tag{15}$$

both in probability.

The proof of Theorems 2.1. 2.2, and 2.3 will be carried out in Section 4. In multiple parts of the proof, we are able to employ arguments that are similar to the ones used in [15,16] for the three phases of invasion in individual-based models in the context of emergence of homogamy, respectively speciation. A particular additional difficulty of our setting lies in guaranteeing convergence of the underlying dynamical system (6) to its stable equilibrium $(0, \bar{n}_{2a}, \bar{n}_{2d})$, in other words, in verifying certain global attractor properties of this equilibrium. Here, none of the methods of the two aforementioned papers are applicable (see the proof of Lemmas 4.6 and 4.7). Our dynamical system is rather different from the ones considered in [15,16], which have stronger monotonicity properties but also exhibit non-hyperbolic equilibria. The lack of monotonicity in our system is due to the switches between activity and dormancy and to the fact that dormant individuals are not affected by competition. These differences also influence other parts of the proof of our main theorems nontrivially (see e.g. the construction of the couplings in the proofs of Propositions 4.1 and 4.9).

3. Discussion

This section touches the following topics. In Section 3.1 we provide an interpretation of condition (5) that is crucial for our main results and comment on the notion of *invasion fitness*. The relevance of competition-induced vs. spontaneous switching is discussed in Section 3.2, and the case where the first mutant individual is initially dormant instead of active is discussed in Section 3.3. In Section 3.4 we comment on potential experimental studies related to the subject of this paper for model verification.

3.1. Interpretation of the condition of the theorems

Condition (5) is equivalent to the assertion that the advantage of residents caused by their higher birth rate is less than the advantage of the mutants caused by their ability to become dormant under competitive pressure, at the beginning of the invasion where the mutants are rare. Indeed, the right-hand side of (5) equals the rate at which those active mutant individuals move to the seed bank that afterwards become active again before dying. Indeed, active mutants become dormant at rate $p\alpha\bar{n}_1$, and given that they have become dormant, the probability that they turn active again (instead of dying in the seed bank) is $\frac{\sigma}{\kappa\mu+\sigma}$. In the case $\kappa = 0$ of no death in the seed bank, (5) reduces to

$$\frac{\lambda_1 - \mu}{1} < \frac{\lambda_2 - \mu}{1 - p},$$

where $1 - p$ is the probability that a mutant affected by a competitive event dies. On the complementary event, this mutant will eventually become active again.

Note that $\lambda_2 > \mu$ automatically follows from (5) given that $\lambda_1 > \mu$. Thus, our model is free from evolutionary suicide: mutants who are not able to survive on their own will not make the resident population go extinct with asymptotically positive probability.

The *invasion fitness* is the exponential growth rate of a mutant born with a given trait in the presence of the current equilibrium population [8, Section 1.3.2]. In the present setting, the precise formulation of such a quantity is not immediate, for the following reasons. First, the total mutant population size process $(K N_{2,t}^K)_{t \geq 0}$ is not Markovian and hence has no well-defined exponential rate. Second, the pair of active and dormant coordinates $((K N_{2a,t}^K, K N_{2d,t}^K))_{t \geq 0}$ is Markovian, but its initial growth rate depends delicately on the initial condition. More precisely, for $\kappa > 0$, the mutant population has a lower probability to survive if it starts with one dormant and no active individual than if it starts with one active and no dormant one (see Section 3.3 for further details). Nevertheless, if we define the invasion fitness as the principal eigenvalue (a.k.a. Lyapunov exponent) $\widetilde{\lambda}$ of the mean matrix J, then this eigenvalue is positive if and only if the condition (5) holds, in other words, it has the same sign as the expression

$$p(\lambda_1 - \mu)\frac{\sigma}{\kappa\mu + \sigma} - \lambda_1 + \lambda_2.$$

This sign is positive (respectively zero or negative) if and only if the approximating branching process $(\widehat{Z}_{2a}(t), \widehat{Z}_{2d}(t))_{t \geq 0}$ is supercritical (respectively critical or subcritical). Further, according to [1, Section 7], $\widetilde{\lambda}$ is equal to the mean growth rate of the approximating branching process $(\widehat{Z}_{2a}(t), \widehat{Z}_{2d}(t))$, which makes it rightful to call this eigenvalue the invasion fitness.

3.2. A comparison between spontaneous and competition-induced switching, and the case without dormancy trait

We have seen that the bi-type mutant population is able to survive on its own if $\lambda_2 > \mu$, and if (5) holds, then the mutants will invade the population with positive probability even if $\lambda_2 < \lambda_1$. Let us note that without the mutants having a dormancy trait (i.e., for $p = 0$), even though mutants can still survive on their own as soon as $\lambda_2 > \mu$, invasion is not possible as long as $\lambda_2 \leq \lambda_1$. This is true because the approximating branching process is not supercritical in this case.

For $\kappa > 0$, it is not even the case that mutants are fit on their own if the switching from activity to dormancy is not competition-induced but *spontaneous*, i.e., if an active mutant individual switches to dormancy at some fixed rate $\sigma' > 0$. There, in absence of residents, for large K, the rescaled mutant population is approximated by the system of ODEs

$$\begin{aligned}\dot{n}_{2a}(t) &= n_{2a}(t)(\lambda_2 - \mu - \alpha n_{2a}(t) - \sigma') + \sigma n_{2d}(t), \\ \dot{n}_{2d}(t) &= \sigma' n_{2a}(t) - (\kappa\mu + \sigma)n_{2d}(t).\end{aligned} \tag{16}$$

Hence, the determinant of the corresponding Jacobi matrix at the equilibrium $(0, 0)$ is $(\lambda_2 - \mu - \sigma')(-\kappa\mu - \sigma) - \sigma\sigma'$. This is positive if and only if

$$\lambda_2 < \mu + \frac{\kappa\mu\sigma'}{\kappa\mu + \sigma}. \tag{17}$$

In this case, the trace of the matrix is negative because it equals

$$\lambda_2 - \mu - \sigma' - \kappa\mu - \sigma < \frac{\kappa\mu\sigma'}{\kappa\mu + \sigma} - \sigma' - \kappa\mu - \sigma = -\frac{\sigma\sigma'}{\kappa\mu + \sigma} - \kappa\mu - \sigma < 0,$$

and therefore both eigenvalues of the matrix have negative real parts, which implies that the equilibrium $(0, 0)$ is asymptotically stable.

I.e., there are values $\lambda_2 > \mu$ such that the mutant population dies out with high probability if $K \to \infty$. The right-hand side of (17) is the *effective death rate*: indeed, an active individual dies at rate μ, but additionally at rate σ' it becomes dormant, where it dies with probability $\frac{\kappa\mu}{\kappa\mu+\sigma}$ before ever becoming active (and capable of reproducing) again.

In the case of spontaneous switching, it is easy to show that the matrix defined analogously to J (cf. (4)) has no positive eigenvalue for $\lambda_2 < \lambda_1$. I.e., mutant invasion is only possible if the birth rate of mutants is higher than the one of the residents.

We expect that in case both spontaneous and competition-induced switching are present in the model, the behaviour of the system remains similar to the case of purely competition-induced switching, however, with a higher effective death rate, and hence condition (5) is not satisfactory for invasion; λ_2 has to satisfy a stronger condition, which can be derived similarly to (5). In order to keep the notation simple, we do not consider this case of combined switching in the present paper.

3.3. Starting with one dormant individual

Let us recall that s_a is the extinction probability of the approximating bi-type branching process $(\widehat{Z}_{2a}(t), \widehat{Z}_{2d}(t))_{t \geq 0}$ starting from $(1, 0)$, and s_d the same probability starting from $(0, 1)$. Note that the second equation of (8) reads as

$$s_d = \frac{\sigma s_a + \kappa\mu}{\kappa\mu + \sigma}. \tag{18}$$

Note that for $\kappa = 0$, (18) reads as $s_d = s_a$. Thanks to the Markov property of our population process, (18) can be interpreted as follows: given that $(\widehat{Z}_{2a}(0), \widehat{Z}_{2d}(0)) = (0, 1)$, with probability $\frac{\kappa\mu}{\kappa\mu+\sigma}$ the process dies out immediately at the first jump time that affects this single dormant individual. Else (i.e., with probability $\frac{\sigma}{\kappa\mu+\sigma}$), it jumps to $(1, 0)$, where it has probability s_a to die out. This argumentation also implies the following. Let $T_{1,0}$ be the expected extinction time of the mutant population starting from $(1, 0)$ and $T_{0,1}$ the same starting from $(0, 1)$. Then we have

$$\mathbb{E}\big[T_{0,1}\mathbb{1}\{T_{0,1} < \infty\}\big] = \frac{1}{\kappa\mu + \sigma} + \frac{\sigma}{\kappa\mu + \sigma}\mathbb{E}\big[T_{1,0}\mathbb{1}\{T_{1,0} < \infty\}\big],$$

where $\frac{1}{\kappa\mu+\sigma}$ is the expected time of the first jump of the Markov chain. Hence, extinction probabilities and extinction times started from $(0, 1)$ can easily be handled using the same quantities started from $(1, 0)$. This is why our main results describe only the latter case.

3.4. Experimental studies

It would be highly interesting to check the results of the present paper experimentally. In the spirit of the mathematical analysis of the Lenski experiment [10,28] (that also exhibits the three phases of adaptive dynamics invasion), one could think of setting up a controlled experiment where the environment is kept constant over time, with a relatively high but fixed amount of resources. Now, one would need to find two types of microorganisms such that both of them are able to survive on their own in this environment, but the first type reproduces faster, whereas only the second one has a dormancy trait, in such a way that condition (5) holds for the parameters estimated in the experiment. Then, one would first have to establish a resident population of the first type, then augment it by a single individual (or several individuals) of the second type, and continue the experiment until one of the types becomes extinct. Repeating this experiment several times, it would become apparent whether the invasion of the second

type has a positive probability, and whether the invasion probability would come close to the one predicted by our model.

Certainly, the model presented in this paper captures only a small number of features of natural populations. Hence, scenarios excluded by our model such as coexistence of the two types may occur in the experiment. This could lead to interesting feed-back and theoretical model extensions.

4. Proofs

This section is split into four parts: Section 4.1 investigates the first phase of the invasion: the growth or extinction of the mutants. The next two phases only occur if the mutants survive the first phase. Section 4.2 deals with the second phase, where the rescaled population size process is approximated by the system of ODEs (6), and Section 4.3 describes the third phase where the resident population dies out. Using all these, we complete the proof of our theorems in Section 4.4. Throughout the proof we will assume that $\beta \in (0, \min\{\bar{n}_{2a}, \bar{n}_{2d}\})$.

4.1. The first phase of invasion: growth or extinction of the mutant population

The analysis of this phase proceeds similarly to [15, Section 3.1]. However, the presence of dormancy induces nontrivial changes in some coupling arguments (see e.g. the construction of the coupled process appearing in (32)). On the other hand, since we have a monomorphic resident population, some arguments can be simplified or omitted, and the order of proof ingredients will change accordingly.

We now define additional stopping times that will be relevant for this phase. The first one is the time when the resident population first leaves a small-neighbourhood of its equilibrium: for any $\varepsilon > 0$,

$$R_\varepsilon := \inf\left\{t \geq 0 \colon \left|N_{1,t}^K - \bar{n}_1\right| > \varepsilon\right\}.$$

Then our goal is to verify the following proposition.

Proposition 4.1. *Assume that* (5) *holds with* $\lambda_1 > \lambda_2 > \mu$. *Let* $K \mapsto m_1^K$ *be a function from* $(0, \infty)$ *to* $[0, \infty)$ *such that* $m_1^K \in \frac{1}{K}\mathbb{N}_0$ *and* $\lim_{K \to \infty} m_1^K = \bar{n}_1$. *Then there exists a function* $f \colon (0, \infty) \to (0, \infty)$ *tending to zero as* $\varepsilon \downarrow 0$ *such that for any* $\xi \in [1/2, 1]$,

$$\limsup_{K \to \infty}\left|\mathbb{P}\left(T_{\varepsilon^\xi}^2 < T_0^2 \wedge R_{2\varepsilon}, \left|\frac{T_{\varepsilon^\xi}^2}{\log K} - \frac{1}{\tilde{\lambda}}\right| \leq f(\varepsilon)\;\middle|\;\mathbf{N}_0^K = \left(m_1^K, \frac{1}{K}, 0\right)\right) - (1 - q)\right| \tag{19}$$
$$= o_\varepsilon(1)$$

and

$$\limsup_{K \to \infty}\left|\mathbb{P}\left(T_0^2 < T_{\varepsilon^\xi}^2 \wedge R_{2\varepsilon}\;\middle|\;\mathbf{N}_0^K = \left(m_1^K, \frac{1}{K}, 0\right)\right) - q\right| = o_\varepsilon(1), \tag{20}$$

where $o_\varepsilon(1)$ *tends to zero as* $\varepsilon \downarrow 0$.

In order to prove the proposition, we first verify the following lemma.

