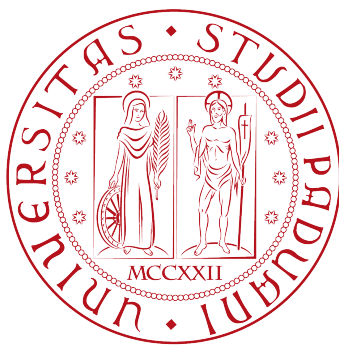




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Spatial Models for Ecological Communities

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Abstract

Equilibrium-based and large-population deterministic approaches, often formulated in well-mixed settings, are widely used in theoretical ecology, yet many ecologically relevant outcomes are shaped by transient amplification, long-lived metastable regimes, and stochastic effects that are not captured by mean-field steady states and linear stability alone. Within this context, this thesis addresses theoretical models of spatially distributed populations that extend beyond these baseline descriptions by relaxing selected underlying assumptions.

Across distinct modeling frameworks, it adopts a mechanism-oriented perspective to derive population-level behavior from elementary microscopic processes – such as reproduction, dispersal, colonization–extinction events, and threshold-driven interactions. On this basis, the analysis develops tractable reduced descriptions and minimal models that retain key mechanistic features, enabling the characterization of dynamical regimes and transitions, ranging from survival–extinction thresholds to the onset of outbreak dynamics.

Three case studies are developed here. In stochastic metapopulations, finite local carrying capacities replace deterministic persistence with metastable survival, yielding extinction-time statistics and finite-size scaling near the persistence threshold. In discrete-time models of dispersal evolution, demographic fluctuations coupled to nonlinear updates reshape invasion thresholds and long-run outcomes beyond mean-field predictions. Finally, bark-beetle outbreaks in spruce forests provide a biologically motivated setting, where disturbances trigger rapid transient amplification and recurrent outbreak regimes arise from ecological feedbacks. A spatial extension of this minimal model is outlined to study localized outbreak waves and emergent aggregation.

Overall, this work presents a dynamical-systems perspective on ecological populations shaped by dispersal, finite-size fluctuations, and nonlinear feedbacks, drawing on tools from statistical physics to analyze population behavior.

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1

Introduction

1.1 Motivation and approach

This thesis investigates ecological dynamics of spatially distributed populations beyond baseline large-population deterministic approximations and equilibrium-based analyses. Rather than constructing a single detailed model tailored to a specific system, it adopts a mechanism-oriented perspective. Starting from simple individual-level processes—such as reproduction and dispersal, colonization and extinction events, and threshold-driven interactions—it examines how their interplay gives rise to population-level regimes, transitions, and dynamical responses. Across the different modeling frameworks considered, a recurring theme is that ecological dynamics is often governed by processes away from equilibria and over finite time scales.

In the context of finite populations, stochastic fluctuations are not merely a source of noise around deterministic predictions, but a structured ingredient that shapes system behavior on ecologically relevant timescales, often promoting long-lived transients and potentially shifting qualitative predictions relative to large-population deterministic limits. This motivates a systematic effort to derive reduced and effective descriptions of stochastic dynamics – through quasi-stationary reductions or moment-based closures – that remain analytically tractable while retaining the signatures of finite-size effects.

Complementarily, ecological systems governed by nonlinear feedbacks and thresholds can exhibit pronounced non-asymptotic dynamics even in the absence of stochasticity. Bark-beetle outbreaks in spruce forests provide a concrete illustration, with disturbances triggering rapid transient amplification and threshold crossing. In such settings, finite-time responses to perturbations play a central role, motivating an analysis of the dynamical mechanisms underlying outbreak initiation and recurrence.

From this standpoint, the thesis emphasizes three closely related aspects: (i) dynamical regime transitions and thresholds separating extinction and persistence; (ii) finite-size scaling behavior and universal signatures in extinction-time statistics near such transitions; and (iii) transient and out-of-equilibrium dynamical regimes beyond fixed points, including metastability, perturbation amplification, and self-sustained oscillations.

By integrating tools from stochastic processes and dynamical systems theory, this work aims to elucidate how finite population effects, nonlinear interactions, and dispersal jointly generate rich ecological dynamics. The remainder of this introduction briefly situates these contributions within existing approaches in spatial and theoretical ecology, providing the minimal context required for

the developments presented in this thesis.

1.2 Context and existing frameworks

Ecological populations are rarely well mixed. Individuals are distributed in space, occupy discrete habitat units, and interact locally with conspecifics, other species, and resources. As a result, population-level dynamics emerges from the coupling between local demographic processes and dispersal across space¹ [3–5].

Spatial ecology has developed complementary modeling frameworks to capture these effects [6]. In patch-based and network approaches, landscapes are represented as sets of discrete habitat patches coupled by colonization and extinction processes [7]. Classic deterministic formulations clarified how spatial coupling can promote persistence even when local extinctions are frequent [8, 9], and later developments made dispersal explicitly dependent on distance, connectivity, and patch quality [10]. Within this class of models, the metapopulation framework developed by Hanski and later generalized by Ovaskainen introduced the concept of *metapopulation capacity* [11, 12] as a landscape-level quantity determining a sharp persistence threshold in the deterministic limit [13].

In parallel, continuum descriptions treat populations as density fields evolving in space and time. When individual motion can be approximated as a random walk at large scales, dispersal leads naturally to diffusion, yielding reaction–diffusion equations in which local demographic interactions are coupled to spatial transport [14, 15]. These models provide a tractable setting to study spatial propagation and large-scale dynamical patterns [16], and admit a wide range of extensions, including density-dependent transport [17].

Alongside these well-established frameworks, spatial ecological systems may display nontrivial forms of spatial organization, such as clustering, patchiness, and long-range correlations [3, 18, 19]. Several theoretical perspectives have been developed to analyze and interpret such structures. These include pattern-forming instabilities in reaction–diffusion systems [20, 21], connectivity and percolation-based perspectives relevant to spatial spread [22, 23], as well as correlation-based and statistical measures of spatial order [24, 25]. While these approaches are not developed as primary analytical tools in the present thesis, they provide a useful conceptual background for interpreting the emergence of large-scale spatial structure in ecological systems.

Crucially, many spatial and metapopulation models rely on deterministic approximations that implicitly assume large local population sizes [26]. In ecologically realistic settings, however, populations are finite, and demographic fluctuations become an intrinsic component of the dynamics [27]. A direct consequence is metastability, whereby deterministic persistence is replaced by noise-induced transient survival characterized by extinction probabilities and extinction-time distributions, rather than by a binary outcome [28]. More generally, stochasticity does not merely broaden deterministic predictions, but can shift effective thresholds and introduce dynamical effects beyond those captured by mean-field approximations [29]. A substantial body of work has addressed finite-size effects and intrinsic stochasticity using mesoscopic and system-size expansion techniques, both in spatially structured systems [30–34] and in well-mixed stochastic population models [35, 36]. These approaches consistently show that fluctuations can qualitatively

¹Dispersal has also been extensively studied as an evolving trait in spatially structured populations, shaped by trade-offs between local competition, kin structure, and the costs and benefits of movement [1]. A large theoretical literature has investigated the conditions under which dispersal strategies are favored, typically within deterministic and equilibrium-based frameworks, using tools from invasion analysis and adaptive dynamics [2].

alter dynamical behavior, generate long-lived transients, and induce oscillatory or noise-sustained regimes beyond deterministic predictions. Extensions to discrete-time systems further highlight the generality of fluctuation-driven mechanisms across different modeling formalisms [37, 38].

Taken together, spatial coupling, finite population sizes, and nonlinearities inherent to ecological interactions shift the focus away from purely asymptotic properties and toward dynamical behavior on finite time scales. More broadly, asymptotic stability alone is often an incomplete descriptor of ecological behavior, even in deterministic large-population settings. This encourages shifting attention from steady states and their linear stability to finite-time responses, transients, and out-of-equilibrium regimes as integral components of ecological dynamics [39–41].

1.3 Scope and organization of the thesis

This thesis develops a bottom-up investigation of ecological dynamics in systems featuring spatial structure, nonlinear feedbacks, and finite-size effects. Rather than advancing a single comprehensive model, it is structured around a set of complementary case studies that combine these ingredients across different modeling settings.

Chapter 2 develops these ideas in the context of stochastic metapopulations. Starting from microscopic colonization–extinction processes on spatial networks, it shows how finite local carrying capacities transform deterministic persistence into metastable survival and allow for analytical predictions of the scaling behavior of extinction times and their variability near the persistence threshold, in homogeneous landscapes with effectively mean-field dispersal. This chapter establishes a quantitative link between deterministic persistence criteria and stochastic extinction statistics, highlighting universal scaling signatures close to the extinction transition.

Chapter 3 investigates dispersal strategies in discrete-time stochastic populations. Here, nonlinear update rules and demographic fluctuations interact to generate effective dynamics that differ systematically from naive mean-field predictions. By deriving variance-corrected descriptions, this chapter shows how population fluctuations can reshape invasion thresholds and long-run outcomes, leading to sharp, transition-like changes in dispersal behavior. More generally, the analysis explores how dispersal evolution is shaped by the interplay between demographic stochasticity and environmental heterogeneity. These findings provide a dynamical basis for interpreting dispersal outcomes in evolutionary terms, without relying on an explicit adaptive-dynamics framework.

While the first two parts of the thesis focus on abstract population models, designed to isolate general mechanisms linking dispersal, stochasticity, and nonlinear dynamics, Chapter 4 turns to a biologically motivated case study: bark beetle outbreaks in conifer forests. Within a minimal deterministic framework, the model captures threshold-driven mass attacks and feedbacks between beetle populations and host availability. The analysis goes beyond equilibrium behavior to characterize reactivity, transient outbreaks triggered by perturbations, and intrinsically recurrent outbreak regimes arising from ecological feedbacks. Finally, in Section 4.9, a spatially explicit extension of the bark beetle model is outlined as a perspective. This extension naturally brings together the main themes of the thesis within a single framework and provides a setting to explore how dispersal and local interactions can generate spatial aggregation, propagating waves of elevated outbreak activity, and localized outbreaks.

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2

Stochastic metapopulations and finite-size extinction statistics

Abstract. Spatial metapopulation models are fundamental to theoretical ecology, enabling to study how landscape structure influences global species dynamics. Traditional models, including recent generalizations, often rely on the deterministic limit of stochastic processes, assuming large population sizes. However, stochasticity - arising from dispersal events and population fluctuations - profoundly shapes ecological dynamics. In this chapter, we extend the classical metapopulation framework to account for finite populations, examining the impact of stochasticity on species persistence and dynamics. Specifically, we analyze how the limited capacity of local habitats influences survival, deriving analytical expressions for the finite-size scaling of the survival probability near the critical transition between survival and extinction. Crucially, we demonstrate that the deterministic metapopulation capacity plays a fundamental role in the statistics of survival probability and extinction time moments. These results provide a robust foundation for integrating demographic stochasticity into classical metapopulation models and their extensions.

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Structure. In Section 2.2, we present a deterministic generalization of the classical Hanski–Ovaskainen metapopulation framework, derived from microscopic colonization–extinction processes on a spatial network. In Section 2.3, we incorporate stochasticity associated with finite carrying capacities and derive a reduced one-dimensional model, which we use to characterize universal finite-size scaling laws for extinction times and fluctuations in Section 2.4. Finally, Section 2.5 discusses coarse-grained indicators that connect the results to ecologically interpretable quantities.

2.1 Introduction

Understanding the dynamics of populations distributed across fragmented habitats is a longstanding challenge in ecology and conservation biology. Metapopulation theory provides a foundational framework for examining how local extinctions and landscape-mediated colonization processes

shape the collective dynamics of spatially structured populations over time [1–10]. The concept of metapopulation, first introduced by Levins [11], describes a “population of populations”, i.e., a set of distinguished subpopulations that are spatially separated, but interconnected by the ongoing exchange of individuals. This exchange occurs across a spatial network of habitat patches, varying in quality, connectivity, and area [2]. Both field and theoretical studies have highlighted the validity of this approach, showing that landscape topology significantly influences the flow of individuals between habitats, ultimately determining the survival or extinction of the metapopulation [12–16].

In particular, to capture the effects of spatial structure and habitat fragmentation on species persistence, Hanski and Ovaskainen introduced a fundamental measure known as metapopulation capacity [17–19], which determines the survival of a focal species within a given landscape. This measure is defined as the maximum eigenvalue of an appropriate landscape matrix, and allows for a direct comparison between theoretical models and real-world networks of habitat fragments [20]. Although the application of network theory to spatial ecology [21–23] has advanced the study of complex dispersal network structures [5, 24–28], metapopulation capacity has traditionally been defined within deterministic models. Crucially, such models overlook fluctuations arising from demographic and environmental stochasticity [29–31]. Early contributions by Lande [32] and Hanski [33] pioneered the integration of stochasticity into metapopulation dynamics, emphasizing the increased risk of extinction posed by random fluctuations at low population levels. Migration through spatially connected patches, by contrast, provides insurance against simultaneous global extinction, underscoring the fundamental role of dispersal network topology. Classical approaches to studying these dynamics, such as Stochastic Patch Occupancy Model [34, 35], the Incidence Function Model [33] and their extensions [36–39], have enabled the computation of extinction times and quasi-stationary occupancy distributions. However, these approaches predominantly rely on purely numerical methods due to the complexity of stochastic processes, spatial heterogeneity, and variability in the parameter space [40]. As a consequence, in metapopulation dynamics, qualitative results are often obtained from deterministic approximations of stochastic processes, which lead to theoretically tractable models and provide broad qualitative insights [4].

In this work, we rigorously extend the traditional deterministic metapopulation framework by explicitly incorporating the stochasticity of individual-level processes to investigate analytically their potential impact on metapopulation dynamics and persistence. To incorporate stochasticity from the ground up, we focus on the role of finite carrying capacity, i.e., the maximum size of the subpopulations that compose the metapopulation. This approach offers a precise way to control fluctuations, allowing us to disentangle the effects of local demographic stochasticity and dispersal network topology. Specifically, we examine whether critical thresholds in carrying capacity exist beyond which stochastic fluctuations become catastrophic, or conversely, whether there are local system sizes beyond which population persistence is significantly enhanced. To address this question, we build upon our previous work, which extends the deterministic spatial metapopulation model developed by Hanski and Ovaskainen to arbitrary landscape structures [5]. We adopt a bottom-up approach, starting from a microscopic model describing colonization, extinction, and dispersal of a focal species at the individual level.

To analytically study the stochastic dynamics of the system, we perform a Van Kampen inverse system-size expansion of the corresponding master equation [41], selecting the inverse of the carrying capacity of the patches - i.e., the maximum local population size supported by each patch - as the expansion parameter. We then introduce a series of simplifying hypotheses to derive analytical insights from the resulting Fokker-Planck equation. In particular, we assume translational invariance within a complete network and marginalize to capture the effective behavior of representative

single-site variables. By imposing a separation of timescales [42] between dispersal and local processes, we derive an effective one-dimensional quasi-stationary (QSS) Langevin equation that accurately captures the overall metapopulation dynamics. In the deterministic limit, we recover the expected absorbing phase transition [43, 44] between extinction and survival regimes, as determined by the system's metapopulation capacity. Stochasticity, however, renders the survival regime metastable - a key result especially relevant for systems with small carrying capacity. Moreover, the effective QSS equation enables us to analytically study the general scaling behavior of the survival probability in the vicinity of the extinction transition. We demonstrate that near this transition point, the survival probability for different carrying capacities exhibits a universal behavior consistent with finite-size scaling [45, 46]. Furthermore, we analytically derive the scaling of the first and second moments of extinction time with varying carrying capacity, showing that they similarly collapse to a universal form.

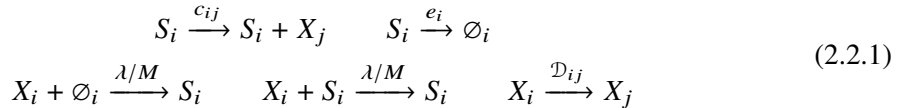
Through this analysis, we bridge results from the deterministic metapopulation framework with its stochastic counterpart. We demonstrate that the metapopulation capacity - a deterministic measure - still plays a crucial role in the statistics of survival probability and extinction time moments.

2.2 Deterministic metapopulation model

We introduce a model that describes the microscopic dynamics of a single species within a metapopulation. Individuals undergo processes such as birth, death, reproduction, and dispersal across a network of habitat patches, as illustrated in Figure 2.1. This model was proposed in [5], where the connection between its deterministic limit and the Hanski and Ovaskainen model [2, 18] was demonstrated. In this section, we first provide a detailed description of the microscopic processes governing the dynamics and then briefly recall the derivation of the macroscopic deterministic equations, as outlined in [5]. This is instrumental in the analysis of the full stochastic model, which we analyze in the following section.

2.2.1 Microscopic ecological dynamics

We consider a dispersal network of N interconnected habitat patches, corresponding to the nodes of the dispersal network, inhabited by a given focal species. We separately model the behavior of two kinds of individuals: settled individuals (denoted by S), which reside on the nodes of the network, and explorers (X), which diffuse through the edges of the network. We denote the vector comprising all local abundances of individuals in each node by $\vec{n} = (n_{X_1}, \dots, n_{X_N}; n_{S_1}, \dots, n_{S_N})$, where n_{X_i} and n_{S_i} are the numbers of explorers and settled individuals in patch i , respectively. By assuming that each patch has a maximum carrying capacity of M settled individuals - i.e., $n_{S_i} + n_{\emptyset_i} = M \quad \forall i$, where $\emptyset_i$ denotes an empty site in patch i - we define the following microscopic reactions:



where the indices $i, j = 1, \dots, N$ label the network patches. The rate e_i accounts for the death of a settled individual in patch i , while c_{ij} represents the rate at which an explorer in patch j is produced by a settled individual in a neighboring node i . An explorer in i can move to a connected patch j at rate $\mathcal{D}_{ij}$, and it may attempt to colonize a randomly chosen site in its current patch at a rate λ/M . In this process, the explorer does not necessarily target only available sites. Rather, if the chosen site is empty, the explorer settles, whereas if the site is already occupied, the explorer dies. This formulation ensures that the total rate of explorer removal reflects both successful colonization

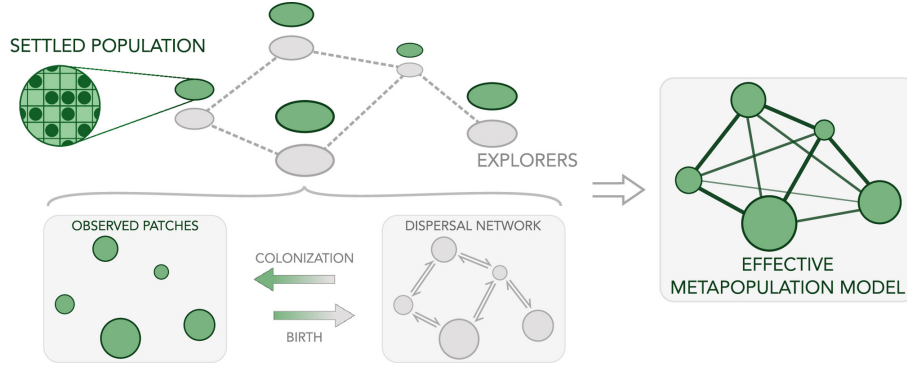


FIG. 2.1. Schematic representation of the deterministic metapopulation model introduced in [5]. The model describes a population of settled individuals residing in habitat patches and a population of explorers moving across a dispersal network and attempting colonization. In the fast-exploration regime, the dynamics reduces to an effective deterministic equation for the settled population, characterized by a topology-dependent colonization kernel. The figure is reproduced from [5] with permission from the authors.

and death due to an occupied site, while the rescaling of λ with M guarantees that such rate is independent of M . Diffusion rates are set in the form $\mathcal{D}_{ij} = \mathcal{D} \mathcal{A}_{ij}$ with $\mathcal{A}_{ij}$ the adjacency matrix of the dispersal network, denoting a possibly weighted connection between node j and node i . Similarly, the colonization rate c_{ij} is given by $c_{ij} = c_i h(\mathcal{D}/\lambda) \mathcal{A}_{ij}$, where $h(f)$ is a function that encodes feasibility of exploration and $f = \mathcal{D}/\lambda$ controls exploration efficiency. A Monod function $h(f) = \frac{\xi_0}{1+1/f}$ is typically chosen to model the saturation effect of exploration feasibility, where ξ_0 represents the maximal explorability.

2.2.2 Deterministic equations

The deterministic equations resulting from the microscopic model defined in Eq. (2.2.1) are given by:

$$\begin{aligned} \dot{\rho}_i &= -e_i \rho_i + \lambda (1 - \rho_i) x_i \\ \dot{x}_i &= -\lambda x_i + h(f) \sum_{j=1}^N \mathcal{A}_{ji} c_j \rho_j + \mathcal{D} \sum_{j=1}^N (\mathcal{A}_{ji} x_j - \mathcal{A}_{ij} x_i) \end{aligned} \quad (2.2.2)$$

where ρ_i , x_i are the average population densities, $\langle n_{S_i} \rangle / M$ and $\langle n_{X_i} \rangle / M$, respectively. In the limit in which the explorers' dynamics is much faster than the dynamics of the settled population, one obtains an effective model describing the evolution of the settled population:

$$\dot{\rho}_i = -e_i \rho_i + (1 - \rho_i) \sum_{j=1}^N c_j K_{ji} \rho_j \quad (2.2.3)$$

where the kernel matrix K encodes the dependence of the population density on the topology of the dispersal network. We have that

$$K_{ji} = \sum_{k=1}^N C_{jk} F_{ik}^{-1} \quad (2.2.4)$$

where we introduced the matrix $F = \mathbb{I} + f L^T$ that depends on the out-degree Laplacian of the network, $L_{ij} = \delta_{ij} \sum_{k=1}^N \mathcal{A}_{ik} - \mathcal{A}_{ij}$. The kernel matrix, K , introduces an effective coupling between

settled populations residing in different patches. In particular, in [5] it was shown that

$$K_{ji} = h(f) \sum_{l=1}^N A_{jl} \sum_{k=1}^N \frac{V_{ik}(V^{-1})_{kl}}{1 + f\omega_k} \quad (2.2.5)$$

where ω_k is the k -th eigenvalue of the transpose out-degree Laplacian of the dispersal network, and $V_{ij} = v_i^{(j)}$ with $\mathbf{v}^{(k)}$ the corresponding right eigenvector. Furthermore, from the deterministic model in Eq. (2.2.3), one can show that if $e_i = e$ and $c_i = c$ for all patches, the survival of the species is uniquely determined by the maximum eigenvalue of the dispersal kernel, i.e., the metapopulation capacity λ_M proposed by Hanski and Ovaskainen [17]. If $\lambda_M > e/c$, the species survives; otherwise, it goes extinct. A similar condition has been shown to hold when e_i explicitly depends on the patch index [27].

2.3 Stochastic model

In deriving the deterministic dynamics given by Eq. (2.2.2), we have implicitly assumed a large carrying capacity, i.e., $M \rightarrow \infty$. However, to investigate the effect of stochasticity on population persistence, we need to extend the deterministic model to account for finite carrying capacities, which introduce demographic fluctuations. For a general model defined by a set of microscopic processes, the complete stochastic dynamics is governed by the master equation [47]

$$\partial_t \mathcal{P}(\vec{n}, t) = \sum_{\vec{n}' \neq \vec{n}} \left[W(\vec{n}|\vec{n}') \mathcal{P}(\vec{n}', t) - W(\vec{n}'|\vec{n}) \mathcal{P}(\vec{n}, t) \right] \quad (2.3.1)$$

where $\mathcal{P}(\vec{n}, t)$ is the probability that the system is in state $\vec{n}$ at time t , and $W(\vec{n}'|\vec{n})$ are the rates at which the system transitions from state $\vec{n}$ to state $\vec{n}'$. The transition rates for our model can be straightforwardly derived from the reactions Eq. (2.2.1), leading to:

$$\begin{aligned} W(n_{S_i} - 1; n_{X_i} | n_{S_i}; n_{X_i}) &= e_i n_{S_i} \\ W(n_{S_i} + 1; n_{X_i} - 1 | n_{S_i}; n_{X_i}) &= \frac{\lambda}{M} n_{X_i} (M - n_{S_i}) \\ W(n_{S_i}; n_{X_i} - 1 | n_{S_i}; n_{X_i}) &= \frac{\lambda}{M} n_{X_i} n_{S_i} \\ W(n_{S_i}, n_{S_j}; n_{X_i} + 1, n_{X_j} | n_{S_i}, n_{S_j}; n_{X_i}, n_{X_j}) &= c_{ji} n_{S_j} \\ W(n_{S_i}, n_{S_j}; n_{X_i} + 1, n_{X_j} - 1 | n_{S_i}, n_{S_j}; n_{X_i}, n_{X_j}) &= \mathcal{D}_{ji} n_{X_j} \end{aligned} \quad (2.3.2)$$

where, for the sake of brevity, we explicitly write only the number of individuals at the nodes involved in the transition.

2.3.1 Fokker-Planck equation

Although no closed-form solution for the master equation of our model exists, the corresponding stochastic dynamics can be simulated exactly using the Gillespie algorithm [48]. However, we can obtain analytical insight into the effects of stochasticity by means of a Van Kampen system size expansion [41, 49]. We take $1/M$ as the natural expansion parameter, so that in the $M \rightarrow \infty$ limit we recover the deterministic equations. To perform this expansion, it is convenient to rewrite the master equation in terms of step operators, defined by their action on a generic function $f(\vec{n})$ as:

$$\xi_{A_i}^{\pm 1} f(n_{A_1}, \dots, n_{A_i}, \dots, n_{A_N}) = f(n_{A_1}, \dots, n_{A_i} \pm 1, \dots, n_{A_N}) \quad (2.3.3)$$

(see Appendix 2.A for details). In terms of step operators, the master equation becomes:

$$\begin{aligned} \frac{\partial}{\partial t} \mathcal{P}(\vec{n}, t) = & \sum_{i=1}^N \left\{ \left[\left(\xi_{S_i}^{+1} - 1 \right) W(n_{S_i} - 1; n_{X_i} | n_{S_i}; n_{X_i}) + \left(\xi_{S_i}^{-1} \xi_{X_i}^{+1} - 1 \right) W(n_{S_i} + 1; n_{X_i} - 1 | n_{S_i}; n_{X_i}) \right. \right. \\ & + \left. \left(\xi_{X_i}^{+1} - 1 \right) W(n_{S_i}; n_{X_i} - 1 | n_{S_i}; n_{X_i}) \right] \mathcal{P}(n_{S_i}; n_{X_i}) \Big\} \\ & + \sum_{i=1}^N \sum_{j=1}^N \left\{ \left[\left(\xi_{X_i}^{-1} - 1 \right) W(n_{S_i}, n_{S_j}; n_{X_i} + 1, n_{X_j} | n_{S_i}, n_{S_j}; n_{X_i}, n_{X_j}) \right. \right. \\ & + \left. \left(\xi_{X_i}^{-1} \xi_{X_j}^{+1} - 1 \right) W(n_{S_i}, n_{S_j}; n_{X_i} + 1, n_{X_j} - 1 | n_{S_i}, n_{S_j}; n_{X_i}, n_{X_j}) \right] \mathcal{P}(n_{S_i}, n_{S_j}; n_{X_i}, n_{X_j}) \Big\}. \end{aligned} \quad (2.3.4)$$

Note that the step operators act on the entire product $W\mathcal{P}$ (i.e., both on W and $\mathcal{P}$), but we have grouped $\mathcal{P}$ to keep the expression more compact. If we define the population densities with respect to the system size parameter M as $\rho_i = n_{S_i}/M$, $x_i = n_{X_i}/M$, the expansion of the master equation up to second order in powers of $1/M$, for fixed densities, yields the Fokker-Planck (FP) equation:

$$\begin{aligned} \partial_t \mathcal{P}(\vec{\rho}, \vec{x}, t) = & - \sum_{i=1}^N \partial_{\rho_i} [A_i^\rho(\vec{\rho}, \vec{x}) \mathcal{P}(\vec{\rho}, \vec{x}, t)] - \sum_{i=1}^N \partial_{x_i} [A_i^x(\vec{\rho}, \vec{x}) \mathcal{P}(\vec{\rho}, \vec{x}, t)] + \\ & + \frac{1}{2} \sum_{i,j=1}^N \partial_{\rho_i} \partial_{\rho_j} [\mathbb{D}_{i,j}^{\rho\rho}(\vec{\rho}, \vec{x}) \mathcal{P}(\vec{\rho}, \vec{x}, t)] + \frac{1}{2} \sum_{i,j=1}^N \partial_{x_i} \partial_{x_j} [\mathbb{D}_{i,j}^{xx}(\vec{\rho}, \vec{x}) \mathcal{P}(\vec{\rho}, \vec{x}, t)] \\ & + \sum_{i,j=1}^N \partial_{\rho_i} \partial_{x_j} [\mathbb{D}_{i,j}^{\rho x}(\vec{\rho}, \vec{x}) \mathcal{P}(\vec{\rho}, \vec{x}, t)]. \end{aligned} \quad (2.3.5)$$

Here, the subscripts i, j, k label the network patches while the superscripts ρ, x refer to the settled and explorer population, respectively. The drift vector's components correspond to the deterministic model:

$$\begin{aligned} A_i^\rho &= \lambda x_i (1 - \rho_i) - e_i \rho_i \\ A_i^x &= \sum_j (\mathcal{D}_{ji} x_j - \mathcal{D}_{ij} x_i + c_{ji} \rho_j) - \lambda x_i \end{aligned} \quad (2.3.6)$$

and the Fokker-Planck diffusion matrix has the following block structure

$$\mathbb{D} = \begin{pmatrix} \mathbb{D}^{\rho\rho} & \mathbb{D}^{\rho x} \\ \mathbb{D}^{x\rho} & \mathbb{D}^{xx} \end{pmatrix} \quad (2.3.7)$$

with blocks given by

$$\begin{aligned} \mathbb{D}_{ij}^{\rho\rho} &= \frac{1}{M} [e_i \rho_i + \lambda x_i (1 - \rho_i)] \delta_{ij} \\ \mathbb{D}_{ij}^{\rho x} &= \mathbb{D}_{ij}^{x\rho} = -\frac{1}{M} \lambda x_i (1 - \rho_i) \delta_{ij} \\ \mathbb{D}_{ij}^{xx} &= \frac{1}{M} \left[\sum_k (\rho_k c_{ki} + x_i \mathcal{D}_{ik} + x_k \mathcal{D}_{ki}) + \lambda x_i \right] \delta_{ij} + \\ & - \frac{1}{M} (x_i \mathcal{D}_{ij} + x_j \mathcal{D}_{ji}) (1 - \delta_{ij}). \end{aligned} \quad (2.3.8)$$

where δ_{ij} is the Kronecker delta. We highlight that all entries in the Fokker-Planck diffusion matrix are proportional to the inverse of the carrying capacity, explicitly showing that the leading order of the Van Kampen expansion yields the deterministic dynamics.

Although Eq. (2.3.5) provides an analytical description of our stochastic model in the limit of large system size M , a general analytical treatment remains cumbersome for large networks, as it would require integrating $2N$ variables. Additionally, the explorers' noise strength, $\mathbb{D}^{xx}$, has non-zero off-diagonal entries, coupling their dynamics across patches. Hence, we resort to a further simplification of Eq. (2.3.5) to obtain a more direct understanding of the system's behavior.

2.3.2 Effective SDE

To simplify the dynamics and reduce the number of variables, we assume a fully connected dispersal network $\mathcal{A}_{ij} = \mathcal{A}(1 - \delta_{ij})$, and homogeneous habitat patches $c_i = c$, $e_i = e \forall i$, implying that the system is invariant under translations. $\mathcal{A}$ is set to $1/N$ to ensure a well-defined limit for $N \rightarrow \infty$. To gain analytical insight, we focus on the marginalized probability distribution, by integrating out all variables except those associated with a single site, $(\rho_1, x_1) \equiv (\rho, x)$:

$$\int \prod_{i \geq 2} [d\rho_i dx_i] \mathcal{P}(\vec{\rho}, \vec{x}, t) = P(\rho, x, t). \quad (2.3.9)$$

Motivated by our assumption of a fully connected dispersal network, we adopt the following approximation for each ρ_j, x_j :

$$\begin{aligned} \int \prod_{i \geq 2} [d\rho_i dx_i] \mathcal{P}(\vec{\rho}, \vec{x}, t) x_j &\approx P(\rho, x, t) x \\ \int \prod_{i \geq 2} [d\rho_i dx_i] \mathcal{P}(\vec{\rho}, \vec{x}, t) \rho_j &\approx P(\rho, x, t) \rho \end{aligned} \quad (2.3.10)$$

Finally, we take the limit $N \rightarrow \infty$, obtaining the simplified equation:

$$\begin{aligned} \frac{\partial}{\partial t} P(\rho, x, t) &= -\partial_\rho \{ [\lambda x (1 - \rho) - e \rho] P(\rho, x, t) \} \\ &\quad - \partial_x \{ [c h(f) \rho - \lambda x] P(\rho, x, t) \} \\ &\quad + \frac{1}{2M} \partial_\rho^2 \{ [e \rho + \lambda x (1 - \rho)] P(\rho, x, t) \} \\ &\quad + \frac{1}{2M} \partial_x^2 \{ [c h(f) \rho + (\lambda + 2\mathcal{D}) x] P(\rho, x, t) \} \\ &\quad - \frac{1}{M} \partial_x \partial_\rho [\lambda x (1 - \rho) P(\rho, x, t)] \end{aligned} \quad (2.3.11)$$

as shown in Appendix 2.B. Eq. (2.3.11) is a two-dimensional Fokker-Planck equation in the representative variables ρ and x . Hence, the corresponding Langevin equation can be straightforwardly derived, adopting the Itô prescription:

$$\begin{cases} \dot{x} = c h(f) \rho - \lambda x + \mathbb{B}^{xx} \eta_x \\ \dot{\rho} = \lambda x (1 - \rho) - e \rho + \mathbb{B}^{\rho\rho} \eta_\rho + \mathbb{B}^{\rho x} \eta_x \end{cases} \quad (2.3.12)$$

where $\vec{\eta} = (\eta_\rho, \eta_x)$ are uncorrelated white noises and the two-dimensional matrix $\mathbb{B}$ is related to the Fokker-Planck diffusion matrix $\hat{\mathbb{D}}$ of Eq. (2.3.11) through $\hat{\mathbb{D}} = \mathbb{B}\mathbb{B}^T$:

$$\hat{\mathbb{D}} = \frac{1}{M} \begin{pmatrix} c h(f) \rho + (\lambda + 2\mathcal{D})x & -\lambda x(1 - \rho) \\ -\lambda x(1 - \rho) & e \rho + \lambda x(1 - \rho) \end{pmatrix}. \quad (2.3.13)$$