Lemma 4.2. *Under the assumptions of Proposition* 4.1, *there exists a positive constant* ε_0 *such that for any* $\xi \in [1/2, 1]$ *and* $0 < \varepsilon \leq \varepsilon_0$,

$$\limsup_{K \to \infty}\mathbb{P}\left(R_{2\varepsilon} \leq T_{\varepsilon^\xi}^2 \wedge T_0^2\right) = 0.$$

Proof. We verify this lemma via coupling the rescaled population size $N_{1,t}^K$ with two birth-and-death processes, $Y_{1,t}^1$ and $Y_{1,t}^2$, on time scales where the mutant population is still small compared to K. More precisely, following [15, Section 3.1.2],

$$Y_{1,t}^1 \leq N_{1,t}^K \leq Y_{1,t}^2, \qquad \text{a.s.} \qquad \forall t \leq T_0^2 \wedge T_{\varepsilon^\xi}^2. \tag{21}$$

The latter processes will also depend on K, but we omit the notation K from their nomenclature for simplicity. In order to satisfy (21), the processes $Y_1^1 = (Y_{1,t}^1)_{t \geq 0}$ and $Y_1^2 = (Y_{1,t}^2)_{t \geq 0}$ can be chosen with the following birth and death rates

$$Y_{1,t}^1: \quad \begin{aligned} \frac{i}{K} &\to \frac{i+1}{K} \quad \text{at rate} \quad i\lambda_1, \\ \frac{i}{K} &\to \frac{i-1}{K} \quad \text{at rate} \quad i\left(\mu + \alpha \frac{i}{K} + \alpha\varepsilon^\xi\right). \end{aligned}$$

and

$$Y_{1,t}^2: \quad \begin{aligned} \frac{i}{K} &\to \frac{i+1}{K} \quad \text{at rate} \quad i\lambda_1, \\ \frac{i}{K} &\to \frac{i-1}{K} \quad \text{at rate} \quad i\left(\mu + \alpha \frac{i}{K}\right). \end{aligned}$$

Let us estimate the time until which the processes Y_1^1 and Y_2^1 stay close to the value $\bar{n}_1$. We define the stopping times

$$R_\varepsilon^i := \inf\{t \geq 0: Y_{1,t}^i \notin [\bar{n}_1 - \varepsilon, \bar{n}_1 + \varepsilon]\}, \qquad i \in \{1, 2\}, \ \varepsilon > 0.$$

For large K, according to [19, Theorem 2.1, p. 456], the dynamics of $Y_{1,t}^1$ is close to the one of the unique solution to

$$\dot{n} = n(\lambda_1 - \mu - \alpha n - \alpha\varepsilon^\xi).$$

The equilibria of this ODE are 0 and $\bar{n}_1^{(\varepsilon)} = \frac{\lambda_1 - \mu - \alpha\varepsilon^\xi}{\alpha} = \bar{n}_1 - \varepsilon^\xi$. Since $\lambda_1 > \mu$, the latter equilibrium is positive for all sufficiently small $\varepsilon > 0$. Linearizing implies that for all small enough $\varepsilon > 0$ (namely, for ε such that $\alpha\varepsilon^\xi < \lambda_1 - \mu$), the equilibrium 0 is unstable and the one $\bar{n}_1^{(\varepsilon)}$ is asymptotically stable. A direct analysis of the sign of $n(\lambda_1 - \mu - \alpha n - \alpha\varepsilon^\xi)$ implies that for such ε, any solution with a positive initial condition converges to the stable equilibrium $\bar{n}_1^{(\varepsilon)}$ as $t \to \infty$. These also imply that there exists $\varepsilon_0 > 0$ such that for all $0 < \varepsilon \leq \varepsilon_0$,

$$\left|\bar{n}_1 - \bar{n}_1^{(\varepsilon)}\right| = \varepsilon^\xi \qquad \text{and} \qquad 0 \notin [\bar{n}_1 - 2\varepsilon, \bar{n}_1 + 2\varepsilon].$$

Now, using a result about exit of jump processes from a domain by Freidlin and Wentzell [21, Chapter 5], there exists a family (over K) of Markov jump processes $\widetilde{Y}_1^1 = (\widetilde{Y}_{1,t}^1)_{t \geq 0}$ whose transition rates are positive, bounded, Lipschitz continuous, and uniformly bounded away from 0 such that for

$$\widetilde{R}_\varepsilon^1 = \inf\{t \geq 0: \widetilde{Y}_{1,t}^1 \notin [\bar{n}_1 - \varepsilon, \bar{n}_1 + \varepsilon]\}, \qquad i \in \{1, 2\}, \ \varepsilon > 0,$$

there exists $V > 0$ such that

$$\mathbb{P}(R_{2\varepsilon}^1 > e^{KV}) = \mathbb{P}(\widetilde{R}_{2\varepsilon}^1 > e^{KV}) \xrightarrow[K \to \infty]{} 0. \tag{22}$$

Using similar arguments for N_1^2, we derive that for $\varepsilon > 0$, $V > 0$ small enough, we have that

$$\mathbb{P}(R_{2\varepsilon}^1 > e^{KV}) \xrightarrow[K \to \infty]{} 0. \tag{23}$$

Now, on the event $\{R_{2\varepsilon} \leq T_0^2 \wedge T_{\varepsilon\xi}^2\}$ we have $R_{2\varepsilon} \geq R_{2\varepsilon}^1 \wedge R_{2\varepsilon}^2$. Using (22) and (23), we derive that

$$\limsup_{K \to \infty} \mathbb{P}(R_{2\varepsilon} \leq e^{KV}, R_{2\varepsilon} \leq T_0^2 \wedge T_{\varepsilon\xi}^2) = 0.$$

Moreover, using Markov's inequality,

$$\begin{aligned}
\mathbb{P}(R_{2\varepsilon} \leq T_0^2 \wedge T_{\varepsilon\xi}^2) &\leq \mathbb{P}(R_{2\varepsilon} \leq e^{KV}, R_{2\varepsilon} \leq T_0^2 \wedge T_{\varepsilon\xi}^2) \\
&\quad + \mathbb{P}(R_{2\varepsilon} \wedge T_0^2 \wedge T_{\varepsilon\xi}^2 \geq e^{KV}) \\
&\leq \mathbb{P}(R_{2\varepsilon} \leq e^{KV}, R_{2\varepsilon} \leq T_0^2 \wedge T_{\varepsilon\xi}^2) + e^{-KV}\mathbb{E}(R_{2\varepsilon} \wedge T_0^2 \wedge T_{\varepsilon\xi}^2).
\end{aligned}$$

Since we have

$$\mathbb{E}[R_{2\varepsilon} \wedge T_0^2 \wedge T_{\varepsilon\xi}^2] \leq \mathbb{E}\left[\int_0^{R_{2\varepsilon} \wedge T_0^2 \wedge T_{\varepsilon\xi}^2} K N_{2,t}^K \mathrm{d}t\right],$$

it suffices to show that there exists $C > 0$ such that

$$\mathbb{E}\left[\int_0^{R_{2\varepsilon} \wedge T_0^2 \wedge T_{\varepsilon\xi}^2} K N_{2,t}^K \mathrm{d}t\right] \leq C\varepsilon^\xi K. \tag{24}$$

This can be done similarly to [15, Section 3.1.2]. Indeed, let $\mathcal{L}$ be the infinitesimal generator of $(\mathbf{N}_t^K)_{t \geq 0}$. We want to show that there exists a function $g \colon (\frac{1}{K}\mathbb{N}_0)^3 \to \mathbb{R}$ defined as

$$g(n_1, n_{2a}, n_{2d}) = \gamma_1 n_{2a} + \gamma_2 n_{2d} \tag{25}$$

such that

$$\mathcal{L}g(\mathbf{N}_t^K) \geq N_{2,t}^K. \tag{26}$$

If (26) holds, then (24) follows because thanks to Dynkin's formula,

$$\begin{aligned}
\mathbb{E}\left[\int_0^{R_{2\varepsilon} \wedge T_0^2 \wedge T_{\varepsilon\xi}^2} K N_{2,t}^K \mathrm{d}t\right] &\leq \mathbb{E}\left[\int_0^{R_{2\varepsilon} \wedge T_0^2 \wedge T_{\varepsilon\xi}^2} K \mathcal{L}g(\mathbf{N}_t^K)\mathrm{d}t\right] \\
&= \mathbb{E}[K g(\mathbf{N}_{R_{2\varepsilon} \wedge T_0^2 \wedge T_{\varepsilon\xi}^2}^K) - K g(\mathbf{N}_0^K)] \\
&\leq (\gamma_1 \vee \gamma_2)\varepsilon^\xi K - (\gamma_1 \wedge \gamma_2),
\end{aligned}$$

which implies (24), independently of the signs of γ_1 and γ_2. Let us apply the infinitesimal generator $\mathcal{L}$ to the function g defined in (25). We obtain

$$\begin{aligned}
\mathcal{L}g(\mathbf{N}_t^K) = N_{2a,t}^K\big[(\lambda_2 - \mu - \alpha(N_{1,t}^K + N_{2a,t}^K))\gamma_1 + p\alpha(N_{1,t}^K + N_{2a,t}^K)\gamma_2\big] \\
+ N_{2d,t}^K\big[\sigma\gamma_1 - (\kappa\mu + \sigma)\gamma_2\big].
\end{aligned}$$

Hence, according to (26), it suffices to show that there exists $\gamma_1, \gamma_2 \in \mathbb{R}$ such that the following system of inequalities is satisfied:

$$(\lambda_2 - \mu - \alpha(N_{1,t}^K + N_{2a,t}^K))\gamma_1 + p\alpha(N_{1,t}^K + N_{2a,t}^K)\gamma_2 > 1, \tag{27}$$

$$\sigma\gamma_1 - (\kappa\mu + \sigma)\gamma_2 > 1. \tag{28}$$

Since $N_{1,t}^K + N_{2a,t}^K$ varies in t, the system (27)–(28) of inequalities is not easy to handle. However, for $t \in [0, R_{2\varepsilon} \wedge T_0^2 \wedge T_{\varepsilon\xi}^2]$, we have $\alpha N_t^K \leq \alpha(\bar{n}_1 + 2\varepsilon + \varepsilon^\xi)$ and $p\alpha N_t^K \geq p\alpha(\bar{n}_1 - 2\varepsilon)$. Hence,

$$\begin{aligned}
&(\lambda_2 - \mu - \alpha(N_{1,t}^K + N_{2a,t}^K))\gamma_1 + p\alpha(N_{1,t}^K + N_{2a,t}^K)\gamma_2 \\
&\geq (\lambda_2 - \mu - \alpha(\bar{n}_1 + 2\varepsilon + \varepsilon^\xi))\gamma_1 + p\alpha(\bar{n}_1 - 2\varepsilon)\gamma_2,
\end{aligned}$$

which implies that (27) is satisfied as soon as

$$(\lambda_2 - \mu - \alpha(\bar{n}_1 + 2\varepsilon + \varepsilon^\xi))\gamma_1 + p\alpha(\bar{n}_1 - 2\varepsilon)\gamma_2 > 1,$$

which, according to the definition of $\bar{n}_1$, can also written as

$$(\lambda_2 - \lambda_1 - 2\varepsilon - \varepsilon^\xi)\gamma_1 + p(\lambda_1 - \mu - 2\varepsilon)\gamma_2 > 1. \tag{29}$$

Let us verify the existence of γ_1 and γ_2 satisfying (29) and (28). First of all, we can rewrite (28) as follows

$$\gamma_2 < \frac{\sigma\gamma_1 - 1}{\kappa\mu + \sigma}. \tag{30}$$

Hence, let us first consider the equation

$$(\lambda_2 - \lambda_1 - 2\varepsilon - \varepsilon^\xi)\gamma_1 + p(\lambda_1 - \mu - 2\varepsilon)\frac{\sigma\gamma_1 - 1}{\kappa\mu + \sigma} > 1. \tag{31}$$

The inequality (5) is satisfied by assumption, and hence there exists $\varepsilon > 0$ such that

$$(\lambda_2 - \lambda_1 - 2\varepsilon - \varepsilon^\xi) + p(\lambda_1 - \mu - 2\varepsilon)\frac{\sigma}{\kappa\mu + \sigma} > 0.$$

Hence, $(\lambda_2 - \lambda_1 - 2\varepsilon - \varepsilon^\xi)\gamma_1 + p(\lambda_1 - \mu - 2\varepsilon)\frac{\sigma\gamma_1}{\kappa\mu + \sigma}$ tends to infinity as $\gamma_1 \to \infty$, in particular, for all sufficiently large γ_1 it is strictly larger than $1 + \frac{p(\lambda_1 - \mu - 2\varepsilon)}{\kappa\mu + \sigma}$, and thus (31) holds. By continuity of the function $x \mapsto p(\lambda_1 - \mu - 2\varepsilon)x$, this implies that for any γ_1 satisfying (31) there exists γ_2 satisfying (30) such that (29) holds. We conclude the lemma. □

Proof of Proposition 4.1. In what follows, we consider our population process on the event

$$A_\varepsilon := \{T_0^2 \wedge T_{\varepsilon^\xi}^2 < R_{2\varepsilon}\}$$

for sufficiently small $\varepsilon > 0$. On this event, the invasion or extinction of the mutant population will happen before the resident population substantially deviates from its equilibrium size. We couple on A_ε the process $(KN_{2a,t}^K, KN_{2d,t}^K)$ with two bi-type branching processes $(Z_{2a,t}^{\varepsilon,-}, Z_{2d,t}^{\varepsilon,-})$ and $(Z_{2a,t}^{\varepsilon,+}, Z_{2d,t}^{\varepsilon,+})$ on $\mathbb{N}_0^2$ (these processes again depend on K, but we omit that from the notation for readability) such that almost surely, for any $t < t_\varepsilon := T_0^2 \wedge T_{\varepsilon^\xi}^2 \wedge R_{2\varepsilon}$ and $\upsilon \in \{a, d\}$,

$$\begin{aligned} Z_{2\upsilon,t}^{\varepsilon,-} &\leq \widehat{Z}_{2\upsilon}(t) \leq Z_{2\upsilon,t}^{\varepsilon,+}, \\ Z_{2\upsilon,t}^{\varepsilon,-} &\leq KN_{2\upsilon,t}^K \leq Z_{2\upsilon,t}^{\varepsilon,+}, \end{aligned} \tag{32}$$

where we recall the approximating branching process $(\widehat{Z}_{2a}(t), \widehat{Z}_{2d}(t))$ defined in Section 2.2. We claim that in order to satisfy (32), these processes can be defined with the following jump rates:

$(Z_{2a,t}^{\varepsilon,-}, Z_{2d,t}^{\varepsilon,-})$:

$(i, j) \to (i + 1, j)$	at rate $i\lambda_2$,
$(i, j) \to (i - 1, j)$	at rate $i(\mu + (1 - p)\alpha(\varepsilon^\xi + \bar{n}_1 + 2\varepsilon) + p\alpha(4\varepsilon + \varepsilon^\xi))$,
$(i, j) \to (i - 1, j + 1)$	at rate $ip\alpha(\bar{n}_1 - 2\varepsilon)$,
$(i, j) \to (i + 1, j - 1)$	at rate $j\sigma$,
$(i, j) \to (i, j - 1)$	at rate $j\kappa\mu$,

and

$(Z_{2a,t}^{\varepsilon,+}, Z_{2d,t}^{\varepsilon,+})$:

$(i, j) \rightarrow (i + 1, j)$ at rate $i\lambda_2$,

$(i, j) \rightarrow (i - 1, j)$ at rate $i(\mu + (1 - p)\alpha(\bar{n}_1 - 2\varepsilon) - p\alpha(4\varepsilon + \varepsilon^\xi))$,

$(i, j) \rightarrow (i - 1, j + 1)$ at rate $ip\alpha(\bar{n}_1 + 2\varepsilon + \varepsilon^\xi)$,

$(i, j) \rightarrow (i + 1, j - 1)$ at rate $j\sigma$,

$(i, j) \rightarrow (i, j - 1)$ at rate $j\kappa\mu$.