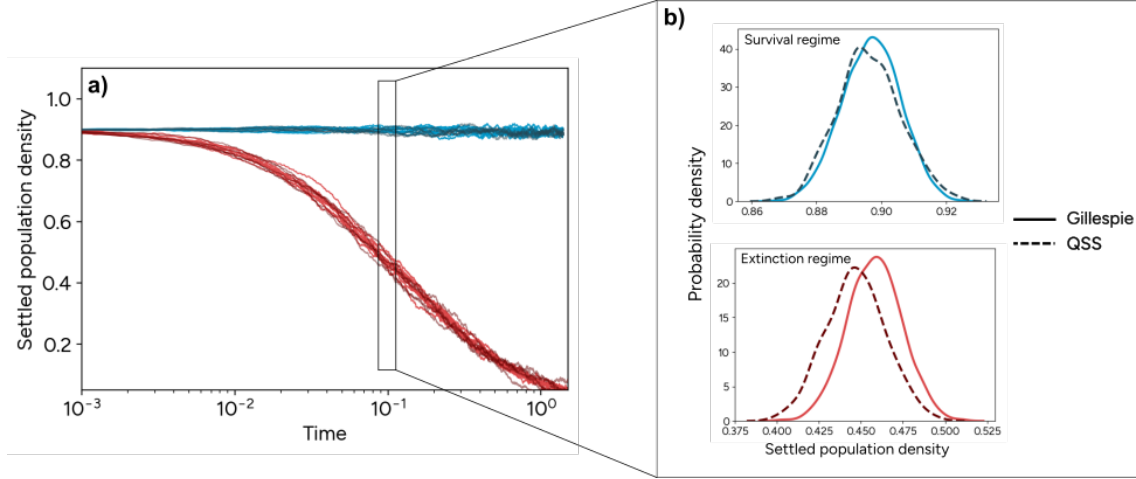


FIG. 2.2. Comparison between **a)** 5 realizations of the trajectories resulting from the mean-field quasi-stationary SDE Eq. (2.3.14) (integrated with the Euler-Maruyama method) and the Gillespie simulation reproducing the exact dynamics of the microscopic model Eq. (2.2.1). The parameters of the model are $M = 1000$, $N = 20$, $f = 1$ which imply an effective metapopulation capacity of $\lambda_M \sim 9.5$. Survival regime ($e/c < \lambda_M$): $e = 1$, $c = 1.5$, extinction regime ($e/c > \lambda_M$): $e = 10$, $c = 1$.

We note that the diffusion matrix $\hat{\mathbb{D}}$ contains negative off-diagonal entries, corresponding to cross terms coupling ρ and x . These originate from microscopic reactions that simultaneously increase one population while decreasing the other. In particular, colonization events ($X \rightarrow S$) induce anti-correlated fluctuations between explorers and settled individuals, resulting in negative covariance terms, while diagonal terms encode the variance of fluctuations in each population arising from colonization, death, and dispersal. Despite the presence of negative off-diagonal entries, the diffusion matrix (2.3.13) is positive semidefinite, as can be verified explicitly (Appendix 2.B), ensuring that the stochastic fluctuations of the reduced dynamics are well defined.

Since we are primarily interested in the persistence of settled populations, we further assume a separation of timescales in the dynamics of the explorers and the settled population. This results in a one-variable effective Langevin equation for the settled population (2.2.3), mirroring the deterministic generalization of the Hanski and Ovaskainen metapopulation model derived in [5]. The elimination of the variable x is, however, more involved than in the deterministic case, due to the presence of noise. We report the detailed calculations in Appendix 2.B, resulting in the following one-dimensional Itô SDE:

$$\dot{\rho} = [c h(f) (1 - \rho) - e] \rho + \sqrt{\frac{\rho}{M} \left\{ e + \frac{c h(f)}{2(1 + \mathcal{D}/\lambda)} \left[1 - \rho^2 + 2 \frac{\mathcal{D}}{\lambda} (1 - \rho) \right] \right\}} \sigma(t) \quad (2.3.14)$$

with $\langle \sigma(t) \rangle = 0$, $\langle \sigma(t) \sigma(s) \rangle = \delta(t - s)$. To verify our derivation and assumptions, we numerically compare the trajectories resulting from the stochastic QSS equation Eq. (2.3.14) with those obtained from a Gillespie simulation of the complete Master equation, which samples the exact microscopic dynamics of the model described in Eq. (2.2.1). As shown in Figure 2.2, we achieve a very good matching between the different trajectories in the survival regime. In the extinction regime, the mean densities are similar. However, the Gillespie trajectory reaches extinction more slowly due to the absorbing boundary, which causes the explorer densities to always deviate from the quasi-stationary value. This suggests that the simplification methods considered up to this point are still able to reproduce the average behavior of the stochastic model under different parameters.

We can now exploit Eq. (2.3.14) to analyze the stochastic dynamics of the model. In particular, the mean-field settled population density ρ has domain $(0, 1]$, with an absorbing boundary at $\rho = 0$, that corresponds to population extinction. $\rho = 1$ is instead a reflecting boundary, corresponding to the maximum number M of individuals that each patch can sustain. Deterministically, Eq. (2.3.14) yields an effective metapopulation capacity $\lambda_M = h(f)$, which still allows us to distinguish two regimes. When $e/c > \lambda_M$, the deterministic stationary solution is $\rho_{\text{st}} = 0$, corresponding to widespread extinction. If $e/c < \lambda_M$ the stationary solution is instead given by $\rho_{\text{st}} = \frac{1}{\lambda_M}(\lambda_M - \frac{e}{c})$, which defines the survival regime in the deterministic mean-field model. However, due to the presence of noise, survival and extinction are no longer deterministic. In particular, if one solves the full stochastic equation in Eq. (2.3.14), with the specified boundary conditions, the only true stationary solution is $\rho_{\text{st}} = 0$. Indeed, the regime $e/c < \lambda_M$ is now characterized by a long-lasting metastable state in which the population survives (see Figure 2.2). This reflects the well-known fact that phase transitions appear only in the thermodynamic limit of an infinite system size. Since the diffusion terms in the Fokker-Planck equations are inversely proportional to the local population size M , we anticipate that stochasticity will have a more pronounced impact on systems with a small carrying capacity. Indeed, as the population size decreases, the likelihood of a random fluctuation inducing extinction increases.

To investigate these effects, we need to compute the probabilities of survival and the time taken to reach extinction. These quantities provide comprehensive information about the impact of the absorbing boundary and enable us to ascertain whether the regimes defined by the deterministic dynamics remain relevant when stochasticity is considered.

2.4 Scaling close to the transition

From the effective stochastic dynamics given by Eq. (2.3.14), we can investigate how the system size M , which is related to the amount of noise affecting the system, influences the survival probability.

Given an initial condition ρ at time $t = 0$, the survival probability is defined as the probability that the variable is still in its domain $(0, 1]$ at time t [47]:

$$S(t|\rho, M) = \int_0^1 p(\rho', t|\rho, 0) d\rho', \quad (2.4.1)$$

where $p(\rho', t|\rho, 0)$ is the solution of the FP equation related to Eq. (2.3.14), with the initial condition $p(\rho', t = 0|\rho, 0) = \delta(\rho - \rho')$. Then, we introduce the mean exit time and its higher moments,

$$T_n(\rho, M) = \int_0^\infty p(t|\rho) t^n dt, \quad (2.4.2)$$

where $p(t|\rho)$ is the probability distribution of extinction times, given the initial condition ρ . The latter probability distribution is connected to the survival probability through $p(t|\rho) = -\partial_t S(t|\rho)$ [47], which implies

$$T_n(\rho, M) = \int_0^\infty t^{n-1} S(t|\rho, M) dt. \quad (2.4.3)$$

To investigate how the survival probability changes with the carrying capacity, we simulate the dynamics of the mean-field QSS stochastic differential equation corresponding to Eq. (2.3.14) for various values of M , using the Euler-Maruyama algorithm, with a total of 10^7 realizations. Figure 2.3a shows the numerical survival probability curves, with the system set at the boundary between

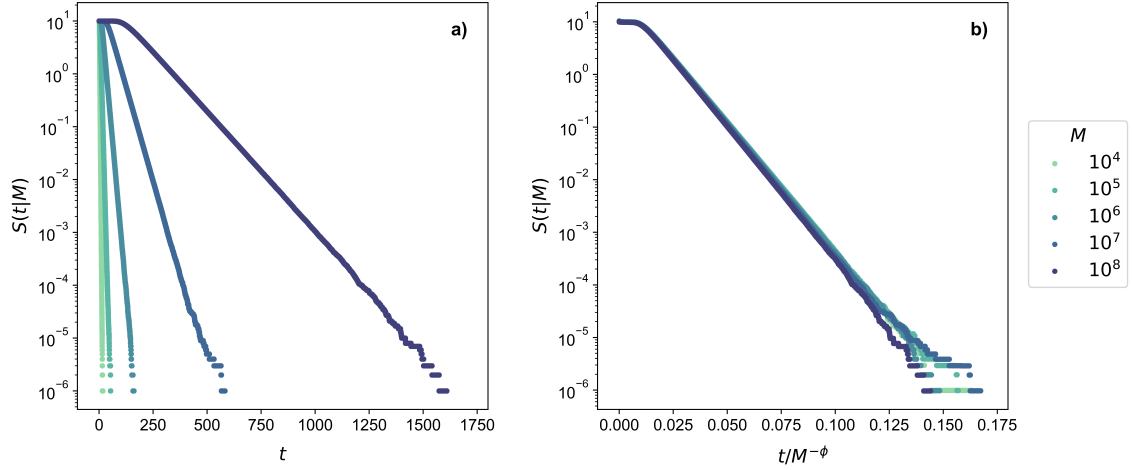


FIG. 2.3. Survival probability of the quasi-stationary SDE as a function of time t and system size M : **(a)** not rescaled. **(b)** rescaled according to Eq. (2.4.4), with the numerical estimates of the scaling exponents given in Eq. (2.4.7). The system is set at criticality and the initial condition is fixed at $\rho = \frac{1}{2}$. The microscopic parameters of the model are $N = 201$, $\lambda = 100$, $D = 100$, $e/c = \lambda_M = 100$. Averages are obtained over 10^7 numerical realizations of the dynamics in Eq. (2.3.14), using Euler-Maruyama algorithm.

the two regimes identified in the deterministic limit, i.e. $e/c \equiv \lambda_M$. We observe that the survival probability curves appear to exhibit a power-law behavior.

Hence, we adopt a typical finite-size scaling ansatz for the survival probability:

$$S(t|\rho, M) \propto \frac{1}{t^\alpha} \mathcal{F}_\rho(t M^\phi). \quad (2.4.4)$$

This corresponds to assuming that, close to the critical point, the survival probability is a generalized homogeneous function of time t and system size M . The scaling function $\mathcal{F}_\rho$ depends on t and M only through their combination $t M^\phi$, and the exponents ϕ and α are expected to be independent of the details of the system. Plugging our ansatz (2.4.4) into Eq. (2.4.3) yields:

$$T_n(\rho, M) = \int_0^\infty \mathcal{F}_\rho(t M^\phi) t^{n-\alpha-1} dt = M^{-\phi(n-\alpha)} C_{n,\alpha}(\rho). \quad (2.4.5)$$

Notice that, by taking the ratio of two consecutive moments - as detailed in Appendix 2.D.2 - we obtain

$$\frac{\langle T^{n+1} \rangle}{\langle T^n \rangle} = \frac{C_{n+1,\alpha}(\rho)}{C_{n,\alpha}(\rho)} M^{-\phi} \quad (2.4.6)$$

where $C_{n,\alpha}(\rho)$ depend only on the initial condition ρ . We can exploit the above relations to numerically verify whether the finite-size scaling ansatz is correct and obtain a preliminary numerical estimate of the scaling exponents α and ϕ . By extracting the time to extinction from each realization of the simulation and fitting the moments' ratios as in Eq. (2.4.6), we can directly obtain the value of ϕ and subsequently estimate α from Eq. (2.4.5):

$$\phi = -0.506 \pm 0.002, \quad \alpha = -0.005 \pm 0.003. \quad (2.4.7)$$

Further details on the numerical derivation are provided in Appendix 2.C. Ultimately, Figure 2.3b shows the collapse of the survival probability curves rescaled according to the numerical exponents in Eq. (2.4.7), which confirms our scaling hypothesis given in Eq. (2.4.4).

Yet, obtaining the scaling behavior of our system away from criticality presents more challenges: indeed, choosing a suitable scaling ansatz is not straightforward in this case. For this reason, we will adopt a more rigorous approach and analytically derive the scaling form of the moments of extinction time directly from the effective stochastic equation (2.4.5). This method yields the exact values of the scaling exponents even when the system is not poised at the critical point.

2.4.1 First and second moments of exit time

We set $T \equiv T_1$ and analytically investigate the scaling behavior of T_n with the carrying capacity M . We rely on the following differential equations, derived from the backward Fokker-Planck equations for the survival probability [47]:

$$A(\rho) \partial_\rho T(\rho) + \frac{1}{2} D(\rho) \partial_\rho^2 T(\rho) = -1 \quad (2.4.8)$$

$$A(\rho) \partial_\rho T_n(\rho) + \frac{1}{2} D(\rho) \partial_\rho^2 T_n(\rho) = -n T_{n-1}(\rho) \quad (2.4.9)$$

where $A(\rho)$ and $D(\rho)$ are the drift and diffusion coefficients of Eq. (2.3.14), respectively, and ρ is the initial condition of the settled population density at time $t = 0$.

We consider a setting in which the system is close to criticality and define the deviation from the critical point ($e/c = \lambda_M$) through

$$\Delta := \frac{1}{\lambda_M} \left(\lambda_M - \frac{e}{c} \right) = \frac{\epsilon}{\lambda_M}, \quad |\epsilon| \ll 1 \quad (2.4.10)$$

where $\lambda_M = h(f)$, as resulting from the deterministic part of the effective quasi-stationary Fokker-Planck Eq. (2.3.14). As shown in Appendix 2.D.1, by rescaling $\rho \rightarrow \hat{\rho} = \rho \sqrt{M}$, $T \rightarrow \hat{T} = \frac{\lambda_M c}{\sqrt{M}} T$ and $\Delta \rightarrow \hat{\Delta} = \Delta \sqrt{M}$, the equation for the first moment of exit time Eq. (2.4.8) becomes

$$\left(\hat{\Delta} - \hat{\rho} \right) \hat{\rho} \partial_{\hat{\rho}} \hat{T} + \frac{\chi}{4} \hat{\rho} \partial_{\hat{\rho}}^2 \hat{T} = -1 \quad (2.4.11)$$

in the limit of large system sizes M . Here, we have introduced $\chi := 3 + \frac{\mathcal{D}}{\mathcal{D} + \lambda}$, which we treat as a fixed constant. Since Eq. (2.4.11) is independent of M , the rescaled extinction time $\hat{T}$ is expected to be a function of the rescaled initial density $\hat{\rho}$ and the rescaled distance from the critical point $\hat{\Delta}$ alone. This implies that, in the limit of large M , T can be written as the scaling form

$$T(\rho, \Delta, M) \propto \sqrt{M} \hat{T} \left(\sqrt{M} \rho, \sqrt{M} \Delta \right) \quad (2.4.12)$$

which implies that it is a homogeneous function of ρ and Δ . The solution of Eq. (2.4.11), with boundary conditions $\hat{T}(0) = 0$, $\partial_{\hat{\rho}} \hat{T}(\hat{\rho})|_{\hat{\rho}=\sqrt{M}} = 0$, is given by the integral Eq. (2.D.5), which can be evaluated analytically at criticality ($\hat{\Delta}=0$) and numerically elsewhere. To test our analytical predictions, we simulate the mean-field QSS SDE over 10^5 realizations, varying the distance from the critical point Δ , the initial condition in the settled population density ρ , and the system size M . As shown in Figure 2.4a, the simulated points distribute within a volume in the three-dimensional space defined by Δ , ρ , and T . Upon rescaling the axes with M according to Eq. (2.4.12), the points

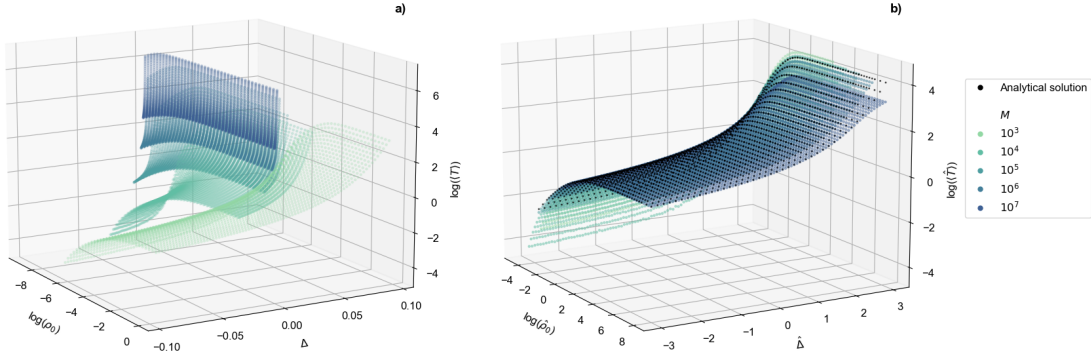


FIG. 2.4. First moment of exit time $\langle T \rangle$ versus initial condition ρ_0 and deviation from criticality Δ for different values of the local carrying capacity M . **a)** not rescaled. **b)** rescaled according to Eq. (2.4.12). The black dots indicate the analytical solution Eq. (2.D.5). Averages are obtained from 10^5 numerical realizations of the MF QSS dynamics in Eq. (2.3.14).

collapse onto a single well-defined surface that encompasses different initial conditions and distances from criticality, consistently with the numerical evaluation of the analytically derived average extinction time (Eq. (2.D.5)). The effectiveness of the collapse can be more clearly visualized through the two-dimensional sections plotted in the left panel of Figure 2.7. We can now apply the same procedure to the equation for the second moment of the exit time, obtained by substituting $n = 2$ into Eq. (2.4.9). The same analysis yields the scaling expression

$$T_2(\rho, \Delta, M) \propto M \hat{T}_2 \left(\sqrt{M} \rho, \sqrt{M} \Delta \right). \quad (2.4.13)$$

Figure 2.6 shows that rescaling the surfaces obtained from simulation data according to Eq. (2.4.13) leads to the collapse of these surfaces. We present further details of the derivation, along with an explicit analytical solution of the differential equation for T_2 , in Appendix 2.D.1.