Informally speaking, (32) holds thanks to the fact that for branching processes having the same kind of transitions as $(KN_{2a,t}^K, KN_{2d,t}^K)_{t\geq 0}$, competition-induced switching to dormancy is more favourable for an active mutant individual than immediate death by competition, but not better, and for $\kappa > 0$ strictly worse, than not being hit by a competitive event at all.

Now, for $\diamond \in \{+, -\}$ and for a fixed initial condition (i, j), the total competitive event rate of $(Z_{2a,t}^{\varepsilon,\diamond}, Z_{2d,t}^{\varepsilon,\diamond})$ is given as the sum of the $(i, j) \rightarrow (i - 1, j)$ and the $(i, j) \rightarrow (i - 1, j + 1)$ jump rate corresponding to the process. Given that a competitive event has happened, the ratio of the probability of death by competition and the one of switching to dormancy is equal to the ratio of the $(i, j) \rightarrow (i - 1, j)$ rate and the $(i, j) \rightarrow (i - 1, j + 1)$ rate. Further, for any fixed initial condition, $(Z_{2a,t}^{\varepsilon,-}, Z_{2d,t}^{\varepsilon,-})$ has higher death rate, higher total competitive event rate, but lower rate for active→dormant switching rate than $(\widehat{Z}_{2a}(t), \widehat{Z}_{2d}(t))$ for any $t \geq 0$ or than $(KN_{2a,t}^K, KN_{2d,t}^K)$ for $t < t_\varepsilon$ on the event A_ε, while all other rates are the same for all these processes. Birth-and-death processes are coordinatewise nonincreasing (for $\kappa > 0$ decreasing) in the rate of competitive events. Indeed, after a competitive event the affected active mutant individual either dies immediately or moves to the seed bank, where it dies with probability less than one (but for $\kappa > 0$ more than zero) before ever becoming active again. On the other hand, the $(i, j) \rightarrow (i - 1, j + 1)$ switching rates are the lowest for $(Z_{2a,t}^{\varepsilon,-}, Z_{2d,t}^{\varepsilon,-})$, which ensures that less individuals enter the seed bank and the couplings (32) hold also for $\upsilon = d$. The corresponding inequalities for $(Z_{2a,t}^{\varepsilon,+}, Z_{2d,t}^{\varepsilon,+})$ in (32) follow similarly since this process has the lowest rate for death and for competitive events in total but the highest rate for active→dormant switching.

For $\diamond \in \{+, -\}$, let $q^{(\varepsilon,\diamond)}$ denote the extinction probability of the process $(Z_{2a,t}^{\varepsilon,\diamond}, Z_{2d,t}^{\varepsilon,\diamond})$ started from $(1, 0)$. The extinction probability of a supercritical branching process is continuous with respect to all kinds of transitions that the mutant population in our model has. Given the total competitive event rate, this probability increases with the rate of active death by competition. Further, given the ratio between the rate of death by competition and the one of active→dormant switching, it increases with the total competitive event rate. These assertions can be proven using the methods of [15, Sections A.3]. Hence, by the first line of (32), we have $q^{(\varepsilon,+)} \leq q \leq q^{(\varepsilon,-)}$ for fixed $\varepsilon > 0$ and

$$0 \leq \liminf_{\varepsilon \downarrow 0} \left| q^{(\varepsilon,\diamond)} - q \right| \leq \limsup_{\varepsilon \downarrow 0} \left| q^{(\varepsilon,\diamond)} - q \right| \leq \limsup_{\varepsilon \downarrow 0} \left| q^{(\varepsilon,-)} - q^{(\varepsilon,+)} \right| = 0, \tag{33}$$

for all $\diamond \in \{+, -\}$, where we recall the extinction probability q defined in (7).

Next, we prove that the probabilities of extinction and invasion of the actual process $(N_{2a,t}^K, N_{2d,t}^K)$ also tend to q and $1 - q$, respectively, with high probability as $K \rightarrow \infty$. We define the stopping times

$$T_x^{(\varepsilon,\diamond),2} := \inf\{t > 0 : Z_{2a}^{(\varepsilon,\diamond)}(t) + Z_{2d}^{(\varepsilon,\diamond)}(t) = \lfloor Kx \rfloor\}, \qquad \diamond \in \{+, -\}, x \in \mathbb{R}.$$

Thanks to the coupling in the second line of (32), which is valid on A_ε, we have

$$\mathbb{P}\big(T_{\varepsilon^\xi}^{(\varepsilon,-),2} \leq T_0^{(\varepsilon,-),2}, A_\varepsilon\big) \leq \mathbb{P}\big(T_{\varepsilon^\xi}^2 \leq T_0^2, A_\varepsilon\big) \leq \mathbb{P}\big(T_{\varepsilon^\xi}^{(\varepsilon,+),2} \leq T_0^{(\varepsilon,+),2}, A_\varepsilon\big) \tag{34}$$

Indeed, if a process reaches the size $K\varepsilon^\xi$ before dying out, then the same holds for a larger process. However, A_ε is independent of $(Z_{2a,t}^{\varepsilon,\diamond}, Z_{2d,t}^{\varepsilon,\diamond})$ for both $\diamond = +$ and $\diamond = -$, and hence

$$\liminf_{K\to\infty} \mathbb{P}\big(T_{\varepsilon^\xi}^{(\varepsilon,-),2} \leq T_0^{(\varepsilon,-),2}, A_\varepsilon\big) = \liminf_{K\to\infty} \mathbb{P}(A_\varepsilon)\mathbb{P}\big(T_{\varepsilon^\xi}^{(\varepsilon,-),2} \leq T_0^{(\varepsilon,-),2}\big)$$
$$\geq (1 - q^{(\varepsilon,-)})(1 - o_\varepsilon(1)) \tag{35}$$

and

$$\limsup_{K\to\infty} \mathbb{P}\big(T_{\varepsilon^\xi}^{(\varepsilon,+),2} \leq T_0^{(\varepsilon,+),2}, A_\varepsilon\big) = \limsup_{K\to\infty} \mathbb{P}(A_\varepsilon)\mathbb{P}\big(T_{\varepsilon^\xi}^{(\varepsilon,+),2} \leq T_0^{(\varepsilon,+),2}\big)$$
$$\leq (1 - q^{(\varepsilon,+)})(1 + o_\varepsilon(1)). \tag{36}$$

Letting $K \to \infty$ in (34) and applying (35) and (36) yields that

$$\limsup_{K\to\infty} \big|\mathbb{P}(T_{\varepsilon^\xi}^2 \leq T_0^2, A_\varepsilon) - (1 - q)\big| = o_\varepsilon(1),$$

as required. Eq. (20) can be derived similarly.

It remains to show that in the case of invasion, the time before reaching size $K\varepsilon^\xi$ is of order $\log K / \widetilde{\lambda}$, where $\widetilde{\lambda}$ was defined in (12) as the maximal eigenvalue of the matrix J defined in (4), which is positive under our assumptions.

Let $\widetilde{\lambda}^{(\varepsilon,\diamond)}$, $\diamond \in \{+,-\}$, denote the maximal eigenvalue of the mean matrix of the process $(Z_{2a,t}^{\varepsilon,\diamond}, Z_{2d,t}^{\varepsilon,\diamond})$. This eigenvalue is positive for all small enough $\varepsilon > 0$ and converges to $\widetilde{\lambda}$ as $\varepsilon \downarrow 0$. Hence, there exists a function $f : (0,\infty) \to (0,\infty)$ with $\lim_{\varepsilon\downarrow 0} f(\varepsilon) = 0$ such that for all $\varepsilon > 0$ sufficiently small,

$$\left|\frac{\widetilde{\lambda}^{(\varepsilon,\diamond)}}{\widetilde{\lambda}} - 1\right| \leq \frac{f(\varepsilon)}{2}. \tag{37}$$

Let us fix ε small enough such that (37) holds. Then from the second line of (32) we deduce that

$$\mathbb{P}\big(T_{\varepsilon^\xi}^{(\varepsilon,-),2} \leq T_0^{(\varepsilon,-),2} \wedge \frac{\log K}{\widetilde{\lambda}}(1 + f(\varepsilon)), A_\varepsilon\big) \leq \mathbb{P}\big(T_{\varepsilon^\xi}^2 \leq T_0^2 \wedge \frac{\log K}{\widetilde{\lambda}}(1 + f(\varepsilon)), A_\varepsilon\big).$$

Using this together with the independence between A_ε and $(Z_{2a,t}^{\varepsilon,\diamond}, Z_{2d,t}^{\varepsilon,\diamond})$ and employing [1, Section 7.5], we obtain for $\varepsilon > 0$ small enough (in particular such that $f(\varepsilon) < 1$)

$$\liminf_{K\to\infty} \mathbb{P}\Big(T_{\varepsilon^\xi}^{(\varepsilon,-),2} \leq T_0^{(\varepsilon,-),2} \wedge \frac{\log K}{\widetilde{\lambda}}(1 + f(\varepsilon)), A_\varepsilon\Big) \geq (1 - q^{(\varepsilon,-)})(1 - o_\varepsilon(1)).$$

This inequality follows from computations that are analogous to [15, Section 3.1.3, first display below (3.41)]. Similarly, using the second line of (32), we derive that for all sufficiently small $\varepsilon > 0$

$$\liminf_{K\to\infty} \mathbb{P}\Big(T_{\varepsilon^\xi}^{(\varepsilon,+),2} \geq T_0^{(\varepsilon,+),2} \wedge \frac{\log K}{\widetilde{\lambda}}(1 + f(\varepsilon)), A_\varepsilon\Big) \geq (1 - q^{(\varepsilon,+)})(1 + o_\varepsilon(1)).$$

These together imply (19), hence the proof of the proposition is finished. $\square$

4.2. The second phase of invasion: Lotka–Volterra phase

4.2.1. Convergence to a dynamical system for large population size

Now we rigorously state in what sense our population process $(\mathbf{N}_t^K)_{t\geq 0}$ is close to the solution $(\mathbf{n}_t)_{t\geq 0} = (n_1(t), n_{2a}(t), n_{2d}(t))_{t\geq 0}$ of the system of ODEs (6) for large K given that the

corresponding initial conditions are close to each other. As for (6), note that the vector field is locally Lipschitz and solutions do not explode in finite time, which guarantees existence and uniqueness for a given initial condition. Let $\mathbf{n}^0 = (n_1^0, n_{2a}^0, n_{2d}^0) \in [0, \infty)^3$ be an initial condition, and let $(\mathbf{n}^{(\mathbf{n}^0)}(t))_{t \geq 0}$ be the unique solution of the ODE started from the initial condition $\mathbf{n}^0$. Then, [19, Theorem 2.1, p. 456] implies the following.

Lemma 4.3. *Let $T > 0$. Assume that $(\mathbf{N}_0^K)_{K \geq 1}$ converge in probability to some deterministic vector $\mathbf{n}^0 = (n_1^0, n_{2a}^0, n_{2d}^0) \in [0, \infty)^3$ as K tends to infinity. Then*

$$\lim_{K \to \infty} \sup_{0 \leq s \leq T} \left| \mathbf{N}^K(s) - \mathbf{n}^{(\mathbf{n}^0)}(s) \right| = 0$$

in probability, where $| \cdot |$ denotes the Euclidean norm on $\mathbb{R}^3$.

4.2.2. Mutant active–dormant proportions

On the event $\{T_{\sqrt{\varepsilon}}^2 < T_0^2 \wedge R_{2\varepsilon}\} \subset A_\varepsilon$, after time T_ε^2 the total mutant population has size close to εK. Note that Proposition 4.1 provides us no coordinatewise information about the mutant population at this point in time. However, in order to guarantee convergence of the rescaled population process $(\mathbf{N}_t^K)_{t \geq 0}$ to a corresponding solution of the system of ODEs (6), we have to guarantee convergence of the initial conditions. We will thus show that with high probability, there exists a point in time in the interval $[T_\varepsilon^2, T_{\sqrt{\varepsilon}}^2]$ such that at this time, the resident population is still close to equilibrium, the total mutant population size is still at least of order εK and the proportion of active and dormant mutants is close to the equilibrium proportion of the approximating branching process $((\widehat{Z}_{2a}(t), \widehat{Z}_{2d}(t)))_{t \geq 0}$. The present section is devoted to this problem. Next, in Section 4.2.3, we show that the ODE system (6) started from the limiting initial condition converges to $(0, \bar{n}_{2a}, \bar{n}_{2d})$ as $t \to \infty$.

Since $\widetilde{\lambda}$ is positive, the Kesten–Stigum theorem (see e.g. [22, Theorem 2.1]) ensures that we have

$$\left(\frac{\widehat{Z}_{2a}(t)}{\widehat{Z}_{2a}(t) + \widehat{Z}_{2d}(t)}, \frac{\widehat{Z}_{2d}(t)}{\widehat{Z}_{2a}(t) + \widehat{Z}_{2d}(t)} \right) \xrightarrow[K \to \infty]{} (\pi_{2a}, \pi_{2d})$$

on the event of survival of the branching process $((\widehat{Z}_{2a,t}, \widehat{Z}_{2d,t}))_{t \geq 0}$, where (π_{2a}, π_{2d}) is the positive left eigenvector of J defined in (4) associated to $\widetilde{\lambda}$ such that $\pi_{2a} + \pi_{2d} = 1$, which can be computed explicitly according to (12). We verify the next proposition, employing some arguments of [15, Proposition 3.2].

Proposition 4.4. *There exists $C > 0$ sufficiently large such that for $\delta > 0$ such that $\pi_{2a} \pm \delta \in (0, 1)$, under the same assumptions as Proposition 4.1,*

$$\liminf_{K \to \infty} \mathbb{P} \left(\exists t \in \left[T_\varepsilon^2, T_{\sqrt{\varepsilon}}^2 \right], \frac{\varepsilon K}{C} \leq K N_{2,t}^K \leq \sqrt{\varepsilon} K, \right.$$
$$\left. \pi_{2a} - \delta < \frac{N_{2a,t}^K}{N_{2a,t}^K + N_{2d,t}^K} < \pi_{2a} + \delta \,\middle|\, T_{\sqrt{\varepsilon}}^2 < T_0^2 \wedge R_{2\varepsilon} \right) \geq 1 - o_\varepsilon(1). \tag{38}$$

Proof. If $\pi_{2a} - \delta < \frac{N_{2a,T_\varepsilon^2}^K}{N_{2a,T_\varepsilon^2}^K + N_{2d,T_\varepsilon^2}^K} < \pi_{2a} + \delta$, then there is nothing to show. Let us assume that

$$\frac{N_{2a,T_\varepsilon^2}^K}{N_{2a,T_\varepsilon^2}^K + N_{2d,T_\varepsilon^2}^K} \leq \pi_{2a} - \delta,$$

the symmetric case $\frac{N_{2a,T_\varepsilon^2}}{N_{2a,T_\varepsilon^2}+N_{2d,T_\varepsilon^2}} \geq \pi_{2a} + \delta$ can be treated similarly. Let us introduce the event

$$\widetilde{A}_\varepsilon := \{T_{\sqrt{\varepsilon}}^2 < T_0^2 \wedge R_{2\varepsilon}\}$$

on which we conditioned in (38). Our first goal is to show that for $\varepsilon > 0$ small, with high probability, once the total mutant population size reaches εK, for sufficiently large $C > 0$ it will not decrease to a level lower than $\varepsilon K / C$ again before it reaches $\sqrt{\varepsilon} K$. To be more precise, for $C > 0$ we introduce the stopping time

$$T_{\varepsilon, \varepsilon/C} = \inf\{t \geq T_\varepsilon^2 : N_{2,t}^K \leq \frac{\varepsilon K}{C}\}.$$

Then our goal is to show that if C is large enough, then $T_{\sqrt{\varepsilon}}^2$ is larger than $T_\varepsilon^2 + \log\log(1/\varepsilon)$ and smaller than $T_{\varepsilon, \varepsilon/C}$. First of all, for all $\varepsilon > 0$ sufficiently small, since the coupling (32) is satisfied on $\widetilde{A}_\varepsilon$ and the branching processes $(Z_{2a,t}^{\varepsilon,-}, Z_{2d,t}^{\varepsilon,-})$ is supercritical, [15, Lemma A.1] implies that for C large enough,

$$\lim_{K \to \infty} \mathbb{P}(T_{\varepsilon, \varepsilon/C} < T_{\sqrt{\varepsilon}}^2 | \widetilde{A}_\varepsilon) = 0. \tag{39}$$

On the other hand, note that the total size of mutant individuals is stochastically dominated from above by a Yule process with birth rate λ_2. Thus, by [15, Lemma A.2], we have

$$\lim_{K \to \infty} \mathbb{P}(T_{\sqrt{\varepsilon}}^2 \leq T_\varepsilon^2 + \log\log(1/\varepsilon) | \widetilde{A}_\varepsilon) \leq \sqrt{\varepsilon}(\log(1/\varepsilon))^{\lambda_2}. \tag{40}$$

Using these, we want to show that the fraction $\frac{N_{2a,t}^K}{N_{2a,t}^K + N_{2d,t}^K}$ cannot stay below $\pi_{2a} - \delta$ on $[T_\varepsilon^2, T_{\sqrt{\varepsilon}}^2]$ with probability close to one. Let us define the following five independent Poisson random measures on $[0, \infty)^2$ with intensity $\mathrm{d}s\mathrm{d}\theta$:

- $P_{2a}^b(\mathrm{d}s, \mathrm{d}\theta)$ representing the birth events of the active mutant individuals,
- $P_{2a}^d(\mathrm{d}s, \mathrm{d}\theta)$ representing the death events of the active mutant individuals,
- $P_{2a \to 2d}^s(\mathrm{d}s, \mathrm{d}\theta)$ representing the active→dormant switching events,
- $P_{2d}^d(\mathrm{d}s, \mathrm{d}\theta)$ representing the death events of the dormant mutant individuals (for $\kappa = 0$ this measure can be omitted),
- $P_{2d \to 2a}^s(\mathrm{d}s\mathrm{d}\theta)$ representing the dormant→active switching events.

The reason why competitive death events can be assumed as independent of active→dormant switches is that the corresponding Poisson random measures can be obtained as an independent thinning of a Poisson random measure with survival probability $1 - p$ respectively the complementary thinning (with survival probability p), which are independent Poisson random measures according to [25, Section 5.1]. Let

$$\widetilde{P}_{2a}^b(\mathrm{d}s, \mathrm{d}\theta) := P_{2a}^b(\mathrm{d}s, \mathrm{d}\theta) - \mathrm{d}s\mathrm{d}\theta, \ldots, \widetilde{P}_{2d \to 2a}^s(\mathrm{d}s, \mathrm{d}\theta) := P_{2d \to 2a}^s(\mathrm{d}s, \mathrm{d}\theta) - \mathrm{d}s\mathrm{d}\theta$$

be the associated compensated measures.

The fraction $\frac{N_{2a,t}^K}{N_{2a,t}^K + N_{2d,t}^K}$ is a semimartingale and can be decomposed as follows

$$\frac{N_{2a,t}^K}{N_{2a,t}^K + N_{2d,t}^K} = \frac{N_{2a,T_\varepsilon^2}^K}{N_{2a,T_\varepsilon^2}^K + N_{2d,T_\varepsilon^2}^K} + M_2(t) + V_2(t), \qquad t \geq T_\varepsilon^2,$$

with M_2 being a martingale and V_2 a finite variation process such that

$$
\begin{aligned}
M_2(t) = &\int_{T_\varepsilon^2}^t \int_{[0,\infty)} \mathbb{1}\{\theta \le \lambda_2 N_{2a,s-}^K\} \frac{N_{2d,s-}^K}{N_{2,s-}^K(N_{2,s-}^K + 1)} \widetilde{P}_{2a}^{\mathrm{b}}(\mathrm{d}s, \mathrm{d}\theta) \\
&- \int_{T_\varepsilon^2}^t \int_{[0,\infty)} \mathbb{1}\{\theta \le N_{2a,s-}^K(\mu + \alpha(1 - p)(N_{1,s-}^K + N_{2a,s-}^K))\} \\
&\quad \times \frac{N_{2d,s-}^K}{N_{2,s-}^K(N_{2,s-}^K - 1)} \widetilde{P}_{2a}^{\mathrm{d}}(\mathrm{d}s, \mathrm{d}\theta) \\
&- \int_{T_\varepsilon^2}^t \int_{[0,\infty)} \mathbb{1}\{\theta \le N_{2a,s-}^K(\alpha p(N_{1,s-}^K + N_{2a,s-}^K))\} \frac{1}{N_{2,s-}^K} \widetilde{P}_{2a\to 2d}^{\mathrm{s}}(\mathrm{d}s, \mathrm{d}\theta) \\
&+ \int_{T_\varepsilon^2}^t \int_{[0,\infty)} \mathbb{1}\{\theta \le \kappa\mu N_{2d,s-}^K\} \frac{N_{2a,s-}^K}{N_{2,s-}^K(N_{2,s-}^K - 1)} \widetilde{P}_{2d}^{\mathrm{d}}(\mathrm{d}s, \mathrm{d}\theta) \\
&+ \int_{T_\varepsilon^2}^t \int_{[0,\infty)} \mathbb{1}\{\theta \le \sigma N_{2d,s-}^K\} \frac{1}{N_{2,s-}^K} \widetilde{P}_{2d\to 2a}^{\mathrm{s}}(\mathrm{d}s, \mathrm{d}\theta)
\end{aligned}
$$

and

$$
\begin{aligned}
V_2(t) = \int_{T_\varepsilon^2}^t \bigg\{ &\lambda_2 N_{2a,s}^K \frac{N_{2d,s}^K}{N_{2,s}^K(N_{2,s}^K + 1)} \\
&- N_{2a,s}^K(\mu + \alpha(1 - p)(N_{1,s}^K + N_{2a,s}^K)) \frac{N_{2d,s}^K}{N_{2,s}^K(N_{2,s}^K - 1)} \\
&- N_{2a,s}^K(\alpha p(N_{1,s}^K + N_{2a,s}^K)) \frac{1}{N_{2,s}^K} \mathrm{d}s + \kappa\mu N_{2d,s}^K \frac{N_{2a,s}^K}{N_{2,s}^K(N_{2,s}^K - 1)} + \sigma N_{2d,s}^K \frac{1}{N_{2,s}^K} \bigg\} \mathrm{d}s.
\end{aligned}
$$

Further, the predictable quadratic variation of the martingale M_2 is given as follows

$$
\begin{aligned}
\langle M_2 \rangle_t = &\int_{T_\varepsilon^2}^t \lambda_2 N_{2a,s}^K \frac{(N_{2d,s}^K)^2}{(N_{2,s}^K)^2(N_{2,s}^K + 1)^2} \mathrm{d}s \\
&+ \int_{T_\varepsilon^2}^t \mu N_{2a,s}^K(\mu + \alpha(1 - p)(N_{1,s-}^K + N_{2a,s-}^K)) \frac{(N_{2d,s}^K)^2}{(N_{2,s}^K)^2(N_{2,s}^K - 1)^2} \\
&+ N_{2a,s}^K \alpha p(N_{1,s-}^K + N_{2a,s-}^K) \frac{1}{(N_{2,s}^K)^2} \mathrm{d}s + \kappa\mu N_{2d,s}^K \frac{(N_{2a,s}^K)^2}{(N_{2,s}^K(N_{2,s}^K - 1))^2} \\
&+ \sigma N_{2d,s}^K \frac{1}{(N_{2,s}^K)^2} \mathrm{d}s.
\end{aligned}
$$

This yields that there exists $C_0 > 0$ such that for all $t \ge T_\varepsilon^2$,

$$
\langle M_2 \rangle_t \le C_0(t - T_\varepsilon^2) \sup_{T_\varepsilon^2 \le s \le t} \frac{1}{N_{2,s}^K - 1}.
$$

This implies

$$
\langle M_2 \rangle_{(T_\varepsilon^2 + \log\log(1/\varepsilon)) \wedge T_{\varepsilon,\varepsilon/C}} \le \frac{C_0 \log\log(1/\varepsilon)}{\frac{\varepsilon K}{C} - 1} \tag{41}
$$

and

$$
\begin{aligned}
&\limsup_{K\to\infty} \mathbb{P}\Big(\sup_{T_\varepsilon^2 \le t \le T_\varepsilon^2 + \log\log(1/\varepsilon)} |M_2(t)| \ge \varepsilon \Big| \widetilde{A}_\varepsilon \Big) \\
&\le \limsup_{K\to\infty} \Big(\mathbb{P}\Big(\sup_{T_\varepsilon^2 \le t \le (T_\varepsilon^2 + \log\log(1/\varepsilon)) \wedge T_{\varepsilon,\varepsilon/C}} |M_2(t)| \ge \varepsilon \Big| \widetilde{A}_\varepsilon \Big) \\
&\qquad\qquad + \mathbb{P}\big(T_{\varepsilon,\varepsilon/C} < T_\varepsilon^2 + \log\log(1/\varepsilon) \big| \widetilde{A}_\varepsilon \big) \Big) \\
&\le \limsup_{K\to\infty} \frac{1}{\varepsilon^2} \mathbb{E}\Big[\langle M_2 \rangle_{(T_\varepsilon^2 + \log\log(1/\varepsilon)) \wedge T_{\varepsilon,\varepsilon/C}} \Big| \widetilde{A}_\varepsilon \Big] + \sqrt{\varepsilon}(\log 1/\varepsilon)^{\lambda_2} \\
&= \sqrt{\varepsilon}(\log 1/\varepsilon)^{\lambda_2},
\end{aligned}
\tag{42}
$$

where in the first inequality of the last line we used Doob's martingale inequality for the first term and (39) together with (40) for the second term, and the last inequality of the last line is due to (41).