2.4.2 Survival probability

Having found $\langle T \rangle \propto \sqrt{M}$ (Eq. (2.4.12)) and $\langle T^2 \rangle \propto M$ (Eq. (2.4.13)), we can determine the scaling of the survival probability at criticality ($\Delta = 0$). The ϕ exponent is obtained from Eq. (2.4.6) as

$$\frac{\langle T^2 \rangle}{\langle T \rangle} \propto \sqrt{M} \Rightarrow \phi \equiv -\frac{1}{2}, \quad (2.4.14)$$

and, similarly, we can calculate the α exponent (2.4.5) as

$$\langle T \rangle \propto M^{-\phi(1-\alpha)} \Rightarrow \alpha = 0 \quad (2.4.15)$$

which yields the scaling form

$$S(t|M) \propto f(t M^{-\frac{1}{2}}). \quad (2.4.16)$$

It is worth noting that the scaling exponents derived analytically and the ones obtained numerically reported in Eq. (2.4.7) agree remarkably well.

The technique we employed to analyze moments of extinction time can also be replicated for the survival probability. The starting point is once more the backward Fokker-Planck equation for the survival probability [47],

$$\partial_t S = A(\rho) \partial_\rho S + \frac{1}{2} D(\rho) \partial_\rho^2 S. \quad (2.4.17)$$

Since Eq. (2.4.17) involves a time derivative, it is necessary to rescale both the initial condition and the time as

$$\rho \rightarrow \hat{\rho} = \rho M^\gamma \quad t \rightarrow \hat{t} = t \lambda_M c M^\phi. \quad (2.4.18)$$

After setting $\phi = -\frac{1}{2}$ and $\gamma = \frac{1}{2}$, we obtain the size-independent equation

$$\partial_{\hat{t}} S = (\hat{\Delta} - \hat{\rho}) \hat{\rho} \partial_{\hat{\rho}} S + \frac{\chi}{4} \hat{\rho} \partial_{\hat{\rho}}^2 S \quad (2.4.19)$$

from which we derive

$$S = S\left(\frac{t}{\sqrt{M}}, \sqrt{M}\rho, \sqrt{M}\Delta\right) \quad (2.4.20)$$

as detailed in Appendix 2.D.2. This scaling is consistent with our previous findings regarding the first and second moments of extinction time, but it now offers a more general form that relates to the entire distribution of extinction times rather than its specific moments. By fixing the distance from the critical point $\Delta = 0$ and the initial condition ρ , we recover our result in Eq. (2.4.16).

Overall, the scaling relations of survival probability at criticality and moments of extinction time away from criticality can be summarized as follows:

$$\begin{aligned} S(t|M) &= t^{-\alpha} \hat{S}(tM^\phi) \\ T_1(\rho, \Delta, M) &= M^\beta \hat{T}_1(\rho M^\gamma, \Delta M^\eta) \\ T_2(\rho, \Delta, M) &= M^\delta \hat{T}_2(\rho M^\gamma, \Delta M^\eta) \end{aligned} \quad (2.4.21)$$

with the exponents connected through the scaling relations

$$\beta = -\phi(1 - \alpha), \quad \delta = -\phi(2 - \alpha). \quad (2.4.22)$$

Their numerical values are reported in Table 2.1.

α	ϕ	γ	η	β	δ
0	$-\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	1

TAB. 2.1. Scaling exponents characterizing the survival probability S and the first and second moments of the exit time, T_1 and T_2 in the vicinity of the critical point.

2.5 Coarse-grained simplifications for ecological directions

Thus far, our analysis has considered a mean-field setting with a fully connected dispersal network. While analytically tractable, these assumptions are typically unrealistic in natural ecosystems. In

this section, we develop tools based on mean-field framework that can nonetheless yield ecologically meaningful insights.

We first consider the coefficient of variation (CV) of the time to extinction, defined as the ratio of the standard deviation to the mean i.e., $CV(T) = \sqrt{\langle T^2 \rangle - \langle T \rangle^2} / \langle T \rangle$. This estimate, which captures relative fluctuations, provides a way to quantify the uncertainty and sensitivity of ecological time series. Figures 2.5a and b show that the CV exhibits a collapse behavior similar to that of the moments, as expected. Interestingly, we also observe the emergence of an optimal value: increasing the rescaled distance from criticality, $\hat{\Delta}$, causes the CV to rise, reaching a maximum at $\hat{\Delta} > 0$. We recall that $\hat{\Delta} = 0$ corresponds to the critical point separating extinction and survival regimes, which are defined for the deterministic dynamics obtained for $M \rightarrow \infty$. Here, we see that a finite M may lead to an additional transition point, associated with the variability in the time to extinction, namely the point at which the CV attains its maximum. This behavior is further highlighted in the two-dimensional slices of the CV collapse in Figure 2.8. This transition point warrants further investigation, especially in more realistic networks for which the coefficient of variation is obtainable from time-series data.

As observed in Figure 2.2, once the system transitions into the survival regime, it enters a metastable state in which the settled population fluctuates around a well-defined mean. The corresponding quasi-stationary dynamics, described by the stochastic differential equation in Eq. (2.3.14), involves nonlinear drift and a diffusion term with higher-order polynomial dependence. To simplify this description, we ask whether the fluctuations near the deterministic metastable state can be approximated by a linearized, effective process. This would enable analytical predictions about variability and responses to environmental perturbations—potentially applicable beyond the fully connected mean-field case [50]. To this end, we consider an Ornstein–Uhlenbeck (OU) approximation to the stochastic dynamics. Neglecting the absorbing boundary, this leads to a Gaussian approximation of the stationary distribution. For the deterministic dynamics, Eq. (2.3.14) admits a stable survival solution at $\rho_* = 1 - \frac{e}{c h(f)}$. Thus, linearizing the drift term and evaluating the noise term at ρ_* yields the effective drift rate κ and diffusion coefficient D_{eff} :

$$\begin{aligned} \kappa &= \left| \frac{\partial}{\partial \rho} A(\rho) \right|_{\rho_*} = |e - c h(f)| \\ D_{\text{eff}} &= D(\rho_*) = \frac{\rho_*}{M} \left\{ e + \frac{c h(f)}{2(1 + \mathcal{D}/\lambda)} \left[1 - \rho_*^2 + 2 \frac{\mathcal{D}}{\lambda} (1 - \rho_*) \right] \right\} \\ &= \frac{1}{2M} \frac{e[e - c h(f)][e\lambda - 4c h(f)(\mathcal{D} + \lambda)]}{[c h(f)]^2(\mathcal{D} + \lambda)} \\ \sigma_{\text{eff}} &= \sqrt{\frac{D_{\text{eff}}}{2\kappa}} \end{aligned} \tag{2.5.1}$$

and the resulting linearized dynamics is governed by the effective OU equation:

$$\dot{\rho}_{\text{OU}} = -\kappa \rho_{\text{OU}} + \sqrt{2\sigma_{\text{eff}}} \eta(t) \tag{2.5.2}$$

where $\eta(t)$ is gaussian white noise. To evaluate the validity of this approximation, we fit the stationary settled densities to a Gaussian distribution and compare the resulting standard deviation with that predicted by the OU process with the effective drift and diffusion coefficients. As shown in Figure 2.5c, the empirical distribution in the metastable state is well approximated by a Gaussian. In Figure 2.5d, we compare the standard deviation predicted by the OU approximation to that obtained from Gaussian fits across a range of parameter ratios e/c , finding excellent agreement.

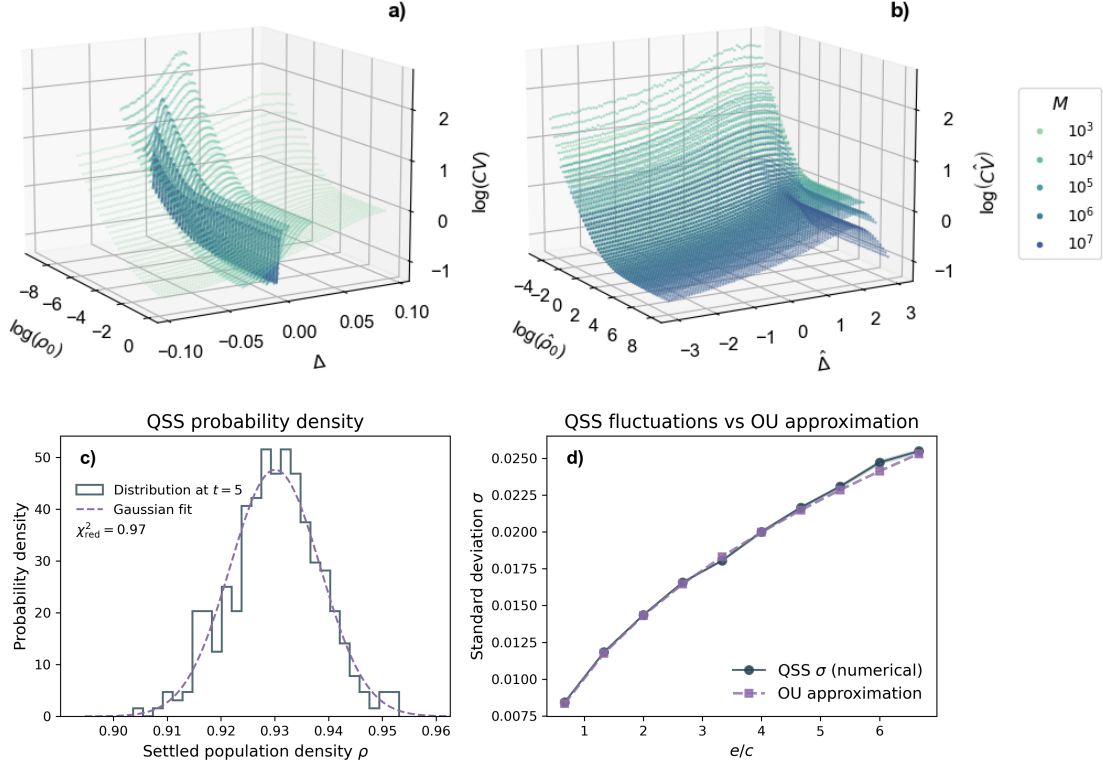


FIG. 2.5. Top: Coefficient of variation (CV) versus initial condition ρ_0 and deviation from criticality Δ for different values of the local carrying capacity M . **a)** not rescaled. **b)** rescaled according to Eq. (2.4.12) and Eq. (2.4.13). Averages are obtained from 10^5 numerical realizations of the QSS dynamics in Eq. (2.3.14). **Bottom:** Fluctuations in the survival regime of the QSS dynamics given by Eq. (2.3.14). **c)** Probability distribution of the settled population density at $t \approx 5$, along with a Gaussian fit. The same parameters are used as in the survival trajectories shown in Figure 2.2, and the distribution is obtained from 350 independent realizations. The reduced chi-squared of the fit is $\chi^2_{\text{red}} = 0.97$. **d)** Standard deviation σ as a function of e/c , comparing results from direct numerical integration of the QSS dynamics with the linearized analytical estimate based on the Ornstein–Uhlenbeck (OU) approximation. The numerical values of σ are obtained from Gaussian fits to distributions built from 250 independent realizations.

This indicates a potential simplification of the metastable dynamics, which may hold beyond our simplistic model assumptions.

2.6 Conclusions

In this work, we extended the traditional metapopulation framework to incorporate stochasticity, with the aim of investigating its impact on metapopulation persistence. We focused on understanding the role of finite carrying capacity in the subpopulation size, which is directly associated with the strength of demographic fluctuations. In doing so, we were able to quantitatively address the dynamics of finite metapopulations and study their stochastic evolution.

Our results suggest that, for a simple colonization-death dynamics in homogeneous landscapes governed by mean-field dispersal networks, the introduction of stochasticity does not lead to strong

deviations from the deterministic population dynamics. Yet, we uncovered the unexpected appearance of an absorbing boundary even in the regime in which the population would deterministically survive. Hence, the stochastic metapopulation always faces eventual extinction due to the finite carrying capacity. Additionally, we have found strong consistency with finite-size scaling predictions, as evidenced by the collapse of the survival probability and extinction time moments curves. The scaling exponents governing this collapse have been analytically derived from the backward Fokker-Planck equation of the model (Table 2.1) as well as verified through numerical simulations. These results provide a baseline expectation for further studies into stochastic metapopulation models. The bottom-up derivation of the Fokker-Planck equation and the effective Langevin equation present immediate numerical applications beyond mean-field networks to incorporate interesting topological factors which we omitted for the sake of analytical simplicity. Changes in the scaling exponents will not only provide possible connections to universality classes but also connect network topology and average time to extinction induced by demographic stochasticity.

Despite the fact that natural ecosystems are far more complex than the simplified scenario considered here, our results provide a quantitative link between a system's proximity to the extinction threshold, as well as both the expected time to extinction and the variability around that time. In particular, we have shown that survival time increases sharply as the system moves away from the critical point, while relative fluctuations (as measured by the coefficient of variation) become smaller only after a transition point that is higher than the metapopulation capacity. This relationship is especially useful when independent estimates of the deterministic metapopulation capacity are available (e.g., from connectivity measures or colonization-extinction data) alongside the local carrying capacity. Our results demonstrate how these two parameters alone can offer meaningful predictions about extinction time statistics in finite systems both above and below the critical value. This aspect is particularly significant because the classic metapopulation capacity does not carry any information at all regarding timescales. These timescales can be a proxy for the robustness to fluctuation-induced extinction events. In this respect, we emphasize that the noise term we derived, which can cause extinctions also in the deterministic persistence scenario, goes beyond the usual demographic noise from pure birth-and-death processes, incorporating the effective contribution of colonization dynamics. Non-trivial network topologies are also expected to play an important role in shaping the fluctuations of the metapopulation density. For example, dendritic river networks affect ecological dynamics [51, 52], and the spatial structure of the diffusion network can influence the probability of fixation of a mutation in stochastic metapopulation models of microbial communities [53, 54]. Similarly, environmental cofactors, such as wildfires that influence forest dynamics [55], and stochastic or time-varying dispersal [56–58], can significantly alter the impact of demographic stochasticity. Our effective SDE provides a framework to capture these effects by appropriately modeling boundary conditions [59–61]. Given a simplified dynamics of the metastable state, we can also expect to understand the effect of ecologically relevant networks through their distance from the effective drift and diffusion parameters. In time series data, where local carrying capacity information is also available, more involved methods can be used to infer the drift and diffusion terms [62] which may enable the quantification of the distance from mean-field connectivity. Such methods could be used as indirect measures of the connectivity of a landscape. The existence of long metastable states also facilitates the study of the response to environmental perturbations on both dynamics of population and its persistence [63]. In this sense, demographic noise is not merely a complicating factor — it carries early-warning information about system stability.

Finally, a key insight from our analysis is the universality of the scaling behavior. The mathematical

structure governing the relationship between capacity, fluctuations, and extinction time does not depend on the fine details of the system. As a result, data collected in one habitat could be used to predict survival time statistics in another, provided the key parameters—capacity and carrying size—are known. Although the present framework relies on highly idealized assumptions, it may provide a baseline for empirical tests beyond what is captured by the deterministic metapopulation capacity λ_M alone. Natural settings could include experimental or controlled systems in which habitat patches differ in effective local capacity—such as patch area or resource availability—while retaining comparable dispersal conditions. The predicted finite-size scaling near the persistence threshold, together with the maximal variability at $\hat{\Delta} > 0$, could serve as reference signatures for interpreting empirical extinction statistics. Overall, this universality provides practical value for the theory, enabling better generalization across species or landscapes without requiring full system-specific modeling each time. An exciting direction for future work is to investigate whether this universality holds beyond the mean-field approach pursued here.