Let us now consider the finite variation process V_2. This can be written as

$$
V_2(t) = \int_{T_\varepsilon^2}^t P\Big(\frac{N_{2a,s}^K}{N_{2,s}^K}\Big) \frac{N_{2,s}^K}{N_{2,s}^K + 1} + Q^{(s)}\Big(\frac{N_{2a,s}^K}{N_{2,s}^K}\Big) \frac{N_{2,s}^K}{N_{2,s}^K - 1} + R^{(s)}\Big(\frac{N_{2a,s}^K}{N_{2,s}^K}\Big) ds,
\tag{43}
$$

with

$$
P(x) = \lambda_2 x(1-x), \quad Q^{(s)}(x) = (\kappa\mu - \mu - \alpha(1-p)(N_{1,s}^K + N_{2a,s}^K))x(1-x),
$$
$$
R^{(s)}(x) = \sigma(1-x) - p\alpha(N_{1,s}^K + N_{2a,s}^K)x.
$$

For $\varepsilon > 0$ small, on $[T_\varepsilon^2, T_{\sqrt{\varepsilon}}^2]$, $Q^{(s)}$ and $R^{(s)}$ are close on $[0,1]$, respectively, to the polynomial functions Q, R given as follows

$$
Q(x) = (\kappa\mu - \mu - \alpha(1-p)\bar{n}_1)x(1-x) = (\kappa\mu - \mu - (1-p)(\lambda_1 - \mu))x(1-x),
$$
$$
R(x) = \sigma(1-x) - p\alpha\bar{n}_1 x = \sigma(1-x) - p(\lambda_1 - \mu)x.
$$

Thus, for given $\varepsilon > 0$, for all sufficiently large K, the integrand in (43) is close to the polynomial function

$$
S(x) = (\lambda_2 + \kappa\mu - \mu - (1-p)(\lambda_1 - \mu))x(1-x) + \sigma(1-x) - p(\lambda_1 - \mu)x.
$$

Since $S(0) > 0$ and $S(1) < 0$, further, S is of degree 2, the equation $\dot{x} = S(x)$ has a unique equilibrium in $(0,1)$. Now, let (π_{2a}, π_{2d}) be the left eigenvector of the matrix J defined in (4) corresponding to the eigenvalue $\widetilde{\lambda}$ such that $\pi_{2a} + \pi_{2d} = 1$. A direct computation implies that π_{2a} is a root of S and thus equal to this equilibrium. Thus, we can choose $\delta > 0$ and $\theta > 0$ such that $\pi_{2a} - \delta > 0$ and for all $x < \pi_{2a} - \delta$, $S(x) > \theta/2$. By continuity, this implies that for all sufficiently small $\varepsilon > 0$ and accordingly chosen sufficiently large $K > 0$, on the event $\widetilde{A}_\varepsilon$ the following relation holds for all $s \in [T_\varepsilon^2, T_{\sqrt{\varepsilon}}^2]$ and $x \in (0, \pi_{2a} - \delta)$:

$$
P(x)\frac{N_{2,s}^K + 1}{N_{2,s}^K} + Q^{(s)}(x)\frac{N_{2,s}^K - 1}{N_{2,s}^K} + R^{(s)}(x) \ge \frac{\theta}{2} > 0.
\tag{44}
$$

Let us define

$$
\mathfrak{t}_{2a}^{(\varepsilon)} := \inf\Big\{ t \ge T_\varepsilon^2 : \frac{N_{2a,t}^K}{N_{2d,t}^K} \ge \pi_{2a} - \delta \Big\}.
$$

From (42) and (44) we obtain that on the event $\widetilde{A}_\varepsilon$, for any $t \in [T_\varepsilon^2, (T_\varepsilon^2 + \log\log(1/\varepsilon)) \wedge \mathfrak{t}_{2a}^{(\varepsilon)}]$,

$$\pi_{2a} - \delta \geq \frac{N_{2a,t}^K}{N_{2,t}^K} \geq \frac{\theta}{2}\left(\log\log(1/\varepsilon) \wedge (\mathfrak{t}_{2a}^{(\varepsilon)} - T_\varepsilon^2)\right) - \varepsilon$$

with a probability higher than $1 - \sqrt{\varepsilon}(\log(1/\varepsilon))^{\lambda_2}$. Since $\frac{\theta}{2}\log\log(1/\varepsilon)$ tends to ∞ as $\varepsilon \downarrow 0$, it follows that for $\varepsilon > 0$ small, $\mathfrak{t}_{2a}^{(\varepsilon)}$ is smaller than $T_\varepsilon^2 + \log\log(1/\varepsilon)$ and thus smaller than $T_{\sqrt{\varepsilon}}^2$ with a probability close to 1 on the event $\widetilde{A}_\varepsilon$, where we also used (40).

Lastly, note that each jump of the process $N_{2a,t}^K/N_{2,t}^K$ is smaller than $(\varepsilon K/C + 1)^{-1}$, and hence smaller than δ for all K sufficiently large (given ε). Thus, after the time $\mathfrak{t}_{2a}^{(\varepsilon)}$, the process will be contained in the interval $[\pi_{2a} - \delta, \pi_{2a} + \delta]$ for some positive amount of time. Hence, we conclude the proposition. $\square$

4.2.3. Convergence of the dynamical system for large times

In this section, we first investigate the stability of the equilibria of the system of ODEs (6) via linearization. Then we show convergence of the solution of the system to $(0, \bar{n}_{2a}, \bar{n}_{2d})$ for initial conditions corresponding to Proposition 4.4, and for the two-dimensional projection of the system even for any nonnegative initial condition that has at least one nonzero coordinate. As mentioned before, the behaviour of the dynamical system is rather different from the ones described in [15,16].

Proposition 4.5. *Assume that (5) holds. Then the system of ODEs (6) admits precisely three equilibria: $(0, 0, 0)$, $(\bar{n}_1, 0, 0)$ and $(0, \bar{n}_{2a}, \bar{n}_{2d})$, the first two of which are unstable, whereas the third one is asymptotically stable.*

Proof. We easily identify the equilibria $(0, 0, 0)$, $(\bar{n}_1, 0, 0)$ and $(0, \bar{n}_{2a}, \bar{n}_{2d})$, and we claim that further equilibria do not exist. Indeed, it is easy to see that apart from $(0, 0, 0)$, the only possible coordinatewise nonnegative equilibrium of the form $(0, \cdot, \cdot)$ is $(0, \bar{n}_{2a}, \bar{n}_{2d})$ and the only possible one of the form $(\cdot, 0, \cdot)$ or $(\cdot, \cdot, 0)$ is $(\bar{n}_1, 0, 0)$. Hence, it remains to exclude the existence of equilibria with three positive coordinates. For such equilibria (n_1, n_{2a}, n_{2d}), expressing n_1 from the first line of (6) and substituting it into the second and third line divided by n_{2a} yields

$$\frac{n_{2d}}{n_{2a}} = \frac{\lambda_1 - \lambda_2}{\sigma} = \frac{1}{\kappa\mu + \sigma}p(\lambda_1 - \mu),$$

but the last inequality contradicts with (5). We conclude the claim.

We continue with checking stability of the three equilibria. At any equilibrium (n_1, n_{2a}, n_{2d}), the Jacobian matrix is given as

$$B(n_1, n_{2a}, n_{2d}) = \begin{pmatrix} \lambda_1 - \mu - 2\alpha n_1 - \alpha n_{2a} & -\alpha n_1 & 0 \\ -\alpha n_{2a} & \lambda_2 - \mu - 2\alpha n_{2a} - \alpha n_1 & \sigma \\ p\alpha n_{2a} & 2p\alpha n_{2a} + p\alpha n_1 & -(\kappa\mu + \sigma) \end{pmatrix}.$$

As for the origin, B takes the block diagonal form

$$B(0, 0, 0) = \begin{pmatrix} \lambda_1 - \mu & 0 & 0 \\ 0 & \lambda_2 - \mu & \sigma \\ 0 & 0 & -(\kappa\mu + \sigma) \end{pmatrix}.$$

Its spectrum is the union of the spectra of the two blocks, hence $\lambda_1 - \mu$ is an eigenvalue (with eigenvector $(1, 0, 0)$). Since this eigenvalue is positive, the origin is unstable. At $(\bar{n}_1, 0, 0)$, since

$\alpha \bar{n}_1 = \lambda_1 - \mu$, the Jacobian matrix is

$$B(\bar{n}_1, 0, 0) = \begin{pmatrix} -\lambda_1 + \mu & -\lambda_1 + \mu & 0 \\ 0 & \lambda_2 - \lambda_1 & \sigma \\ 0 & p(\lambda_1 - \mu) & -(\kappa \mu + \sigma) \end{pmatrix}. \tag{45}$$

The determinant of this matrix is

$$\det B(\bar{n}_1, 0, 0) = -(\lambda_1 - \mu)((\lambda_2 - \lambda_1)(-\kappa \mu - \sigma) - p(\lambda_1 - \mu)\sigma).$$

Now, since $\lambda_1 > \mu$, further, thanks to (5),

$$(\lambda_1 - \lambda_2)(\kappa \mu + \sigma) - p(\lambda_1 - \mu)\sigma < 0,$$

the determinant is positive. Hence, in order to conclude that the equilibrium is unstable, it suffices to show that all eigenvalues are real. This follows from the fact that by (45), $\det B(\bar{n}_1, 0, 0)/(\mu - \lambda_1)$ is negative. Since this quotient equals the product of the two other eigenvalues of the matrix, it is impossible that these eigenvalues are complex (and thus conjugate). Finally, let us consider the equilibrium $(0, \bar{n}_{2a}, \bar{n}_{2d})$. We have

$$B(0, \bar{n}_{2a}, \bar{n}_{2d}) = \begin{pmatrix} \lambda_1 - \mu - \alpha \bar{n}_{2a} & 0 & 0 \\ 0 & \lambda_2 - \mu - 2\alpha \bar{n}_{2a} & \sigma \\ p\alpha \bar{n}_{2a} & 2p\alpha \bar{n}_{2a} & -(\kappa \mu + \sigma) \end{pmatrix}.$$

We have already seen in Section 2.2 that $\lambda_1 - \mu - \alpha \bar{n}_{2a} < 0$ under condition (5), and this quantity is clearly an eigenvalue of the matrix $B(0, \bar{n}_{2a}, \bar{n}_{2d})$. The other two ones are the eigenvalues of the matrix $A(\bar{n}_{2a}, \bar{n}_{2d})$ (cf. (2)), which are negative since $\lambda_2 > \mu$, see also Section 2.2. We conclude that $B(0, \bar{n}_{2a}, \bar{n}_{2d})$ is negative definite and hence the equilibrium $(0, \bar{n}_{2a}, \bar{n}_{2d})$ is asymptotically stable under condition (5). $\square$

Now, for the two-dimensional variant

$$\dot{n}_{2a}(t) = n_{2a}(t)(\lambda_2 - \mu - \alpha n_{2a}(t)) + \sigma n_{2d}(t),$$
$$\dot{n}_{2d}(t) = p\alpha n_{2a}^2(t) - (\kappa \mu + \sigma)n_{2d}(t), \tag{46}$$

of the system, introduced in (1), which corresponds to starting the system (6) from $\{0\} \times [0, \infty)^2$ and ignoring the invariant first coordinate, $(\bar{n}_{2a}, \bar{n}_{2d})$ turns out to be the limit of the solution started from any nonnegative initial condition apart from $(0, 0)$. Let us recall that this system has an asymptotically stable equilibrium $(\bar{n}_{2a}, \bar{n}_{2d})$ and an unstable one $(0, 0)$ under the assumption that $\lambda_2 > \mu$.

Lemma 4.6. *In case* $(n_{2a}(0), n_{2d}(0)) \in [0, \infty)^2 \setminus \{(0, 0)\}$, *we have*

$$\lim_{t \to \infty} (n_{2a}(t), n_{2d}(t)) = (\bar{n}_{2a}, \bar{n}_{2d}).$$

Proof. Observe that the active coordinate of the stable equilibrium,

$$\bar{n}_{2a} = \frac{(\lambda_2 - \mu)(\kappa \mu + \sigma)}{\alpha(\kappa \mu + (1 - p)\sigma)} > 0$$

satisfies

$$\frac{\lambda_2 - \mu}{\alpha} < \bar{n}_{2a} \leq \frac{\lambda_2 - \mu}{(1 - p)\alpha}, \tag{47}$$

where the second inequality is an equality if and only if $\kappa = 0$. Further, the dormant coordinate $\bar{n}_{2d}$ is positive. Note further that the divergence of the system is given as

$$\lambda_2 - \mu - 2\alpha n_{2a}(t) - (\kappa\mu + \sigma).$$

This is certainly negative if $n_{2a} \geq \frac{\lambda_2 - \mu}{2\alpha}$, $n_{2d} \geq 0$, and at least one of the latter two inequalities is strict. In particular, the Bendixson criterion [18, Theorem 7.10] implies that there is no nontrivial periodic solution in the open and simply connected set

$$U = \left\{ (n_{2a}, n_{2d}) \in \mathbb{R}^2 \colon n_{2a} > \tfrac{\lambda_2 - \mu}{2\alpha}, n_{2d} > 0 \right\}.$$

Since this is a two-dimensional system and all solutions of the system with coordinatewise nonnegative initial conditions are bounded, this implies that any solution starting from U converges to the equilibrium $(\bar{n}_{2a}, \bar{n}_{2d}) \in U$. It remains to show that any solution started from $[0, \infty)^2 \setminus (\{(0, 0)\} \cup U)$ will enter the open set U after finite time.

Now, observe that if $n_{2a}(0) > 0$ and $n_{2d}(0) \geq 0$, then $\dot{n}_{2a}$ is positive and bounded away from zero until n_{2a} reaches $\frac{\lambda_2 - \mu}{2\alpha}$, hence n_{2a} will reach this level. If $n_{2d}(0) > 0$ and $n_{2a}(0) = 0$, then there exists $\delta > 0$ such that $n_{2a}(\delta) > 0$ and $n_{2d}(\delta) > 0$, and hence n_{2a} will also reach the level $\frac{\lambda_2 - \mu}{2\alpha}$ in finite time. Further, for $t > 0$, if $n_{2a}(t) = \frac{\lambda_2 - \mu}{2\alpha}$ and $n_{2d}(t) \geq 0$, then plugging in the first inequality of (47) to the first equation of (46) implies that $\dot{n}_{2a}(t) > 0$. This implies that if $n_{2d}(t) > 0$, then

$$(n_{2a}(t + \varepsilon), n_{2d}(t + \varepsilon)) \in U, \qquad \forall \varepsilon > 0 \text{ sufficiently small.} \tag{48}$$

Else, $\dot{n}_{2a}(t) = 0$ but $\dot{n}_{2d}(t) > 0$, and hence the observations of the previous case imply that $\dot{n}_{2a}(t + \varepsilon) > 0$ for all sufficiently small $\varepsilon > 0$, thus (48) also holds. □

Finally, we show convergence of the original 3-dimensional system to the equilibrium $(0, \bar{n}_{2a}, \bar{n}_{2d})$ as $t \to \infty$ for initial conditions corresponding to Proposition 4.4. In other words, we verify some global attractor properties of this equilibrium, which are not as general as for the two-dimensional system but sufficient for the goals of the present paper.

Lemma 4.7. *Let us consider the system of ODEs* (6). *If the initial condition* $(n_1, n_{2a}, n_{2d}) = (n_1(0), n_{2a}(0), n_{2d}(0))$ *satisfies*

$$\frac{p\alpha(n_1 + n_{2a})}{\kappa\mu + \sigma} > \frac{n_{2d}}{n_{2a}} > \frac{\mu - \lambda_2 + \alpha(n_1 + n_{2a})}{\sigma}, \qquad n_1 \geq 0, n_{2a}, n_{2d} > 0, \tag{49}$$

then

$$\lim_{t \to \infty} (n_1(t), n_{2a}(t), n_{2d}(t)) = (0, \bar{n}_{2a}, \bar{n}_{2d}). \tag{50}$$

Note that in the two-dimensional case $n_1(0) = 0$, Lemma 4.7 is weaker than Lemma 4.6. We will use the stronger assertion (more precisely, an approximative version of it) when handling the third phase of invasion in Section 4.3, where perturbations of the system (16) need to be treated.

Proof. Let us assume that for some $t \geq 0$, $(n_1(t), n_{2a}(t), n_{2d}(t)) = (n_1, n_{2a}, n_{2d})$. Then the first inequality in (49) is equivalent to the statement that $\dot{n}_{2d}(t) > 0$ and the second one is equivalent to the statement that $\dot{n}_{2a}(t) > 0$. Hence, as long as (49) holds, $t \mapsto n_{2a}(t)$ and $t \mapsto n_{2d}(t)$ are strictly increasing.

Let us assume that condition (49) is satisfied for

$$(n_1, n_{2a}, n_{2d}) = (n_1(0), n_{2a}(0), n_{2d}(0)).$$

We claim that this implies that the condition also holds for all $t > 0$ with $(n_1, n_{2a}, n_{2d}) = (n_1(t), n_{2a}(t), n_{2d}(t))$, unless $(n_{2a}(t), n_{2d}(t)) = (\bar{n}_{2a}, \bar{n}_{2d})$ holds eventually. Indeed, let us assume that for some $t > 0$, $(n_1(t), n_{2a}(t), n_{2d}(t))$ lies on the boundary of the set

$$\{(n_1, n_{2a}, n_{2d}) \in [0, \infty) \times (0, \infty) \times (0, \infty) : (n_1, n_{2a}, n_{2d}) \text{ satisfies (49)}\} \tag{51}$$

with $n_{2a}, n_{2d} \geq 0$, in such a way that $(n_1(s), n_{2a}(s), n_{2d}(s))$ is contained in the set (51) for all $0 \leq s < t$. Then $n_{2a}, n_{2d} > 0$ holds because $n_{2a}(0), n_{2d} > 0$ by assumption, moreover, $s \mapsto n_{2a}(s)$ and $s \mapsto n_{2d}(s)$ are increasing on $[0, t)$. Hence, one of the following conditions holds:

(i) $\dot{n}_{2d}(t) = 0$, $\dot{n}_{2a}(t) > 0$,
(ii) $\dot{n}_{2a}(t) = 0$, $\dot{n}_{2d}(t) > 0$,
(iii) $\dot{n}_{2a}(t) = \dot{n}_{2d}(t) = 0$.

In case (i) we have

$$\left(\tfrac{\dot{n}_{2d}}{n_{2a}}\right)(t) = \frac{-\dot{n}_{2a}(t) n_{2d}(t)}{n_{2a}(t)^2} < 0.$$

The case (ii) yields

$$\left(\tfrac{\dot{n}_{2d}}{n_{2a}}\right)(t) = \frac{\dot{n}_{2d}(t) n_{2a}(t)}{n_{2a}(t)^2} > 0.$$

In case (iii) we have (thanks to the condition that $n_{2a}, n_{2d} > 0$) that $(n_{2a}, n_{2d}) = (\bar{n}_{2a}, \bar{n}_{2d})$. We conclude that if $(n_1, n_{2a}, n_{2d}) = (n_1(0), n_{2a}(0), n_{2d}(0))$ satisfies (49), then $t \mapsto (n_1(t), n_{2a}(t), n_{2d}(t))$ never enters the complement of the closure of the set (51) apart from $(\bar{n}_{2a}, \bar{n}_{2d})$, which implies the claim.

Now, given that condition (49) is satisfied for $(n_1, n_{2a}, n_{2d}) = (n_1(0), n_{2a}(0), n_{2d}(0))$, $t \mapsto n_{2a}(t)$ and $t \mapsto n_{2d}(t)$ are nonnegative, bounded, increasing, and strictly increasing unless $(n_{2a}(t), n_{2d}(t)) = (\bar{n}_{2a}, \bar{n}_{2d})$ eventually, in which case both coordinates would immediately become constant. Further, $t \mapsto n_1(t)$ is also bounded and nonnegative. Hence, $(n_1(t), n_{2a}(t), n_{2d}(t))$ converges along a subsequence to $(n_1^*, \bar{n}_{2a}, \bar{n}_{2d})$ for some $n_1^* \geq 0$. Now we argue that n_1^* must be equal to zero. Indeed, taking limits of (49) implies that

$$\frac{p\alpha(n_1^* + \bar{n}_{2a})}{\kappa\mu + \sigma} \geq \frac{\bar{n}_{2d}}{\bar{n}_{2a}} \geq \frac{\mu - \lambda_2 + \alpha(n_1^* + \bar{n}_{2a})}{\sigma}. \tag{52}$$

Observe that both inequalities in (52) holds with equality for $n_1^* = 0$ thanks to (3). Taking this into account, any subsequential limit n_1^* has to satisfy

$$\frac{p\alpha n_1^*}{\kappa\mu + \sigma} \geq 0 \geq \frac{\alpha n_1^*}{\sigma}.$$

Since by our assumptions, $\frac{p}{\kappa\mu+\sigma} < \frac{1}{\sigma}$, we conclude that $n_1^* = 0$. Hence, (50) follows. □

The last auxiliary result corresponding to the second phase of invasion states that the state of the population process reached thanks to Proposition 4.4 belongs to the domain of attraction of the stable equilibrium $(0, \bar{n}_{2a}, \bar{n}_{2d})$.

Lemma 4.8. *Let C be chosen according to Proposition 4.4, further, n_1, n_{2a}, n_{2d} positive such that $n_1 \in (\bar{n}_1 - 2\varepsilon, \bar{n}_1 + 2\varepsilon)$, $n_{2a} + n_{2d} \in (\varepsilon/C, \sqrt{\varepsilon})$, and $\frac{n_{2d}}{n_{2a}} = \frac{\pi_{2d}}{\pi_{2a}}$. Then, if $\varepsilon > 0$ is sufficiently small, then (n_1, n_{2a}, n_{2d}) satisfies (49).*

Proof. Since (π_{2a}, π_{2d}) is a left eigenvector of J corresponding to the eigenvalue $\widetilde{\lambda}$, we have

$$(\lambda_2 - \lambda_1) + \sigma \frac{\pi_{2d}}{\pi_{2a}} = \widetilde{\lambda} = p(\lambda_1 - \mu)\frac{\pi_{2a}}{\pi_{2d}} - (\kappa\mu + \sigma).$$

Hence, since $\widetilde{\lambda} > 0$, given that $\varepsilon > 0$ is small enough, we obtain

$$\frac{\pi_{2d}}{\pi_{2a}} = \frac{\widetilde{\lambda} - \lambda_2 + \lambda_1}{\sigma} = \frac{\widetilde{\lambda} - \lambda_2 + \mu + \alpha\left(\frac{\lambda_1 - \mu}{\alpha}\right)}{\sigma} > \frac{-\lambda_2 + \mu + \alpha\left(\frac{\lambda_1 - \mu}{\alpha} + 3\sqrt{\varepsilon}\right)}{\sigma}$$

$$\geq \frac{\mu - \lambda_2 + \alpha(n_1 + n_{2a})}{\sigma}$$

and

$$\frac{\pi_{2d}}{\pi_{2a}} = \frac{p\alpha\left(\frac{\lambda_1 - \mu}{\alpha}\right)}{\widetilde{\lambda} + \kappa\mu + \sigma} < \frac{p\alpha\left(\frac{\lambda_1 - \mu}{\alpha} - 2\varepsilon\right)}{\kappa\mu + \sigma} \leq \frac{p\alpha(n_1 + n_{2a})}{\kappa\mu + \sigma},$$

as asserted. $\square$

4.3. The third phase of invasion: extinction of the resident population

At the end of the second phase, the rescaled process $\mathbf{N}_t^K$ is close to the state $(0, \bar{n}_{2a}, \bar{n}_{2d})$. In particular, $N_{1,t}^K$ is at most εK for some $\varepsilon > 0$ small. In this subsection, we estimate the time of the extinction of the resident population. We also need to check that the mutant population stays close to $(\bar{n}_{2a}, \bar{n}_{2d})$ during its time. We recall the set S_β (9) and the time T_{S_β} (10). We have the following proposition.

Proposition 4.9. *There exist $\varepsilon_0, C_0 > 0$ such that for all $\varepsilon \in (0, \varepsilon_0)$, under condition (5) with $\lambda_1 > \lambda_2 > \mu$, if there exists $\eta \in (0, 1/2)$ that satisfies*

$$\left|N_{2a}^K(0) - \bar{n}_{2a}\right| \leq \varepsilon \quad and \quad \left|N_{2d}^K(0) - \bar{n}_{2d}\right| \leq \varepsilon \quad and \quad \eta\varepsilon/2 \leq N_1^K(0) \leq \varepsilon/2,$$

then

$$\forall \widetilde{C} > (\mu + \alpha\bar{n}_{2a} - \lambda_1)^{-1} + C_0\varepsilon, \qquad\qquad \mathbb{P}(T_{S_\varepsilon} \leq \widetilde{C} \log K) \xrightarrow[K \to \infty]{} 1,$$

$$\forall 0 \leq \widetilde{C} < (\mu + \alpha\bar{n}_{2a} - \lambda_1)^{-1} - C_0\varepsilon, \qquad\qquad \mathbb{P}(T_{S_\varepsilon} \leq \widetilde{C} \log K) \xrightarrow[K \to \infty]{} 0.$$

Proof. We first show that the rescaled population size vector $(N_{2a,t}^K, N_{2d,t}^K)$ stays close to its equilibrium $(\bar{n}_{2a}, \bar{n}_{2d})$ for long times, given that the resident population is small. To this aim, we employ arguments similar to the ones of [16, Proof of Proposition 4.1, Step 1]. For $\varepsilon > 0$ we define the stopping times

$$R_{\varepsilon,i} = \inf\left\{t \geq 0 \colon \left|N_{2i,t}^K - \bar{n}_{2i}\right| > \varepsilon\right\}, \qquad i \in \{a, d\},$$

$$T_0^1 = \inf\{t \geq 0 \colon N_{1,t}^K = 0\},$$

and

$$T_\varepsilon^1 = \inf\{t \geq 0 \colon N_{1,t}^K \geq \varepsilon\}.$$

These stopping times depend on K, but we omit the K-dependence from the notation for readability.

We couple $(N_{2a,t}^K, N_{2d,t}^K)$ with two bi-type birth-and-death processes, denoted by $(Y_{2a,t}^{\varepsilon,\le}, Y_{2d,t}^{\varepsilon,\le})$ and $(Y_{2a,t}^{\varepsilon,\ge}, Y_{2d,t}^{\varepsilon,\ge})$, such that

$$Y_{2\upsilon,t}^{\varepsilon,\le} \le N_{2\upsilon,t}^K \le Y_{2\upsilon,t}^{\varepsilon,\ge}, \qquad a.s. \qquad \forall \upsilon \in \{a,d\}, \ \forall 0 \le t \le T_\varepsilon^1. \tag{53}$$

In order to satisfy (53), these processes can be defined with the following rates:

$$(Y_{2a,t}^{\varepsilon,\le}, Y_{2d,t}^{\varepsilon,\le}): \left(\frac{i}{K}, \frac{j}{K}\right) \to \left(\frac{i+1}{K}, \frac{j}{K}\right) \qquad \text{at rate} \quad i\lambda_2,$$
$$\left(\frac{i}{K}, \frac{j}{K}\right) \to \left(\frac{i-1}{K}, \frac{j}{K}\right) \qquad \text{at rate} \quad i(\mu + \alpha((1-p)\tfrac{i}{K} + \varepsilon)),$$
$$\left(\frac{i}{K}, \frac{j}{K}\right) \to \left(\frac{i-1}{K}, \frac{j+1}{K}\right) \qquad \text{at rate} \quad \frac{p\alpha i^2}{K},$$
$$\left(\frac{i}{K}, \frac{j}{K}\right) \to \left(\frac{i+1}{K}, \frac{j-1}{K}\right) \qquad \text{at rate} \quad j\sigma,$$
$$\left(\frac{i}{K}, \frac{j}{K}\right) \to \left(\frac{i}{K}, \frac{j-1}{K}\right) \qquad \text{at rate} \quad j\kappa\mu.$$

and

$$(Y_{2a,t}^{\varepsilon,\ge}, Y_{2d,t}^{\varepsilon,\ge}): \left(\frac{i}{K}, \frac{j}{K}\right) \to \left(\frac{i+1}{K}, \frac{j}{K}\right) \qquad \text{at rate} \quad i\lambda_2,$$
$$\left(\frac{i}{K}, \frac{j}{K}\right) \to \left(\frac{i-1}{K}, \frac{j}{K}\right) \qquad \text{at rate} \quad i(\mu + \alpha(1-p)\tfrac{i}{K} - p\alpha\varepsilon),$$
$$\left(\frac{i}{K}, \frac{j}{K}\right) \to \left(\frac{i-1}{K}, \frac{j+1}{K}\right) \qquad \text{at rate} \quad \frac{p\alpha(i^2+\varepsilon)}{K},$$
$$\left(\frac{i}{K}, \frac{j}{K}\right) \to \left(\frac{i+1}{K}, \frac{j-1}{K}\right) \qquad \text{at rate} \quad j\sigma,$$
$$\left(\frac{i}{K}, \frac{j}{K}\right) \to \left(\frac{i}{K}, \frac{j-1}{K}\right) \qquad \text{at rate} \quad j\kappa\mu.$$

The idea of this coupling is similar to the one in the proof of Proposition 4.1: in order to decrease (increase) the process, one needs higher (lower) total competition event rate and rate of death by competition for the actives and lower (higher) active→dormant switching rate.