Overall, our results provide a foundation for integrating more complex and realistic effects into stochastic metapopulation models. By refining microscopic processes and dispersal network topology, these extensions will further elucidate the critical role of stochasticity in the survival of spatially structured populations.

Appendix

2.A Step-operator form of the master equation

To facilitate the system size expansion, we reformulate the master equation Eq. (2.3.1) using step operators, which shift occupation numbers in the state vector $\vec{n}$. The step operator $\xi_{A_i}^{\pm 1}$ acts on a generic function $f(\vec{n})$ as follows:

$$\xi_{A_i}^{\pm 1} f(n_{A_1}, \dots, n_{A_i}, \dots, n_{A_N}) = f(n_{A_1}, \dots, n_{A_i} \pm 1, \dots, n_{A_N}) \quad (2.A.1)$$

Using this notation, the master equation can be rewritten in a more compact form Eq. (2.3.4). For example, consider the gain term associated with a process in which a settled individual at patch i dies:

$$W(n_{S_i}; n_{X_i} | n_{S_i} + 1; n_{X_i}) \mathcal{P}(n_{S_i} + 1; n_{X_i}) . \quad (2.A.2)$$

This term represents the contribution to the probability $\mathcal{P}(n_{S_i}, n_{X_i})$ due to transitions from state $(n_{S_i} + 1, n_{X_i})$ to the state (n_{S_i}, n_{X_i}) . Applying the step operator $\xi_{S_i}^{+1}$, it can be rewritten as:

$$W(n_{S_i}; n_{X_i} | n_{S_i} + 1; n_{X_i}) \mathcal{P}(n_{S_i} + 1; n_{X_i}) = \xi_{S_i}^{+1} W(n_{S_i} - 1; n_{X_i} | n_{S_i}; n_{X_i}) \mathcal{P}(n_{S_i}; n_{X_i}) . \quad (2.A.3)$$

At the same time, this process under consideration also yields a loss contribution to the probability $\mathcal{P}(n_{S_i}; n_{X_i})$:

$$W(n_{S_i} - 1; n_{X_i} | n_{S_i}; n_{X_i}) \mathcal{P}(n_{S_i}; n_{X_i}) .$$

As a result, the net effect of the settled individual's death process can be compactly expressed as:

$$\left(\xi_{S_i}^{+1} - 1 \right) W(n_{S_i} - 1; n_{X_i} | n_{S_i}; n_{X_i}) \mathcal{P}(n_{S_i}; n_{X_i}) . \quad (2.A.4)$$

Similarly, when multiple variables are involved, a compound operator like $\xi_{S_i}^{-1} \xi_{X_i}^{+1}$ acts by shifting both indices:

$$\begin{aligned} \left(\xi_{S_i}^{-1} \xi_{X_i}^{+1} - 1 \right) W(n_{S_i} + 1; n_{X_i} - 1 | n_{S_i}; n_{X_i}) \mathcal{P}(n_{S_i}; n_{X_i}) &= W(n_{S_i}; n_{X_i} | n_{S_i} - 1; n_{X_i} + 1) \mathcal{P}(n_{S_i} - 1; n_{X_i} + 1) + \\ &\quad - W(n_{S_i} + 1; n_{X_i} - 1 | n_{S_i}; n_{X_i}) \mathcal{P}(n_{S_i}; n_{X_i}) . \end{aligned} \quad (2.A.5)$$

Applying this notation to all the processes with their respective transition rates (Eq. (2.3.2)), the master equation takes the form given in Eq. (2.3.4) of the main text.

To maintain a compact and readable form, we have grouped the probability distribution $\mathcal{P}$ at the end of each term. However, it is important to note that the step operators act on all functions appearing to their right - that is, the full product $W\mathcal{P}$, with the arguments of both the transition rates and the probability being shifted accordingly.

2.B Mean-field model

Let us consider a complete network (whose adjacency matrix is $\mathcal{A}_{ij} = \mathcal{A} (1 - \delta_{ij})$ with $\mathcal{A} = 1/N$) and assume patch homogeneity: $c_i = c \forall i$, $e_i = e \forall i$. Under these hypotheses, the drift Eq. (2.3.6) and diffusion Eq. (2.3.7) coefficients of the Fokker-Planck equation become:

$$\begin{aligned} A_i^\rho &= \lambda x_i (1 - \rho_i) - e \rho_i \\ A_i^x &= \frac{1}{N} \sum_j \left(\mathcal{D}x_j + ch(f)\rho_j \right) - \frac{1}{N} ch(f)\rho_i - (\mathcal{D} + \lambda)x_i \\ \mathbb{D}_{ij}^{\rho\rho} &= \frac{1}{M} [e\rho_i + \lambda x_i (1 - \rho_i)] \delta_{ij} \\ \mathbb{D}_{ij}^{\rho x} &= \mathbb{D}_{ij}^{x\rho} = -\frac{1}{M} \lambda x_i (1 - \rho_i) \delta_{ij} \\ \mathbb{D}_{ij}^{xx} &= \frac{1}{M} \left[\frac{1}{N} \sum_k \left(\mathcal{D}x_k + ch(f)\rho_k \right) + (\mathcal{D} + \lambda)x_i - \frac{1}{N} ch(f)\rho_i \right] \delta_{ij} - \frac{2}{MN} \mathcal{D}x_i (1 - \delta_{ij}) \end{aligned} \quad (2.B.1)$$

After applying the marginalization procedure described in Eq. (2.3.9) and (2.3.10), we obtain a two-dimensional Fokker-Planck equation in the representative variables (x, ρ) , as reported in Eq. (2.3.11). The drift vector and diffusion matrix are given by:

$$\begin{aligned} \vec{A} &= \begin{pmatrix} \lambda x (1 - \rho) - e \rho \\ c h(f) \rho - \lambda x \end{pmatrix} \\ \hat{\mathbb{D}} &= \frac{1}{M} \begin{pmatrix} c h(f) \rho + (\lambda + 2\mathcal{D})x & -\lambda x (1 - \rho) \\ -\lambda x (1 - \rho) & e \rho + \lambda x (1 - \rho) \end{pmatrix} \end{aligned} \quad (2.B.2)$$

To ensure that the reduced stochastic description remains well defined, we verify that the diffusion matrix $\hat{\mathbb{D}}$ is positive semidefinite. Given its symmetric structure, this can be established by checking the non-negativity of its diagonal entries (which is immediate for all admissible values of the variables) and of its determinant, whose explicit expression is:

$$\det \hat{\mathbb{D}} = \frac{1}{M^2} \left\{ [c h(f) \rho + (\lambda + 2\mathcal{D})x] [e \rho + \lambda x (1 - \rho)] - \lambda^2 x^2 (1 - \rho)^2 \right\}. \quad (2.B.3)$$

Since all parameters are positive and $\rho \in [0, 1)$, we have

$$e \rho + \lambda x (1 - \rho) \geq \lambda x (1 - \rho), \quad (2.B.4)$$

which implies

$$\begin{aligned} \det \hat{\mathbb{D}} &\geq \frac{1}{M^2} \left\{ [c h(f) \rho + (\lambda + 2\mathcal{D})x] \lambda x (1 - \rho) - \lambda^2 x^2 (1 - \rho)^2 \right\} \\ &= \frac{\lambda x (1 - \rho)}{M^2} [c h(f) \rho + \lambda x \rho + 2\mathcal{D}x] \geq 0. \end{aligned} \quad (2.B.5)$$

which proves positive semidefiniteness and ensures that the stochastic fluctuations of the reduced dynamics remain well defined.

The corresponding Langevin equation in Eq. (2.3.12) can be derived by imposing $\mathbb{B}\mathbb{B}^T = \hat{\mathbb{D}}$ for $\mathbb{B}$ in the form:

$$\mathbb{B} = \begin{pmatrix} \mathbb{B}^{xx} & 0 \\ \mathbb{B}^{\rho x} & \mathbb{B}^{\rho\rho} \end{pmatrix} \quad (2.B.6)$$

which yields:

$$\begin{aligned}\mathbb{B}^{xx} &= \frac{1}{\sqrt{M}} \sqrt{c h(f) \rho + (\lambda + 2\mathcal{D})x} \\ \mathbb{B}^{\rho x} &= -\frac{1}{\sqrt{M}} \frac{\lambda x(1 - \rho)}{\sqrt{c h(f) \rho + (\lambda + 2\mathcal{D})x}} \\ \mathbb{B}^{\rho\rho} &= \frac{1}{\sqrt{M}} \sqrt{e\rho + \lambda x(1 - \rho) - \frac{\lambda^2 x^2 (1 - \rho)^2}{c h(f) \rho + (\lambda + 2\mathcal{D})x}}\end{aligned}\quad (2.B.7)$$

We can now derive the effective equation in the settled population density, by assuming a separation of timescales in the settled and explorer population's dynamics. Consider Eq. (2.3.12) and let $\bar{x}$ be the stationary value of x such that $\dot{x} = 0$:

$$\bar{x} = \frac{c h(f) \rho}{\lambda}, \quad \eta_x \equiv 0 \quad (2.B.8)$$

If we condition ρ on x being fixed at $\bar{x}$, we obtain:

$$\dot{\rho} = c h(f) \rho(1 - \rho) - e \rho + B^{\rho\rho}|_{x=\bar{x}} \eta_\rho \quad (2.B.9)$$

which yields the quasi-stationary stochastic Eq. (2.3.14).

2.C Numerical scaling exponents for the survival probability

Given the finite size scaling assumption Eq. (2.4.4) for the survival probability's time dependence, we can express the n -th moment of exit time as:

$$\begin{aligned}\langle T^n(\rho, M) \rangle &= - \int_0^\infty \partial_t S(t|\rho, M) t^n dt \\ &= \int_0^\infty S(t|\rho, M) t^{n-1} dt\end{aligned}\quad (2.C.1)$$

by substituting the scaling hypothesis Eq. (2.4.4) we obtain:

$$\begin{aligned}\langle T^n(\rho, M) \rangle &\propto \int_0^\infty \mathcal{F}_\rho(t M^\phi) t^{n-\alpha-1} dt \\ &= M^{-\phi(n-\alpha)} \int_0^\infty \mathcal{F}_\rho(z) z^{n-\alpha-1} dz \\ &= M^{-\phi(n-\alpha)} C_{n,\alpha}(\rho)\end{aligned}\quad (2.C.2)$$

and

$$\frac{\langle T^{n+1} \rangle}{\langle T^n \rangle} = \frac{C_{n+1,\alpha}(\rho)}{C_{n,\alpha}(\rho)} M^{-\phi} \quad (2.C.3)$$

where the explicit dependence on the initial condition ρ is included in the $C_{n,\alpha}$ coefficients. The above Eq. (2.C.3) allows to numerically estimate the ϕ exponent. To achieve this, we simulate 10^7 realizations of the MF QSS dynamics given by Eq. (2.3.14) and we compute the moments of extinction time. Specifically, we select the moments of order n ranging from 1 to 8, and consider 20 values for M , spanning from 10^3 to 10^7 . For any two consecutive moments, we fit the logarithm of $\frac{\langle T^{n+1} \rangle}{\langle T^n \rangle}$ as a function of $\log(M)$. In principle, this yields 7 parallel lines. The average of the obtained

slopes provides therefore our estimate for ϕ . The error is taken to be the standard deviation of the slopes.

Once ϕ is determined, we can exploit Eq. (2.C.2) to estimate α . In particular, we now fit the logarithm of $\langle T^n \rangle$ versus $\log(M)$, and α is obtained from the slope m of the fitted lines, namely: $m = -\phi(n - \alpha)$. We consider the standard deviation of α as its error.

However, the estimates of ϕ and α are highly influenced from the values of M considered, the number of realizations of the dynamics and the order of the moments used for the fitting. In particular, higher values of M and a larger number of realizations provide more rigorous estimates, as confirmed by deviations from the linearly expected behavior becoming less pronounced. The errors computed as standard deviations are therefore not fully representative of the true uncertainty in the estimates, as they do not account for these factors, which introduce additional variability.

2.D Scaling analysis

Let us express the mean-field QSS stochastic equation Eq. (2.3.14) in the more convenient Fokker-Planck formalism:

$$\partial_t P(\rho, t) = -\partial_\rho [A(\rho)P(\rho, t)] + \frac{1}{2}\partial_\rho^2 [D(\rho)P(\rho, t)] \quad (2.D.1)$$

This is a one-dimensional time-homogeneous FP equation. The domain of ρ is given by the interval $(0, 1]$, with $\rho = 0$ absorbing boundary and $\rho = 1$ reflecting boundary, as seen in Section 2.3.2. Therefore, the definition of survival probability given in Eq. (2.4.1) implies that it obeys the boundary conditions $S(0, t) = 0$, $\partial_\rho S(\rho, t)|_{\rho=1} = 0$. Through Eq. (2.4.3) we similarly find $T_n(0, t) = 0$, $\partial_\rho T_n(\rho, t)|_{\rho=1} = 0$ for the $n - th$ moment of extinction time.

For the upcoming calculations, we rewrite the drift and diffusion coefficients of the QSS mean-field Fokker-Planck equation in terms of the parameter Δ Eq. (2.4.10), which quantifies the deviation from criticality:

$$\begin{aligned} A(\rho, M, \Delta) &= \lambda_M c (\Delta - \rho) \rho \\ D(\rho, M, \Delta) &= \frac{\lambda_M c}{2M} \rho \left[3 + \frac{\mathcal{D}}{\mathcal{D} + \lambda} - 2\Delta - \frac{2\mathcal{D}}{\mathcal{D} + \lambda} \rho - \frac{\lambda}{\mathcal{D} + \lambda} \rho^2 \right] \end{aligned} \quad (2.D.2)$$

2.D.1 First and second moments of exit time

Consider Eq. (2.4.8) for the first moment of exit time:

$$(\Delta - \rho) \rho \partial_\rho T + \frac{\lambda_M c}{4M} \rho \left(3 + \frac{\mathcal{D}}{\mathcal{D} + \lambda} - 2\Delta - \frac{2\mathcal{D}}{\mathcal{D} + \lambda} \rho - \frac{\lambda}{\mathcal{D} + \lambda} \rho^2 \right) \partial_\rho^2 T = -\frac{1}{\lambda_M c}$$

In order to achieve a common scaling of the LHS with the system size M , it is convenient to rescale $\rho \rightarrow \hat{\rho} = \rho \sqrt{M}$, $T \rightarrow \hat{T} = \frac{\lambda_M c}{\sqrt{M}} T$ and $\Delta \rightarrow \hat{\Delta} = \Delta \sqrt{M}$

$$(\hat{\Delta} - \hat{\rho}) \hat{\rho} \partial_{\hat{\rho}} \hat{T} + \frac{1}{4} \hat{\rho} \left(\chi - 2 \frac{\hat{\Delta}}{\sqrt{M}} - \frac{2\mathcal{D}}{\mathcal{D} + \lambda} \frac{\hat{\rho}}{\sqrt{M}} - \frac{\lambda}{\mathcal{D} + \lambda} \frac{\hat{\rho}^2}{M} \right) \partial_{\hat{\rho}}^2 \hat{T} = -1$$

where we define $\chi := 3 + \frac{\mathcal{D}}{\mathcal{D} + \lambda}$, which we treat as a fixed constant in the following. In the limit of large system size M , the terms $-2 \frac{\hat{\Delta}}{\sqrt{M}}$, $-\frac{2\mathcal{D}}{\mathcal{D} + \lambda} \frac{\hat{\rho}}{\sqrt{M}}$, $-\frac{\lambda}{\mathcal{D} + \lambda} \frac{\hat{\rho}^2}{M}$ can be neglected, yielding the following equation:

$$(\hat{\Delta} - \hat{\rho}) \hat{\rho} \partial_{\hat{\rho}} \hat{T} + \frac{\chi}{4} \hat{\rho} \partial_{\hat{\rho}}^2 \hat{T} = -1 \quad (2.D.3)$$

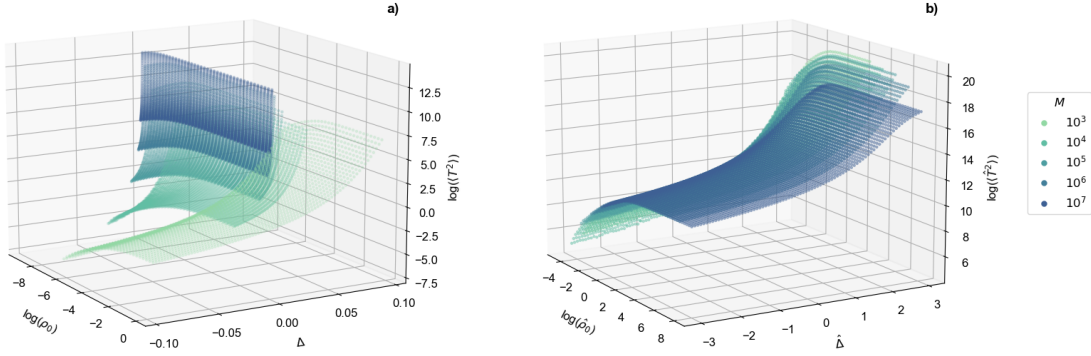


FIG. 2.6. Second moment of exit time $\langle T^2 \rangle$ versus initial condition ρ_0 and deviation from criticality Δ for different values of the local carrying capacity M . **a)** not rescaled. **b)** rescaled according to Eq. (2.4.13). Averages are obtained from 10^5 numerical realizations of the MF QSS dynamics in Eq. (2.3.14).

which is independent of M . Therefore, for large M the first exit time scales as:

$$T(\rho, \Delta, M) \propto \sqrt{M} \hat{T}(\sqrt{M}\rho, \sqrt{M}\Delta) \quad (2.D.4)$$

From the above expression we observe that the rescaled first exit time should depend only on the rescaled initial density $\hat{\rho} = \sqrt{M}\rho$ and the rescaled distance from the critical point $\hat{\Delta} = \sqrt{M}\Delta$. The solution of Eq. (2.D.3) with $\hat{\rho} \in (0, \sqrt{M}]$ and boundary conditions $\hat{T}(0) = 0$, $\partial_{\hat{\rho}} \hat{T}(\hat{\rho})|_{\hat{\rho}=\sqrt{M}} = 0$ is given by the integral:

$$\begin{aligned} \hat{T}(\hat{\rho}, \hat{\Delta}) &= \frac{4}{\chi} \int_0^{\hat{\rho}} dx e^{-G(x, \hat{\Delta})} \int_x^{\sqrt{M}} dy \frac{e^{G(y, \hat{\Delta})}}{y} \\ G(\hat{\rho}, \hat{\Delta}) &= \frac{4}{\chi} \int_{\sqrt{M}}^{\hat{\rho}} dx (\hat{\Delta} - x) = \frac{2}{\chi} \left[2\hat{\Delta}(x - \sqrt{M}) + M - x^2 \right] \end{aligned} \quad (2.D.5)$$

In particular, in the simple case of $\hat{\Delta} = 0$ (criticality) the integral Eq. (2.D.5) can be calculated analytically:

$$\hat{T}(\hat{\rho}) = \frac{4}{\chi} \hat{\rho} {}_2F_2\left(\frac{1}{2}, 1; \frac{3}{2}, \frac{3}{2}; -\frac{2}{\chi} \hat{\rho}^2\right) + \sqrt{\frac{\pi}{2\chi}} \operatorname{erfi}\left[\sqrt{\frac{2}{\chi}} \hat{\rho}\right] \left(\operatorname{Ei}\left(-\frac{2}{\chi} M\right) - \operatorname{Ei}\left(-\frac{2}{\chi} \hat{\rho}^2\right)\right) \quad (2.D.6)$$

where $\operatorname{erfi}(x)$ is the imaginary error function, $\operatorname{Ei}(x)$ is the exponential integral function and ${}_pF_q(\{a_1, \dots, a_p\}; \{b_1, \dots, b_q\}; z)$ is the generalized hypergeometric function.

Consider now the second moment of extinction time ($n = 2$ in Eq. (2.4.9)):

$$(\Delta - \rho) \rho \partial_{\rho} T_2 + \frac{1}{4M} \rho \left(\chi - 2\Delta - \frac{2\mathcal{D}}{\mathcal{D} + \lambda} \rho - \frac{\lambda}{\mathcal{D} + \lambda} \rho^2 \right) \partial_{\rho}^2 T_2 = -2 \frac{T_1}{\lambda M c} \quad (2.D.7)$$

where T_1 is the first moment, which scales according to Eq. (2.4.12). Rescaling $T_2 \rightarrow \hat{T}_2 = \frac{(\lambda M c)^2}{2M} T_2$ and neglecting terms $\sim \mathcal{O}(\frac{1}{\sqrt{M}})$, Eq. (2.D.7) becomes:

$$(\hat{\Delta} - \hat{\rho}) \hat{\rho} \partial_{\hat{\rho}} \hat{T}_2 + \frac{\chi}{4} \hat{\rho} \partial_{\hat{\rho}}^2 \hat{T}_2 = -\hat{T} \quad (2.D.8)$$

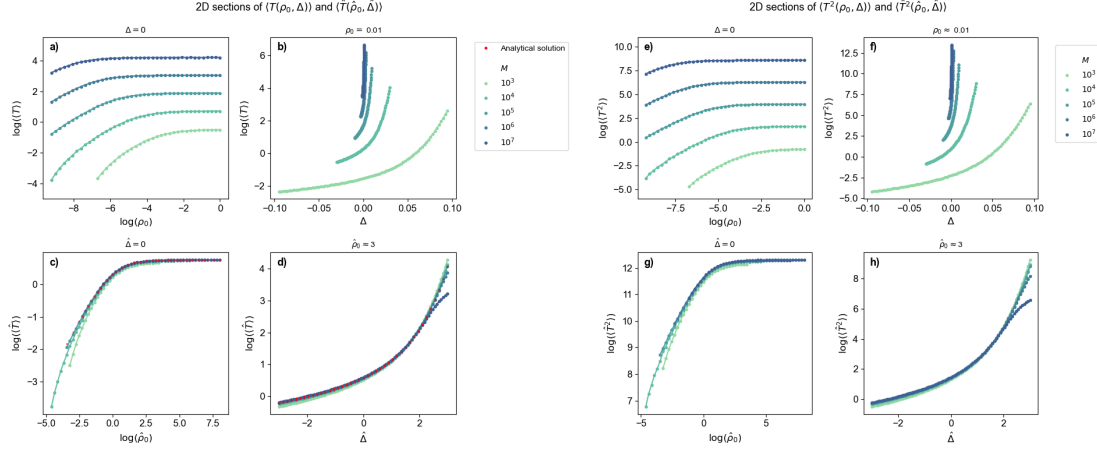


FIG. 2.7. Left: Two-dimensional sections of Figure 2.4, showing the first moment of exit time versus initial condition and deviation from criticality, for different values of the local carrying capacity M . **a)** Section of $\langle T \rangle$ at fixed $\Delta = 0$, not rescaled. **b)** Section of $\langle T \rangle$ at fixed $\rho_0 \approx 0.01$, not rescaled. **c)** Section of $\langle \hat{T} \rangle$ at fixed $\hat{\Delta} = 0$, rescaled according to Eq. (2.4.12). **d)** Section of $\langle \hat{T} \rangle$ at fixed $\hat{\rho}_0 \approx 3$, rescaled according to Eq. (2.4.12). **Right:** Two-dimensional sections of Figure 2.6, showing the second moment of exit time versus initial condition and deviation from criticality, for different values of the local carrying capacity M . **e)** Section of $\langle T^2 \rangle$ at fixed $\Delta = 0$, not rescaled. **f)** Section of $\langle T^2 \rangle$ at fixed $\rho_0 \approx 0.01$, not rescaled. **g)** Section of $\langle \hat{T}^2 \rangle$ at fixed $\hat{\Delta} = 0$, rescaled according to Eq. (2.4.13). **h)** Section of $\langle \hat{T}^2 \rangle$ at fixed $\hat{\rho}_0 \approx 3$, rescaled according to Eq. (2.4.13).

which shows that the second moment of exit time scales as:

$$T_2(\rho, \Delta, M) \propto M \hat{T}_2(\sqrt{M}\rho, \sqrt{M}\Delta) \quad (2.D.9)$$

The analytical solution is given by:

$$\hat{T}_2(\hat{\rho}, \hat{\Delta}) = \frac{4}{\chi} \int_0^{\hat{\rho}} dx e^{-G(x, \hat{\Delta})} \int_x^{\sqrt{M}} dy \frac{\hat{T}(y, \hat{\Delta})}{y} e^{G(y, \hat{\Delta})} \quad (2.D.10)$$

with $G(\hat{\rho}, \hat{\Delta})$ and $\hat{T}(\hat{\rho}, \hat{\Delta})$ defined in Eq. (2.D.5). As done for the mean extinction time, we numerically calculate the second moment of extinction time by simulating 10^5 realizations of the mean-field QSS dynamics given in Eq. (2.3.14), using the Euler-Maruyama algorithm [64]. By applying the proper rescaling, we obtain again a good collapse of the second moment of extinction time as a function of the distance from the critical point Δ , the initial condition ρ and the system size M . The collapse is shown in Figure 2.6, and clarified through two-dimensional sections in the right panel of Figure 2.7.

2.D.2 Survival probability

Starting from Eq. (2.4.17), we apply the rescaling procedure $\rho \rightarrow \hat{\rho} = \rho M^\gamma$, $t \rightarrow \hat{t} = t \lambda_M c M^\gamma$, which yields:

$$\begin{aligned} M^\gamma \partial_{\hat{t}} S &= M^{-\gamma} (\Delta M^\gamma - \hat{\rho}) \hat{\rho} \partial_{\hat{\rho}} S + \\ &+ \frac{1}{4} M^{\gamma-1} \hat{\rho} \left(\chi - 2\Delta - \frac{2\mathcal{D}}{\mathcal{D} + \lambda} \frac{\hat{\rho}}{M^\gamma} - \frac{\lambda}{\mathcal{D} + \lambda} \frac{\hat{\rho}^2}{M^{2\gamma}} \right) \partial_{\hat{\rho}^2} S \end{aligned} \quad (2.D.11)$$

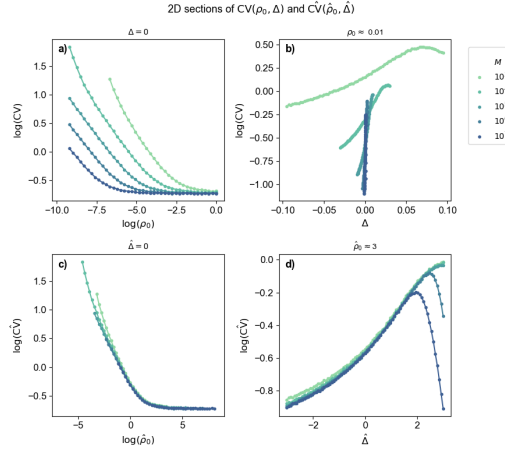


FIG. 2.8. Left: Two-dimensional sections of the top panel of Figure 2.5, showing the coefficient of variation (CV) as a function of the initial condition ρ_0 and deviation from criticality Δ , for different values of the local carrying capacity M . **a)** Section of $\langle CV \rangle$ at fixed $\Delta = 0$, not rescaled. **b)** Section of $\langle CV \rangle$ at fixed $\rho_0 \approx 0.01$, not rescaled. **c)** Section of $\langle \hat{CV} \rangle$ at fixed $\hat{\Delta} = 0$, rescaled according to Eq. (2.4.12) and Eq. (2.4.13). **d)** Section of $\langle \hat{CV} \rangle$ at fixed $\hat{\rho}_0 \approx 3$, rescaled according to Eq. (2.4.12) and Eq. (2.4.13).

It is then convenient to choose ν , γ such that $\nu = -\gamma = \gamma - 1 \rightarrow \gamma = \frac{1}{2}$, $\nu = -\frac{1}{2}$.

$$\partial_{\hat{t}} S = (\hat{\Delta} - \hat{\rho}) \hat{\rho} \partial_{\hat{\rho}} S + \frac{1}{4} \left(\chi - 2 \frac{\hat{\Delta}}{\sqrt{M}} - \frac{2\mathcal{D}}{\mathcal{D} + \lambda} \frac{\hat{\rho}}{\sqrt{M}} - \frac{\lambda}{\mathcal{D} + \lambda} \frac{\hat{\rho}^2}{M} \right) \hat{\rho} \partial_{\hat{\rho}^2} S \quad (2.D.12)$$

where $\hat{\Delta} = \Delta \sqrt{M}$. Neglecting $\mathcal{O}(\frac{1}{\sqrt{M}})$ terms:

$$\partial_{\hat{t}} S = (\hat{\Delta} - \hat{\rho}) \hat{\rho} \partial_{\hat{\rho}} S + \frac{\chi}{4} \hat{\rho} \partial_{\hat{\rho}^2} S \quad (2.D.13)$$

We deduce the following scaling behavior of the survival probability:

$$S(t, \rho, \Delta, M) = S\left(\frac{t}{\sqrt{M}}, \sqrt{M}\rho, \sqrt{M}\Delta\right) \quad (2.D.14)$$

which is consistent with the scaling of S determined through the previous approach.

Code Availability

The code used for the stochastic simulations and numerical analysis presented in this chapter is available at: <https://doi.org/10.5281/zenodo.15188570>

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3

Dispersal strategies in discrete-time stochastic populations

Abstract. Dispersal in patchy environments embodies an exploitation–evasion trade-off: individuals benefit from remaining in favorable patches, but local crowding and kin competition favor movement. While much theory treats dispersal evolution through deterministic selection gradients, here we focus on how demographic fluctuations, filtered through nonlinear updates, reshape dispersal selection. To this end, we study a minimal discrete-time stochastic metapopulation model and derive a variance-corrected effective dynamics that incorporates noise-induced corrections. The reduced theory matches long-run simulations and reveals a finite-size transition at a critical local population size, below which fluctuations can reverse competitive dominance and shift the evolutionarily favored dispersal effort. Preliminary results suggest that carrying-capacity heterogeneity across patches further modulates selection outcomes. Overall, this work provides a tractable framework linking local population size and demographic noise to dispersal outcomes through quantitative size-dependent predictions.

This chapter is based on a collaborative work in preparation with E. Nieto, L. Fant, and M. A. Muñoz.

Structure. Section 3.1 frames dispersal as an exploitation–evasion trade-off and motivates the adopted dynamical viewpoint. Section 3.2 introduces the discrete-time stochastic metapopulation model and Section 3.4.2 derives its moment hierarchy. In Section 3.3 we show the breakdown of naive mean-field theory at finite local population size, and develop a variance-corrected approximation capturing noise-induced drift (Section 3.4) which is then used to analyze invasion and evolutionary stability (Section 3.5). Section 3.6 provides a preliminary extension to environmental heterogeneity.

3.1 Introduction

Organisms in heterogeneous environments must continually balance gaining returns from a favorable local setting with reducing local competition by moving elsewhere. In spatially structured systems, this exploitation–evasion trade-off is especially clear: remaining in a good patch can be profitable, yet crowding and kin competition can erode those gains, creating incentives to disperse [1, 2].

In ecological terms, dispersal changes the conditions individuals experience and therefore the niche they effectively occupy [3]. More generally, niche shifts can be mediated by processes operating on different timescales, including spatial migration among patches as well as temporal dispersal through dormancy [4], both of which reshape the balance between local exploitation and competitive escape. Classical work on the evolution of dispersal is often framed in terms of invasion fitness and selection-gradient arguments, frequently analyzed in island-type models with a large number of patches [5–9].

Here we take a complementary dynamical route. Starting from a minimal discrete-time stochastic life cycle with finite local population size and global dispersal, in the spirit of Hamilton-type island models [1], we first show that the corresponding mean-field description breaks down at finite population size. We then derive a variance-corrected mean-field description that tracks both the mean and the leading fluctuations. This reduced description reproduces long-run stochastic simulations and reveals a finite-size threshold. The key mechanism behind this effect is a Jensen-type drift: the curvature of the nonlinear update rule converts finite-population variance into a systematic shift of the effective dynamics, thereby renormalizing selection. Below a critical local population size, fluctuations can overturn deterministic dominance and shift the evolutionarily favored dispersal effort from low (exploitation-dominated) to high (competition-avoidance) values. The same framework extends naturally to heterogeneous environments, where variability in carrying capacity further modulates these outcomes.

Our results connect to, and extend, classical theory on dispersal evolution. While earlier work established how dispersal can be favored by kin competition even in neutral settings [1], and how persistent spatial heterogeneity can reduce dispersal via variance in patch reproductive potential [9], we emphasize a distinct and broadly applicable mechanism: nonlinear stochastic dynamics convert demographic and environmental variability into systematic shifts of effective growth and stability, thereby reshaping the macroscopic selection pressures that determine optimal dispersal. These questions are ecologically, evolutionarily, and practically important. Our framework points to empirically accessible directions: in heterogeneous environments, strategy shifts could be linked to coarse disorder statistics, and perturbations that alter variability or effective noise strength may tip populations between exploitation-heavy and evasion-heavy regimes. While we focus on spatial dispersal, the same mathematical logic may apply to other forms of niche change (e.g., switching among internal functional states), potentially offering a coarse-grained view of “leave-or-stay” decisions across biological contexts.

3.2 Model

We consider a metapopulation of N habitat patches. In each patch $i = 1, \dots, N$, the adult population size is fixed at k . Individuals are of two types, x and y , which differ only in their dispersal strategy.

At discrete time t , patch i contains X_i^t adults of type x and $Y_i^t = k - X_i^t$ of type y . We work with local frequencies

$$x_i^t = \frac{X_i^t}{k}, \quad y_i^t = 1 - x_i^t, \quad (3.2.1)$$

and denote their spatial averages $\bar{x}^t = \frac{1}{N} \sum_{i=1}^N x_i^t$, $\bar{y}^t = 1 - \bar{x}^t$. Thus, the state of the metapopulation at time t is the vector $\mathbf{x}^t = (x_1^t, \dots, x_N^t)$.