We will show that the processes $(Y_{2a,t}^{\varepsilon,\le}, Y_{2d,t}^{\varepsilon,\le})$ and $(Y_{2a,t}^{\varepsilon,\ge}, Y_{2d,t}^{\varepsilon,\ge})$ will stay close to $(\bar{n}_{2a}, \bar{n}_{2d})$ for at least an exponential (in K) time with a probability close to 1 for large K. To do so, we will study the stopping times

$$R_{\eta,\upsilon}^\diamond = \inf\{t \ge 0: N_{2\upsilon,t}^{\varepsilon,\diamond} \notin [x_\upsilon - \eta, x_\upsilon + \eta]\}$$

for $\eta > 0$, $\upsilon \in \{a,d\}$ and $\diamond \in \{\le, \ge\}$. Let us first study the process $(Y_{2a,t}^{\varepsilon,\le}, Y_{2d,t}^{\varepsilon,\le})$. According to [19, Theorem 2.1, p. 456], the dynamics of this process is close to the dynamics of the unique solution to

$$\dot{n}_{2a} = n_{2a}(\lambda_2 - \mu - \alpha\varepsilon - \alpha n_{2a}) + \sigma n_{2d},$$
$$\dot{n}_{2d} = p\alpha n_{2a}^2 - (\kappa\mu + \sigma)n_{2d}.$$

Similar to point (2) in Section 2.2, we have that for all sufficiently small $\varepsilon > 0$, this system has a unique positive equilibrium, which we denote by $(\bar{n}_{2a}^{\varepsilon,\le}, \bar{n}_{2d}^{\varepsilon,\le})$. Here, analogously to $\bar{n}_{2a}$, we have $\bar{n}_{2a}^{\varepsilon,\le} = \frac{(\lambda_2 - \mu - \alpha\varepsilon)(\kappa\mu + \sigma)}{\alpha(\kappa\mu + (1-p)\sigma)}$, whereas $\bar{n}_{2d}^{\varepsilon,\le}$ depends on ε in a more involved way, but it tends to $\bar{n}_{2d}$ as $\varepsilon \downarrow 0$. For $\varepsilon > 0$ small enough, the equilibrium $(0,0)$ is unstable and $(\bar{n}_{2a}^{\varepsilon,\le}, \bar{n}_{2d}^{\varepsilon,\le})$ is asymptotically stable, further, we can verify convergence of the solution to $(\bar{n}_{2a}^{\varepsilon,\le}, \bar{n}_{2d}^{\varepsilon,\le})$ for any

coordinatewise nonnegative initial condition but $(0, 0)$, as $t \to \infty$, using similar arguments as in the proof of Lemma 4.6. Thus, we can find constants c_0 and ε'_0 such that for any $\varepsilon \in (0, \varepsilon_0)$,

$$\forall i \in \{a, d\} \colon \left| \bar{n}_{2i}^{\varepsilon, \leq} - \bar{n}_{2i} \right| \leq (c_0 - 1)\varepsilon \text{ and } 0 \notin [\bar{n}_{2i} - c_0\varepsilon, \bar{n}_{2i} + c_0\varepsilon].$$

Now, similarly to the proof of Lemma 4.2, we can use results by Freidlin–Wentzell about exit of jump processes from a domain [21, Section 5] in order to construct a family (over K) of Markov processes $(\widetilde{Y}_{2a,t}, \widetilde{Y}_{2d,t})_{t \geq 0}$ whose transition rates are positive, bounded, Lipschitz continuous and uniformly bounded away from 0 such that for

$$\widetilde{R}_{\varepsilon, i}^{\leq} = \inf\{t \geq 0 \colon |\widetilde{Y}_{2i,t}^K - \bar{n}_{2i}| > \varepsilon\}, \qquad i \in \{a, d\},$$

there exists $V > 0$ such that for all $i \in \{a, d\}$ we have

$$\mathbb{P}\big(R_{c_0\varepsilon,a}^{\leq} > \mathrm{e}^{KV}, R_{c_0\varepsilon,d}^{\leq} > \mathrm{e}^{KV}\big) = \mathbb{P}\big(\widetilde{R}_{c_0\varepsilon,a}^{\leq} > \mathrm{e}^{KV}, \widetilde{R}_{c_0\varepsilon,d}^{\leq} > \mathrm{e}^{KV}\big) \xrightarrow[K \to \infty]{} 1. \tag{54}$$

Similarly, we obtain

$$\mathbb{P}\big(R_{c_0\varepsilon,a}^{\geq} > \mathrm{e}^{KV}, R_{c_0\varepsilon,d}^{\geq} > \mathrm{e}^{KV}\big) \xrightarrow[K \to \infty]{} 1, \tag{55}$$

where without loss of generality we can assume that the constant V in (55) is the same as the one in (54). Now note that $R_{c_0\varepsilon,i} \geq R_{c_0\varepsilon,i}^{\leq} \wedge R_{c_0\varepsilon,i}^{\geq}$ on the event $\{R_{c_0\varepsilon,i} \leq T_\varepsilon^1\}$. This together with (54) and (55) implies that

$$\lim_{K \to \infty} \mathbb{P}\big(R_{c_0\varepsilon,i} \leq \mathrm{e}^{KV} \wedge T_\varepsilon^1\big) = 0$$

holds for all $i \in \{a, d\}$, hence

$$\lim_{K \to \infty} \mathbb{P}\big(R_{c_0\varepsilon,a} \wedge R_{c_0\varepsilon,d} \leq \mathrm{e}^{KV} \wedge T_\varepsilon^1\big) = 0. \tag{56}$$

Now, we can find two branching processes $Z_1^{\varepsilon, \leq} = (Z_{1,t}^{\varepsilon, \leq})_{t \geq 0}$ and $Z_1^{\varepsilon, \geq} = (Z_{1,t}^{\varepsilon, \geq})_{t \geq 0}$ such that

$$Z_{1,t}^{\varepsilon, \leq} \leq K N_{1,t}^K \leq Z_{1,t}^{\varepsilon, \geq} \tag{57}$$

almost surely on the time interval

$$I_\varepsilon^K = \big[0, R_{c_0\varepsilon,a} \wedge R_{c_0\varepsilon,d} \wedge T_\varepsilon^1\big].$$

Indeed, in order to satisfy (57), the processes $Z_1^{\varepsilon, \geq}$ and $Z_1^{\varepsilon, \leq}$ can be chosen with the following rates and initial conditions:

$$Z_1^{\varepsilon, \leq} \colon i \to i + 1 \quad \text{at rate } i\lambda_1, \quad i \to i - 1 \text{ at rate } i\Big(\mu + \alpha\big(\bar{n}_{2a} + (c_0 + 1)\varepsilon\big)\Big),$$

started from $\lfloor \frac{\eta\varepsilon K}{2} \rfloor$, and

$$Z_1^{\varepsilon, \geq} \colon i \to i + 1 \quad \text{at rate } i\lambda_1, \quad i \to i - 1 \text{ at rate } i(\mu + \alpha(\bar{n}_{2a} - c_0\varepsilon)),$$

started from $\lfloor \frac{\varepsilon K}{2} \rfloor + 1$.

For all $\varepsilon > 0$ sufficiently small, both of these branching processes are subcritical according to point (5) in Section 2.2. The growth rates of these three processes are $\lambda_1 - \mu - \alpha\bar{n}_{2a} \pm O(\varepsilon)$. From this, analogously to [15, Section 3.3], we deduce that the extinction time of these processes started from $[\lfloor \frac{\eta\varepsilon K}{2} \rfloor, \lfloor \frac{\varepsilon K}{2} \rfloor + 1]$ is of order $(\mu - \lambda_1 + \alpha\bar{n}_{2a} \pm O(\varepsilon)) \log K$. This in turn follows from the general assertion that for a branching process $\mathcal{N} = (\mathcal{N}(t))_{t \geq 0}$ with birth rate $\mathcal{B} > 0$ and death rate $\mathcal{D} > 0$ that is subcritical (i.e., $\mathcal{B} < \mathcal{D}$), given that $\mathcal{N}(0) \in [\lfloor \frac{\eta K\varepsilon}{2} \rfloor, \lfloor \frac{\varepsilon K}{2} \rfloor + 1]$, defining

$$\mathcal{S}_\varepsilon^{\mathcal{N}} = \inf\{t \geq 0 \colon \mathcal{N}(t) \geq \lfloor \varepsilon K \rfloor\}, \qquad \varepsilon > 0,$$

and

$$\mathcal{S}_\varepsilon^{\mathcal{N}} = \inf\{t \geq 0 \colon \mathcal{N}(t) = 0\},$$

the following hold according to [1, p. 202]:

$$\forall \widetilde{C} < (\mathcal{D} - \mathcal{B})^{-1}, \qquad \lim_{K \to \infty} \mathbb{P}(\mathcal{S}_0^{\mathcal{N}} \leq \widetilde{C} \log K) = 0$$

and

$$\forall \widetilde{C} > (\mathcal{D} - \mathcal{B})^{-1}, \qquad \lim_{K \to \infty} \mathbb{P}(\mathcal{S}_0^{\mathcal{N}} \leq \widetilde{C} \log K) = 1.$$

Further, if $\mathcal{N}(0) = \lfloor \frac{\eta K \varepsilon}{2} \rfloor$, then for all sufficiently small $\varepsilon > 0$,

$$\lim_{K \to \infty} \mathbb{P}\left(\mathcal{S}_0^{\mathcal{N}} > K \wedge \mathcal{S}_{\lfloor \varepsilon K \rfloor}^{\mathcal{N}}\right) = 0. \tag{58}$$

Now for $C \geq 0$ we can estimate as follows

$$\begin{aligned}
\mathbb{P}(T_0^1 < \widetilde{C} \log K) &- \mathbb{P}\big(\mathcal{S}_0^{Z_1^{\varepsilon,\leq}} < \widetilde{C} \log K\big) \\
&\leq \mathbb{P}\big(T_0^1 > T_\varepsilon^1 \wedge K\big) + \mathbb{P}\big(T_\varepsilon^1 \wedge K > R_{c_0 \varepsilon, a} \wedge R_{c_0 \varepsilon, d}\big) \\
&\leq \mathbb{P}\big(\mathcal{S}_0^{Z_1^{\varepsilon,\geq}} > \mathcal{S}_{\lfloor \varepsilon K \rfloor}^{Z_1^{\varepsilon,\geq}} \wedge K\big) + \mathbb{P}\big(T_\varepsilon^1 \wedge K > R_{c_0 \varepsilon, a} \wedge R_{c_0 \varepsilon, d}\big).
\end{aligned} \tag{59}$$

Here, the first inequality can be verified as follows:

$$\begin{aligned}
\mathbb{P}(T_0^1 < \widetilde{C} \log K) - \mathbb{P}\big(\mathcal{S}_0^{Z_1^{\varepsilon,\leq}} < \widetilde{C} \log K\big) &= \mathbb{P}\big(T_0^1 < \widetilde{C} \log K \leq \mathcal{S}_0^{Z_1^{\varepsilon,\leq}}\big) \\
&\leq \mathbb{P}(R_{c_0 \varepsilon, a} \wedge R_{c_0 \varepsilon, d} < T_0^1 < \widetilde{C} \log K, R_{c_0 \varepsilon, a} \wedge R_{c_0 \varepsilon, d} < T_\varepsilon^1) \\
&\quad + \mathbb{P}(T_\varepsilon^1 < T_0^1 < \widetilde{C} \log K, R_{c_0 \varepsilon, a} \wedge R_{c_0 \varepsilon, d} > T_\varepsilon^1) \\
&\leq \mathbb{P}(R_{c_0 \varepsilon, a} \wedge R_{c_0 \varepsilon, d} < T_\varepsilon^1 \wedge \widetilde{C} \log K) + \mathbb{P}(T_0^1 > T_\varepsilon^1) \\
&\leq \mathbb{P}(R_{c_0 \varepsilon, a} \wedge R_{c_0 \varepsilon, d} < T_\varepsilon^1 \wedge K) + \mathbb{P}(T_0^1 > T_\varepsilon^1 \wedge K).
\end{aligned}$$

Given that $\varepsilon > 0$ is small enough, the second term in the last line of (59) tends to zero as $K \to \infty$ according to (56) and so does the first one according to (58). We conclude that

$$\limsup_{K \to \infty} \mathbb{P}\big(T_0^1 < \widetilde{C} \log K\big) \leq \lim_{K \to \infty} \mathbb{P}\big(\mathcal{S}_0^{Z_1^{\varepsilon,\leq}} \leq \widetilde{C} \log K\big),$$

and similarly, we deduce

$$\liminf_{K \to \infty} \mathbb{P}\big(T_0^1 < \widetilde{C} \log K\big) \geq \lim_{K \to \infty} \mathbb{P}\big(\mathcal{S}_0^{Z_1^{\varepsilon,\geq}} \leq \widetilde{C} \log K\big),$$

which implies the proposition. □

4.4. Proof of Theorems 2.1, 2.2, and 2.3

Putting together Propositions 4.1, 4.4, and 4.9, we now verify our main results. The structure of this part of our proof is similar to the one of [15, Section 3.4], the main difference lies in the behaviour of the corresponding dynamical systems. Our proof strongly relies on the coupling (32). More precisely, we define a Bernoulli random variable B as the indicator of nonextinction

$$B := \mathbb{1}\{\forall t > 0 \colon \widehat{Z}_{2a}(t) + \widehat{Z}_{2d}(t) > 0\}$$

of the process $(\widehat{Z}_{2a}(t), \widehat{Z}_{2d}(t))_{t \geq 0}$ defined in point 3 of Section 2.2, which is initially coupled with $(K N_{2a,t}^K, K N_{2d,t}^K)_{t \geq 0}$ according to (32). Let f be the function defined in Proposition 4.1. Throughout the rest of the proof, we can assume that $\varepsilon > 0$ is so small that $f(\varepsilon) < 1$.