The dynamics proceeds in discrete generations, each consisting of three steps: reproduction, dispersal, and density-regulated recruitment. First, adults produce offspring locally. A fraction of

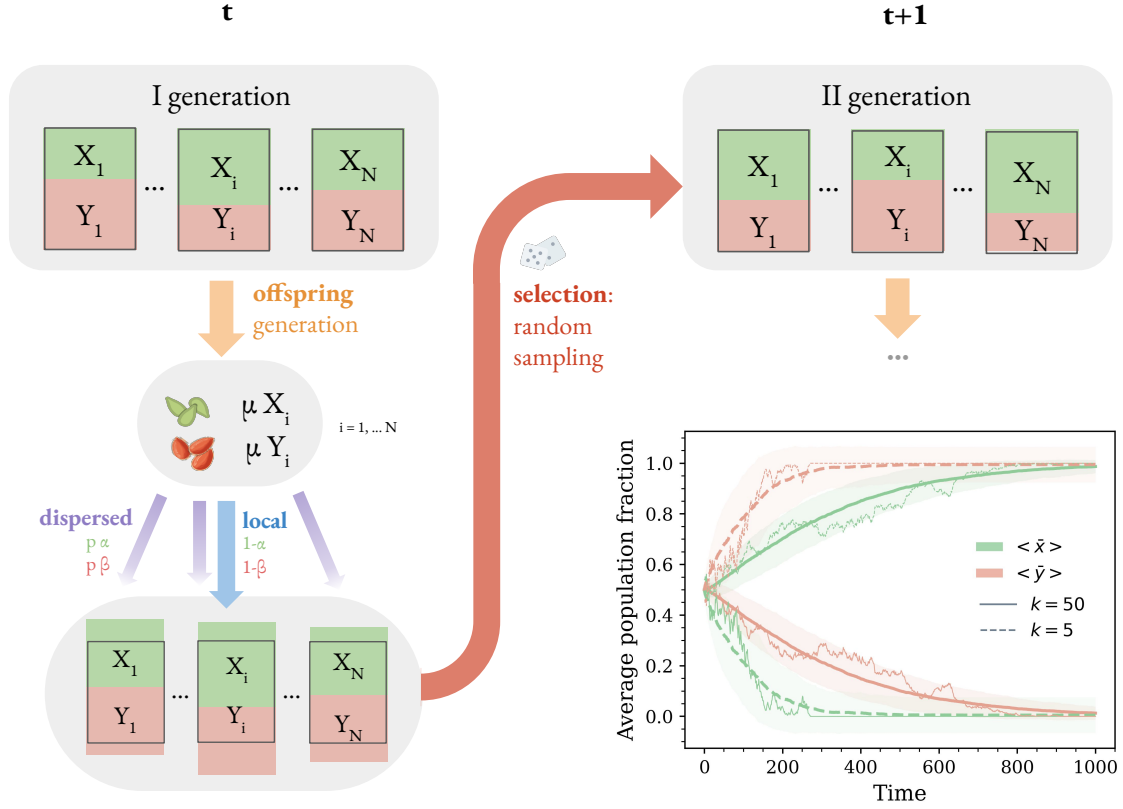


FIG. 3.1. Schematic illustration of the model dynamics, including the reproduction and dispersal steps across generations, together with representative trajectories of the population variables for two different values of the patch size, $k = 5$ and $k = 50$. The remaining model parameters are fixed to $\alpha = 0.5$, $\beta = 0.7$, $p = 0.97$, $\mu = 1000$, and $N = 100$. The shaded areas represent the deviation from the mean obtained from 200 realizations of the stochastic dynamics.

offspring disperses and is redistributed across patches through a global pool. Finally, each patch samples a fixed number k of individuals from the combined pool of residents and immigrants, ensuring constant local population size.

This discrete-time stochastic life cycle, with finite local carrying capacity and density-regulated resampling, follows standard constructions in population genetics and stochastic population models [10, 11]. A schematic representation of the life cycle is shown in Fig. 3.1.

3.2.1 Reproduction and dispersal

Each adult produces μ offspring per generation. A fraction of the offspring remains in the natal patch, while the rest disperses. Dispersal strategy is type-dependent: a fraction α of type- x offspring disperses, whereas β of type- y offspring disperses, with

$$\alpha, \beta \in [0, 1], \quad \Delta\alpha = \beta - \alpha. \quad (3.2.2)$$

Dispersal is global: propagules are redistributed uniformly across all N patches. Migration entails a cost, as only a fraction p of propagules survive dispersal. The surviving propagules form a global dispersal pool whose composition reflects the global averages $\bar{x}^t$ and $\bar{y}^t$.

Conditioned on the adult composition $(x_i^t, \bar{x}^t)$ at time t , the expected numbers of offspring

contributing to patch i are then

$$\text{off}_{x,i}^t = k \left[\mu(1 - \alpha) x_i^t + \mu p \alpha \bar{x}^t \right], \quad (3.2.3)$$

$$\text{off}_{y,i}^t = k \left[\mu(1 - \beta) (1 - x_i^t) + \mu p \beta (1 - \bar{x}^t) \right]. \quad (3.2.4)$$

Here, the first term represents locally retained offspring, while the second accounts for immigrants drawn from the global dispersal pool.

Thus, after reproduction and dispersal, patch i contains a pool of potential recruits consisting of generation- t adults and their redistributed offspring:

$$A_i^t = kx_i^t + \text{off}_{x,i}^t, \quad B_i^t = k(1 - x_i^t) + \text{off}_{y,i}^t, \quad (3.2.5)$$

with total size $T_i^t = A_i^t + B_i^t$. Density regulation then fixes the next-generation $(t + 1)$ adult population at size k by sampling k individuals without replacement from this pool. This resampling step represents strong local competition for limited resources, whereby resident adults and offspring of both x and y types compete for a limited number of recruitment slots in the next generation. Biologically, it captures density-dependent regulation acting after dispersal, analogous to Wright–Fisher-type sampling within each patch [10].

3.2.2 Single-patch update: transition kernel and conditional cumulants

At the recruitment stage, stochasticity arises from finite-size sampling. Formally, conditioned on the current state $(x_i^t, \bar{x}^t)$, the recruitment step defines a stochastic map from x_i^t to x_i^{t+1} through the sampling of k individuals from a finite pool containing A_i^t type- x and B_i^t type- y individuals. Since sampling occurs without replacement from a population of fixed composition, the number of type- x adults at time $t + 1$ follows a hypergeometric distribution,

$$\mathbb{P}\left(x_i^{t+1} = \frac{n}{k} \mid x_i^t, \bar{x}^t\right) = \frac{\binom{A_i^t}{n} \binom{B_i^t}{k-n}}{\binom{T_i^t}{k}}, \quad n = 0, \dots, k. \quad (3.2.6)$$

This expression provides the exact transition kernel at the patch level. The corresponding conditional mean and variance are

$$\begin{aligned} \mathbb{E}\left(x_i^{t+1} \mid x_i^t, \bar{x}^t\right) &= \frac{A_i^t}{T_i^t} \equiv F(x_i^t, \bar{x}^t), \\ \text{Var}\left(x_i^{t+1} \mid x_i^t, \bar{x}^t\right) &= \frac{1}{k} F(x_i^t, \bar{x}^t) [1 - F(x_i^t, \bar{x}^t)] \frac{T_i^t - k}{T_i^t - 1} \equiv G(x_i^t, \bar{x}^t). \end{aligned} \quad (3.2.7)$$

These expressions follow directly from the properties of the hypergeometric distribution. The variance scales as

$$\text{Var}\left(x_i^{t+1} \mid x_i^t, \bar{x}^t\right) = O\left(\frac{1}{k}\right), \quad (3.2.8)$$

showing that fluctuations vanish in the limit of large local population size k (Appendix 3.A).

In the regime $\mu \gg 1$, the offspring pool is large compared to the number of sampled individuals. In this limit, the sampled fraction k/T_i^t is small, so that correlations induced by sampling without

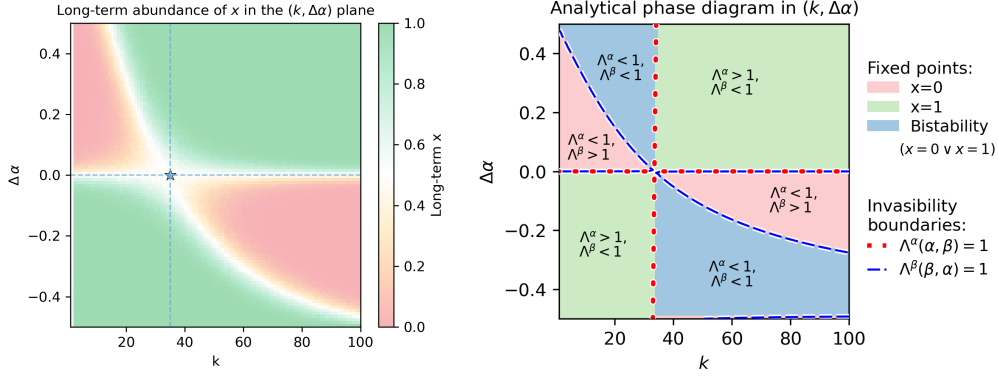


FIG. 3.2. Phase diagrams of x across varying dispersal strategy asymmetry $\Delta\alpha = \beta - \alpha$ and local carrying capacity k , for fixed $\alpha = 0.5$, $p = 0.98$, and $\mu = 1000$. **Left:** numerical phase diagram of the long-term value of $x = \langle f \rangle / k$, obtained by simulating the full stochastic dynamics of the model (Section 3.2) from uniformly distributed initial conditions and averaging over 10^3 realizations. For large k , the outcome matches the mean-field (MF) prediction: the species with the lower dispersal rate fixes while the other goes extinct. As k decreases, however, the system undergoes a transition and, for sufficiently small k , the outcome reverses, so that the species with the higher dispersal rate becomes favored. This illustrates how finite-size fluctuations and the resulting increase in spatial heterogeneity can overturn the MF expectation. The two transition lines intersect at a single point, defining $k_c \simeq 35$, i.e., the local population size at which the fixed strategy $\alpha = 0.5$ is an ESS, marked by a blue star. Notice that the curved transition line shown here is initialization-dependent: within the bistable region of the phase diagram (right panel), the asymptotic outcome depends on the initial conditions, so the transition boundary can shift within this region. **Right:** analytical phase diagram showing the stable fixed points Eq. (3.D.7) of $x = \langle f \rangle / k$ as predicted by the variance-corrected MF model. Green and pink regions indicate fixation of species x ($x=1$) or species y ($x=0$), respectively. The blue region indicates bistability, where both outcomes are locally stable and the final state depends on the initial conditions, consistent with the shift of the transition line observed in stochastic simulations when varying the initial states. The dashed lines represent the rare-mutant invasion boundaries derived in Section 3.5.1.

replacement become negligible. The hypergeometric distribution can therefore be approximated by a binomial one, with success probability $F(x_i^t, \bar{x}^t)$

$$k x_i^{t+1} \sim \text{Binomial}(k, F(x_i^t, \bar{x}^t)), \quad (3.2.9)$$

and variance $F(x_i^t, \bar{x}^t)[1 - F(x_i^t, \bar{x}^t)]/k$ up to corrections of order $O(1/\mu)$. This binomial approximation greatly simplifies some of the analytical calculations, while preserving the qualitative behavior of the system, as commonly done in stochastic population models and related reaction processes [12].

3.3 Naive mean-field dynamics and its breakdown

A natural starting point is a naive deterministic description in which local frequencies evolve according to their expected update, neglecting demographic fluctuations. Using the offspring production and dispersal rules introduced in Section 3.2, the fully deterministic update takes the form

$$x_i^{t+1} = F(x_i^t, \bar{x}^t), \quad (3.3.1)$$

with

$$F(x, \bar{x}) = \frac{x[1 + \mu(1 - \alpha)] + \mu p \alpha \bar{x}}{1 + \mu[1 - \beta(1 - p) + (\beta - \alpha)x]}. \quad (3.3.2)$$

This deterministic map describes how local frequencies are updated in the absence of finite-population noise, while still retaining the coupling among patches through the spatial average $\bar{x}^t$.

A closed mean-field (MF) description is obtained by assuming complete spatial homogeneity, $x_i^t \equiv \bar{x}^t = m_t$ for all patches, i.e., neglecting spatial fluctuations. Under this assumption the dynamics reduces to a one-dimensional map for the global frequency,

$$m_{t+1} = F(m_t, m_t), \quad (3.3.3)$$

which captures the naive MF approximation of the stochastic model. A detailed analysis of this map is reported in Appendix 3.B. The MF dynamics yields a simple and robust outcome: for $p < 1$ and $\beta \neq \alpha$, the strategy with the *lower* dispersal rate always fixes, whereas the more dispersive type is eliminated. Hence, naive MF theory systematically favors low-dispersal strategies in homogeneous environments.

This prediction is confirmed by simulations of the full stochastic model in the limit of large local population size k (left panel of Figure 3.2). However, for smaller k the outcome changes qualitatively. As shown in the plot, there exists a critical carrying capacity k_c at which the transition lines in the phase diagram cross. For $k > k_c$ the MF prediction holds and the low-dispersal type dominates, whereas for $k < k_c$ the species with the *higher* dispersal rate becomes more likely to fix. The location of the transition in the $(k, \Delta\alpha)$ plane also depends on the dispersal cost p , with larger p progressively favoring dispersal, as shown by Figure 3.6 in the Appendix.

This behavior signals a genuine breakdown of the MF approximation: finite-population fluctuations do not merely induce noise around deterministic trajectories, but systematically reshape the effective dynamics, to the point of reversing which dispersal strategy is favored. Within this perspective, the local population size k naturally plays the role of a control parameter. As k decreases, demographic fluctuations grow and feed back into the effective dynamics through the curvature of the update rule. This mechanism generates finite-size-driven transitions between dispersal regimes, which can be naturally interpreted in terms of phase diagrams and invasion boundaries. In the next section we show that this reversal can be understood as a noise-induced drift arising from the curvature of the update rule, i.e., as a Jensen-type correction to mean-field dynamics.

3.4 Noise-induced corrections to mean-field dynamics

The failure of naive mean-field theory at small local population sizes k originates from the interplay of stochasticity and nonlinearity, which generates a systematic mismatch between the averaged update $\mathbb{E}[F(X)]$ and the mean-field prediction $F(\mathbb{E}[X])$. This mismatch, a direct consequence of Jensen's inequality, produces a systematic noise-induced drift in the effective dynamics.

3.4.1 Jensen's force in a generic discrete-time update

To illustrate the origin of noise-induced drift in its simplest form, we consider a generic stochastic discrete-time update for a single variable,

$$x_{t+1} = F(x_t, \bar{x}_t) + \varepsilon_t, \quad (3.4.1)$$

where F is the deterministic update rule and ε_t represents zero-mean fluctuations around it, with

$$\mathbb{E}[\varepsilon_t] = 0, \quad \text{Var}(\varepsilon_t) = G(x_t, \bar{x}_t). \quad (3.4.2)$$

We denote by

$$m_t = \mathbb{E}[x_t], \quad v_t = \text{Var}(x_t) \quad (3.4.3)$$

the first two moments of the process. Expanding $F(x_t, \bar{x}_t)$ to second order around (m_t, m_t) and taking expectations yields

$$\mathbb{E}[F(x_t, \bar{x}_t)] \approx F(m_t, m_t) + \frac{1}{2} F_{xx}(m_t, m_t) v_t + O(v_t/N). \quad (3.4.4)$$

Consequently, the mean evolves according to

$$m_{t+1} \approx F(m_t, m_t) + \frac{1}{2} F_{xx}(m_t, m_t) v_t. \quad (3.4.5)$$

The second term, $\frac{1}{2} F_{xx}(m_t, m_t) v_t$, is the *Jensen's force*: a systematic noise-induced drift of the mean due to the combined effect of fluctuations and curvature of the deterministic map. If $F_{xx} > 0$ (local convexity), fluctuations shift the mean upward; if $F_{xx} < 0$ (local concavity), they shift it downward. This result already suggests that fluctuations can systematically bias the dynamics. In the following, we derive an explicit approximation for our metapopulation model that incorporates this effect.

3.4.2 Moment dynamics from the master equation

In our metapopulation model, the stochastic dynamics is defined at the level of the full probability distribution, rather than through an effective stochastic update such as (3.4.1). To obtain the noise-induced correction, we derive evolution equations for the first two moments of the dynamics. Rather than following all intermediate steps, we directly report the resulting exact recursions and refer to Appendix 3.C for details.

The state of the full metapopulation at time t is described by the configuration $\mathbf{x}^t = (x_1^t, \dots, x_N^t)$, whose distribution $P_t(\mathbf{x})$ evolves according to the master equation [13]:

$$P_{t+1}(\mathbf{x}') = \sum_{\mathbf{x}} K(\mathbf{x}' | \mathbf{x}) P_t(\mathbf{x}). \quad (3.4.6)$$

Because patches update independently given the global state, the transition kernel factorizes across patches. To obtain a reduced description, we focus on the first two moments of the distribution,

$$m_t = \mathbb{E}[x_i^t], \quad v_t = \mathbb{E}[(x_i^t)^2] - m_t^2, \quad (3.4.7)$$

namely the mean and variance of the type- x frequency at a focal patch i . From the master equation (3.4.6), one obtains the following exact (but unclosed) recursions:

$$m_{t+1} = \langle F(x_i^t, \bar{x}^t) \rangle, \quad (3.4.8)$$

$$v_{t+1} = \langle G(x_i^t, \bar{x}^t) + F^2(x_i^t, \bar{x}^t) \rangle - \langle F(x_i^t, \bar{x}^t) \rangle^2, \quad (3.4.9)$$

where $\langle \cdot \rangle$ denotes expectation with respect to $P_t(\mathbf{x})$, and $\bar{x}(\mathbf{x}) = N^{-1} \sum_{j=1}^N x_j$ is the spatial mean of the configuration $\mathbf{x}$.