Our goal is to show that

$$\liminf_{K \to \infty} \mathcal{E}(K, \varepsilon) \geq q - o(\varepsilon) \tag{60}$$

holds for

$$\mathcal{E}(K, \varepsilon) := \mathbb{P}\Big(\frac{T_0^2}{\log K} \leq f(\varepsilon), T_0^2 < T_{S_\beta}, B = 0\Big)$$

and

$$\liminf_{K \to \infty} \mathcal{I}(K, \varepsilon) \geq 1 - q - o(\varepsilon) \tag{61}$$

holds for

$$\mathcal{I}(K, \varepsilon) := \mathbb{P}\Big(\Big|\frac{T_{S_\beta} \wedge T_0^2}{\log K} - \Big(\frac{1}{\tilde{\lambda}} + \frac{1}{\mu - \lambda_1 + \alpha \bar{n}_{2a}}\Big)\Big| \leq f(\varepsilon), T_{S_\beta} < T_0^2, B = 1\Big).$$

These together will imply Theorems 2.1, 2.2, and Eq. (14) in Theorem 2.3. The other assertion of Theorem 2.3, Eq. (15), follows already from (20).

Let us start with the case of mutant extinction in the first phase of invasion and verify (60). Clearly, we have

$$\mathcal{E}(K, \varepsilon) \geq \mathbb{P}\Big(\frac{T_0^2}{\log K} \leq f(\varepsilon), T_0^2 < T_{S_\beta}, B = 0, T_0^2 < T_\varepsilon^2 \wedge R_{2\varepsilon}\Big).$$

Now, considering our initial conditions, for all sufficiently small $\varepsilon > 0$ we have $T_\varepsilon^2 \wedge R_{2\varepsilon} < T_{S_\beta}$, almost surely. Hence,

$$\mathcal{E}(K, \varepsilon) \geq \mathbb{P}\Big(\frac{T_0^2}{\log K} \leq f(\varepsilon), B = 0, T_0^2 < T_\varepsilon^2 \wedge R_{2\varepsilon}\Big). \tag{62}$$

Moreover, analogously to the proof of Proposition 4.1 with $\xi = 1$, we obtain

$$\limsup_{K \to \infty} \mathbb{P}\Big(\{B = 0\}\Delta\{T_0^2 < T_\varepsilon^2 \wedge R_{2\varepsilon}\}\Big) + \mathbb{P}\Big(\{B = 0\}\Delta\{T_0^{(\varepsilon,+),2} < \infty\}\Big) = o_\varepsilon(1), \tag{63}$$

where Δ stands for symmetric difference. Together with (62), these imply

$$\liminf_{K \to \infty} \mathcal{E}(K, \varepsilon)$$
$$\geq \liminf_{K \to \infty} \mathbb{P}\Big(\frac{T_0^2}{\log K} \leq f(\varepsilon), B = 0, T_0^2 \leq T_\varepsilon^2 \wedge R_{2\varepsilon}\Big)$$
$$\geq \liminf_{K \to \infty} \mathbb{P}\Big(\frac{T_0^{(\varepsilon,+),2}}{\log K} \leq f(\varepsilon), B = 0, T_0^2 \leq T_\varepsilon^2 \wedge R_{2\varepsilon}\Big) \tag{64}$$
$$\geq \liminf_{K \to \infty} \mathbb{P}\Big(\frac{T_0^{(\varepsilon,+),2}}{\log K} \leq f(\varepsilon), T_0^{(\varepsilon,+),2} < \infty\Big) + o_\varepsilon(1),$$

where in (64) we used the coupling (32). Thus, using (7) and (33), we conclude (14).

Let us continue with the case of mutant survival in the first phase of invasion and verify (61). Arguing analogously to (63) but for $\xi = 1/2$, we obtain

$$\limsup_{K \to \infty} \mathbb{P}\big(\{B = 1\}\Delta\{T_{\sqrt{\varepsilon}}^2 < T_0^2 \wedge R_{2\varepsilon}\}\big) = o_\varepsilon(1).$$

Thus,

$$
\liminf_{K\to\infty} \mathcal{I}(K,\varepsilon) = \liminf_{K\to\infty} \mathbb{P}\left(\left|\frac{T_{S_\beta}}{\log K} - \left(\frac{1}{\tilde{\lambda}} + \frac{1}{\mu - \lambda_1 + \alpha\bar{n}_{2a}}\right)\right| \leq f(\varepsilon), \tag{65}
$$
$$
T_{S_\beta} < T_0^2, \, T_{\sqrt{\varepsilon}}^2 < T_0^2 \wedge R_{2\varepsilon}\right) + o_\varepsilon(1).
$$

For $\varepsilon > 0$, $\beta > 0$, we introduce the sets

$$
\mathcal{B}_\varepsilon^1 := [\pi_{2a} - \delta, \pi_{2a} + \delta] \times [\varepsilon/C, \sqrt{\varepsilon}] \times [\bar{n}_1 - 2\varepsilon, \bar{n}_1 + 2\varepsilon],
$$
$$
\mathcal{B}_\beta^2 := [0, \beta/2] \times [\bar{n}_{2a} - (\beta/2), \bar{n}_{2a} + (\beta/2)] \times [\bar{n}_{2d} - (\beta/2), \bar{n}_{2d} + (\beta/2)]
$$

and the stopping times

$$
T_\varepsilon' := \inf\left\{t \geq 0 : \left(\frac{N_{2a,t}^K}{N_{2a,t}^K + N_{2d,t}^K}, N_{2,t}^K, N_{1,t}^K\right) \in \mathcal{B}_\varepsilon^1\right\},
$$
$$
T_\beta'' := \inf\left\{t \geq T_\varepsilon' : \mathbf{N}_t^K \in \mathcal{B}_\beta^2\right\}.
$$

Informally speaking, our goal is to show that with high probability the process has to pass through $\mathcal{B}_\varepsilon^1$ and $\mathcal{B}_\beta^2$ in order to reach S_β. Then, thanks to the Markov property, we can estimate T_{S_β} by estimating T_ε', $T_\beta'' - T_\varepsilon'$ and $T_{S_\beta} - T_\beta''$. (65) implies that

$$
\liminf_{K\to\infty} \mathcal{I}(K,\varepsilon) \geq \mathbb{P}\left(\left|\frac{T_\varepsilon'}{\log K} - \frac{1}{\tilde{\lambda}}\right| \leq \frac{f(\varepsilon)}{3}, \left|\frac{T_\beta'' - T_\varepsilon'}{\log K}\right| \leq \frac{f(\varepsilon)}{3},\right.
$$
$$
\left.\left|\frac{T_{S_\beta} - T_\beta''}{\log K} - \frac{1}{\mu - \lambda_1 + \alpha\bar{n}_{2a}}\right| \leq \frac{f(\varepsilon)}{3}, \, T_{\sqrt{\varepsilon}}^2 < T_0^2 \wedge R_{2\varepsilon},\right.
$$
$$
\left. T_\beta'' < T_{S_\beta}, \, T_{S_\beta} < T_0^2 \right) + o_\varepsilon(1),
$$

see [15, display before (3.60)] for further details in a similar setting. Note that for $\varepsilon > 0$ sufficiently small, $R_{2\varepsilon} \leq T_{S_\beta}$ almost surely, further, if $T_\varepsilon' < \infty$, then $T_\varepsilon' < T_\beta''$. Hence, the strong Markov property applied at times T_ε' and T_β'' implies

$$
\liminf_{K\to\infty} \mathcal{I}(K,\varepsilon) \geq \liminf_{K\to\infty}\left[\, \mathbb{P}\left(\left|\frac{T_\varepsilon'}{\log K} - \frac{1}{\tilde{\lambda}}\right| \leq \frac{f(\varepsilon)}{3}, \, T_\varepsilon' < T_0^2, \, T_{\sqrt{\varepsilon}}^2 < T_0^2 \wedge R_{2\varepsilon}\right)\right.
$$
$$
\times \inf_{\substack{\mathbf{n}=(n_1,n_{2a},n_{2d}): \\ \left(\frac{n_{2a}}{n_{2a}+n_{2d}}, n_{2a}+n_{2d}, n_1\right) \in \mathcal{B}_\varepsilon^1}} \mathbb{P}\left(\left|\frac{T_\beta'' - T_\varepsilon'}{\log K}\right| \leq \frac{f(\varepsilon)}{3}, \, T_\beta'' < T_0^2 \,\Big|\, \mathbf{N}_0^K = \mathbf{n}\right) \tag{66}
$$
$$
\left.\times \inf_{\mathbf{n}\in\mathcal{B}_\beta^2} \mathbb{P}\left(\left|\frac{T_{S_\beta} - T_\beta''}{\log K} - \frac{1}{\mu - \lambda_1 + \alpha\bar{n}_{2a}}\right| \leq \frac{f(\varepsilon)}{3}, \, T_{S_\beta} < T_0^2 \,\Big|\, \mathbf{N}_0^K = \mathbf{n}\right)\right] + o_\varepsilon(1).
$$

It remains to show that the right-hand side is close to $1 - q$ as $K \to \infty$ and ε is small. We first consider the first term and verify that

$$
\liminf_{K\to\infty} \mathbb{P}\left(\left|\frac{T_\varepsilon'}{\log K} - \frac{1}{\tilde{\lambda}}\right| \leq \frac{f(\varepsilon)}{3}, \, T_\varepsilon' < T_0^2, \, T_{\sqrt{\varepsilon}}^2 < T_0^2 \wedge R_{2\varepsilon}\right) \geq 1 - q + o_\varepsilon(1). \tag{67}
$$

This can be done analogously to [15, Proof of (3.61)].

Next, we handle the second term on the right-hand side of (66). For $\mathbf{m} = (m_1, m_{2a}, m_{2d}) \in [0, \infty)^3$, let $\mathbf{n}^{(\mathbf{m})}$ denote the unique solution of the dynamical system (6) with initial condition $\mathbf{m}$. Thanks to the continuity of flows of this dynamical system with respect to the initial condition and thanks to the convergence provided by Lemma 4.7, we deduce that there exist

ε_0 and $\delta_0 > 0$ such that for all $\varepsilon \in (0, \varepsilon_0)$ and $\delta \in (0, \delta_0)$, there exists $t_{\beta,\delta,\varepsilon} > 0$ such that for all $t > t_{\beta,\delta,\varepsilon}$,

$$\left| \mathbf{n}^{(\mathbf{n}^0)}(t) - (0, \bar{n}_{2a}, \bar{n}_{2d}) \right| \leq \frac{\beta}{4}$$

holds for any initial condition $n^0 = (n_1^0, n_{2a}^0, n_{2d}^0)$ satisfying $(n_{2a}^0/(n_{2a}^0 + n_{2d}^0), n_{2a}^0 + n_{2d}^0, n_1^0) \in \mathcal{B}_\varepsilon^1$. Indeed, because of Lemma 4.8, n^0 satisfies (49) in case $n_{2a}^0/(n_{2a}^0 + n_{2d}^0)$ is equal to π_{2a}, and for all sufficiently small $\varepsilon > 0$, the same follows by continuity for all $n^0 = (n_1^0, n_{2a}^0, n_{2d}^0)$ such that $(n_{2a}^0/(n_{2a}^0 + n_{2d}^0), n_{2a}^0 + n_{2d}^0, n_1^0) \in \mathcal{B}_\varepsilon^1$.

Now, using Lemma 4.3, we conclude that for all $\varepsilon < \varepsilon_0$,

$$\lim_{K \to \infty} \mathbb{P}\left(T_\beta'' - T_\varepsilon' \leq t_{\beta,\delta,\varepsilon} \,\middle|\, \left(\frac{N_{2a,0}^K}{N_{2a,0}^K + N_{2d,0}^K}, N_{2,0}^K, N_{1,0}^K \right) \in \mathcal{B}_\varepsilon^1 \right) = 1 - o_\varepsilon(1).$$

Thus, the second term on the right-hand side of (66) is close to 1 when K tends to ∞ and $\varepsilon > 0$ is small.

Lastly, we investigate the third term on the right-hand side of (66). By Proposition 4.9, there exists $\beta_0 > 0$ (denoted as ε_0 in Proposition 4.9) such that for all $\beta < \beta_0$, for $\varepsilon > 0$ sufficiently small,

$$\lim_{K \to \infty} \mathbb{P}\left(\left| \frac{T_{S_\beta} - T_\beta''}{\log K} - \frac{1}{\mu - \lambda_1 + \alpha \bar{n}_{2a}} \right| \leq \frac{f(\varepsilon)}{3} \,\middle|\, \mathbf{N}_0^K \in \mathcal{B}_\beta^2 \right) = 1 - o_\varepsilon(1).$$

Further β_0 can be chosen as large as $\min\{\bar{n}_{2a}, \bar{n}_{2d}\}$. Combining (67) with the convergence of the second and the third term on the right-hand side of (66) to 1, we obtain (61), which implies (13).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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