3.4.3 Second-order closure and variance-corrected dynamics

Equations (3.4.8)–(3.4.9) provide an exact description of the moment dynamics. However, they are not closed, since the nonlinear dependence of F and G on x_i^t and $\bar{x}^t$ couples (m_t, v_t) to higher-order cumulants. To obtain a closed approximation, we perform a second-order expansion [13] around a weakly heterogeneous state. Specifically, we write

$$x_i^t = m_t + \delta x_i^t, \quad \mathbb{E}[\delta x_i^t] = 0, \quad \mathbb{E}[(\delta x_i^t)^2] = v_t, \quad (3.4.10)$$

and expand F and G around $(x, \bar{x}) = (m_t, m_t)$. In the large- N limit (exchangeable initial conditions and weak spatial correlations), fluctuations of the global mean $\bar{x}^t$ are subleading. As a result, the dominant correction to naive mean-field theory is the Jensen curvature–variance term. This leads to the following closed recursion for the mean and variance:

$$\begin{cases} m_{t+1} \approx F(m_t, m_t) + \frac{1}{2} F_{xx}(m_t, m_t) v_t, \\ v_{t+1} \approx G(m_t, m_t) + \frac{1}{2} \left[G_{xx}(m_t, m_t) + (F^2)_{xx}(m_t, m_t) - 2F(m_t, m_t) F_{xx}(m_t, m_t) \right] v_t. \end{cases} \quad (3.4.11)$$

This closed two-dimensional map defines our *variance-corrected mean-field* (VCMF) dynamics (derivation in Appendix 3.D). It reduces to naive mean-field theory in the limit $v_t \rightarrow 0$ (or $k \rightarrow \infty$), while for finite k it captures the systematic noise-induced drift generated by Jensen’s force.

The key point is that fluctuations do not merely add noise around deterministic trajectories, but systematically shift the effective dynamics. The direction and magnitude of this shift are controlled by the curvature of the update rule, F_{xx} . In biological terms, this implies that demographic variability biases selection: because recruitment depends nonlinearly on local composition, variability across patches can shift the effective advantage of different dispersal strategies, favoring either increased or reduced dispersal.

Fixed points of the VCMF dynamics can be obtained analytically in the Binomial approximation (Appendix 3.D). They define effective equilibria for the stochastic metapopulation dynamics and reproduce the reversal of competitive dominance between low- and high-dispersal strategies observed in simulations (see Figure 3.2).

3.5 Invasion analysis and evolutionary stability

We now turn to the evolutionary implications of the variance-corrected dynamics, focusing on how finite-population fluctuations shape the selection and stability of dispersal strategies. To this end, we adopt the standard invasion-analysis framework of adaptive dynamics [14, 15].

We consider a resident population using dispersal probability β and a rare mutant with dispersal probability α . For analytical tractability, we adopt the binomial approximation introduced in Eq. (3.2.9), which is accurate in the high-offspring regime $\mu \gg k$.

Figure 3.3 provides an overview of the results obtained from numerical simulations of the model. It shows the long-term outcome of the stochastic dynamics (Section 3.2) in the (α, β) plane across a range of local population sizes k and dispersal survival probabilities p . The key qualitative effect is the progressive deformation of the basins of attraction as k decreases: demographic fluctuations reshape the competitive outcome and shift the evolutionarily stable strategy. This phenomenology motivates the analytical construction developed below, which we formulate in terms of invasion boundaries and evolutionary stability.

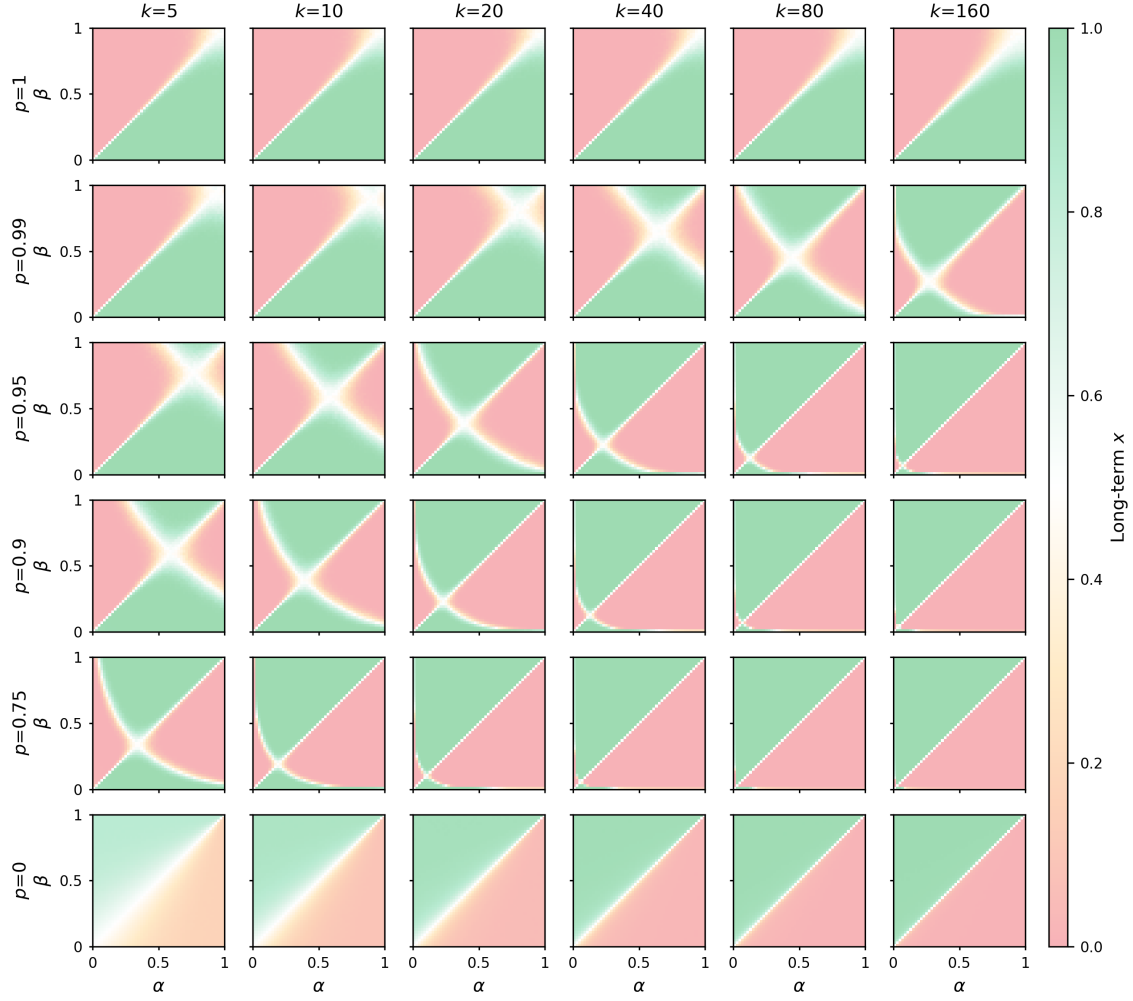


FIG. 3.3. Phase diagrams in the dispersal-trait plane (α, β) across local population size k (columns, increasing left to right) and dispersal survival p (rows, decreasing top to bottom). Colors show the long-term fraction $x = \langle f \rangle / k$, obtained from the stochastic simulations (uniformly distributed initial conditions; $N = 100$, $\mu = 1000$, 10^3 realizations). Green/pink indicate fixation of x ($x \simeq 1$) or y ($x \simeq 0$), respectively; intermediate colors correspond to bistability and sensitive dependence on initial conditions near the transition boundaries. The progressive deformation of the basins of attraction with decreasing k illustrates how demographic fluctuations reshape the competitive outcome and shift the ESS as a function of k and p .

3.5.1 Invasion fitness

We now formalize these observations using invasion analysis (see Appendix 3.E for details). In the adaptive-dynamics framework, the ability of a mutant strategy α to invade a resident population with strategy β is determined by its long-term growth rate when introduced at vanishing frequency. Within the VCMF description, this invasion fitness is obtained by linearising the mutant dynamics (3.4.11) around the resident-only ecological state:

$$\begin{pmatrix} m_{t+1} \\ v_{t+1} \end{pmatrix} = \mathbb{J} \begin{pmatrix} m_t \\ v_t \end{pmatrix}, \quad (3.5.1)$$

where $\mathbb{J}$ is the Jacobian of the VCMF map evaluated at mutant moments $(m, v) = (0, 0)$. The dominant eigenvalue of $\mathbb{J}$ defines the *invasion fitness* $\Lambda^\alpha(\alpha, \beta)$ (analytical expressions can be

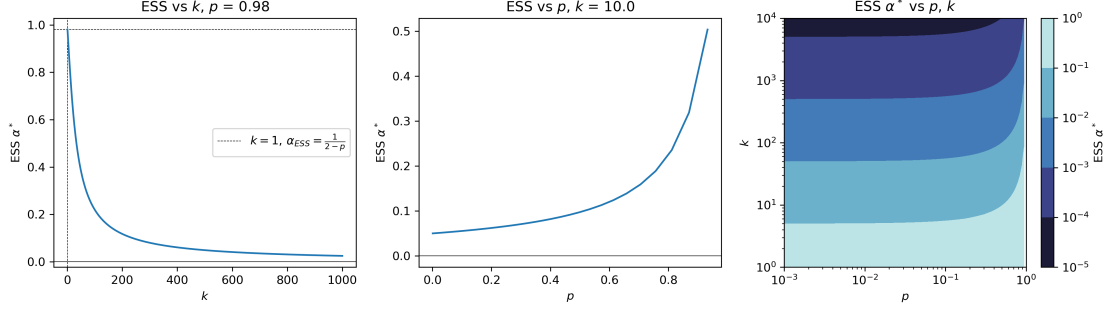


FIG. 3.4. Evolutionary stable strategy as a function of the local population size k and the dispersal mortality p . **Left:** for each value of k , the singular strategy is obtained by solving the selection gradient $s(\beta) = 0$. The curve shows how finite-population effects shift the evolutionarily stable dispersal strategy. The dashed lines demonstrate that in the case $k = 1$ the ESS is $\alpha_{ESS} = 1/2 - p$, consistently with [1]. **Center:** the same is done by varying the parameter p and calculating the ESS. **Right:** lastly, the contour plot shows how the ESS varies as a function of both k and p .

obtained under the binomial approximation).

If $\Lambda^\alpha(\alpha, \beta) > 1$, a mutant with strategy α can invade the resident population. If $\Lambda^\alpha(\alpha, \beta) < 1$, invasion fails and the mutant goes extinct. The condition $\Lambda^\alpha(\alpha, \beta) = 1$ defines the invasion boundary between invadable and uninvadable mutant strategies.

Conversely, invasion of strategy β into a resident population with strategy α is obtained by exchanging the roles of mutant and resident. This corresponds to linearising the dynamics around the fixed point $x = 1$ and yields the boundary $\Lambda^\beta(\beta, \alpha) = 1$.

The two corresponding invasion boundaries are shown in the right panel of Figure 3.2, where they delimit regions of dominance and bistability between dispersal strategies.

3.5.2 Selection gradient and evolutionary singular strategies

To connect invasion analysis with gradual evolutionary change, we compute the *selection gradient* at resident strategy β as the derivative of the invasion fitness with respect to the mutant trait, evaluated at $\alpha = \beta$,

$$s(\beta) = \left. \frac{\partial \Lambda^\alpha(\alpha, \beta)}{\partial \alpha} \right|_{\alpha=\beta}. \quad (3.5.2)$$

The sign of the selection gradient determines the local direction of selection: positive values favor increased dispersal, while negative values favor reduced dispersal. Evolutionary singular strategies β^* are defined by the condition $s(\beta^*) = 0$. Such strategies are evolutionarily stable (ESS) if they cannot be invaded by nearby mutant strategies. We determine singular strategies numerically for each parameter combination (k, p) and assess their evolutionary stability by analysing invasibility in the vicinity of β^* . Technical details are reported in Appendix 3.E.

Figure 3.4 summarizes the resulting evolutionarily stable dispersal strategies. For large local population sizes k , the ESS approaches the mean-field prediction of vanishing dispersal. As k decreases, finite-size fluctuations systematically shift the ESS towards higher dispersal probabilities. For sufficiently small k , this shift reflects the same fluctuation-driven mechanism responsible for the reversal of competitive outcomes observed in the stochastic simulations (Figure 3.2, left). In the limiting case $k = 1$, the ESS reduces to $\alpha_{ESS} = 1/2 - p$, in agreement with classical results [1].

3.6 Environmental heterogeneity

In many metapopulation and spatially structured systems, environmental heterogeneity plays a central role in shaping ecological dynamics [16]. So far we have considered a homogeneous environment in which all patches share the same demographic parameters. In the following, we show how environmental heterogeneity can be incorporated within the same variance-corrected framework, and explore how it qualitatively modifies the selection on dispersal.

In our framework, differences in habitat quality are most naturally represented through heterogeneity in local carrying capacity, which sets the population size of a patch and thus controls both the strength of local kin competition and the magnitude of demographic fluctuations. An alternative form of environmental heterogeneity, acting on the local growth rate μ instead of the carrying capacity, is presented in Appendix 3.G.

We begin by introducing a minimal form of heterogeneity, and then analyse its impact within the variance-corrected framework.

3.6.1 Habitat classes

Specifically, we consider a metapopulation composed of two classes of habitat patches with different carrying capacities. A fraction γ of the N patches has carrying capacity k , while the remaining fraction has capacity

$$h = k + \Delta k. \quad (3.6.1)$$

Thus, γN patches belong to class k and $(1 - \gamma)N$ to class h . At each time step, patch i contains X_i^t individuals of type x and $Y_i^t = K_i - X_i^t$ of type y , where $K_i \in \{k, h\}$ denotes the carrying capacity of patch i . After reproduction and dispersal, K_i individuals are sampled to form the adult population at time $t + 1$, inducing a hypergeometric transition kernel with patch-specific sample size K_i .

3.6.2 Stochastic dynamics in heterogeneous patches

Reproduction and dispersal follow the same rules as in the homogeneous model, with the only difference being the patch-dependent carrying capacity. In patch i , the expected number of offspring of each type is

$$\text{Off}_{X,i}^t = \mu \left[(1 - \alpha) X_i^t + p\alpha \frac{\mathcal{X}^t}{N} \right], \quad (3.6.2)$$

$$\text{Off}_{Y,i}^t = \mu \left[(1 - \beta) Y_i^t + p\beta \frac{\mathcal{Y}^t}{N} \right], \quad (3.6.3)$$

where $\mathcal{X}^t = \sum_i X_i^t$ and $\mathcal{Y}^t = \sum_i Y_i^t$ are the global abundances. After reproduction and dispersal, K_i individuals are sampled to form the adult population at time $t + 1$. As in the homogeneous case, this induces a hypergeometric transition kernel with a patch-specific sample size K_i . To facilitate comparison with the homogeneous case, we introduce the local frequency

$$x_i^t = \frac{X_i^t}{K_i}, \quad K_i \in \{k, h\}. \quad (3.6.4)$$

Conditioned on the current state and on the global abundance, the conditional mean and variance of x_i^{t+1} take the form

$$\mathbb{E}(x_i^{t+1} | x_i^t, \mathcal{X}^t) = F_{K_i}(x_i^t, \mathcal{X}^t), \quad (3.6.5)$$

$$\text{Var}(x_i^{t+1} | x_i^t, \mathcal{X}^t) = G_{K_i}(x_i^t, \mathcal{X}^t), \quad (3.6.6)$$

where the explicit expressions are given in Appendix 3.F. In the limit $\mu \gg k, h$ we again use the binomial approximation, which leaves the conditional mean unchanged and simplifies the conditional variance to $G_{K_i} \sim K_i^{-1} F_{K_i} (1 - F_{K_i})$.

3.6.3 Variance-corrected equations

We now extend the variance-corrected mean-field approach to the heterogeneous setting, following the same steps as in the homogeneous case. We define class-specific mean frequencies and variances as

$$m_t^K = \mathbb{E}[x_i^t \mid K_i = K], \quad v_t^K = \text{Var}(x_i^t \mid K_i = K), \quad K \in \{k, h\}. \quad (3.6.7)$$

The exact moment equations for each habitat class read

$$m_{t+1}^K = \langle F^K(x_i^t, \mathcal{X}^t) \rangle, \quad (3.6.8)$$

$$v_{t+1}^K = \langle G^K(x_i^t, \mathcal{X}^t) + F^K(x_i^t, \mathcal{X}^t)^2 \rangle - \langle F^K(x_i^t, \mathcal{X}^t) \rangle^2, \quad (3.6.9)$$

where F^K and G^K are the class-specific conditional mean and variance. As in the homogeneous case, these equations are exact but not closed. To obtain a closed approximation, we proceed as in the homogeneous case by replacing the global abundance with its deterministic mean

$$\mathcal{X}^t \approx \tilde{\mathcal{X}}_t = \gamma N k m_t^k + (1 - \gamma) N h m_t^h, \quad (3.6.10)$$

and performing a second-order cumulant expansion within each habitat class, neglecting terms of order $O(v_t^K/N)$ and higher. We obtain the class-specific variance-corrected mean-field equations

$$\begin{aligned} m_{t+1}^K &\approx F^K(m_t^K, \tilde{\mathcal{X}}_t) + \frac{1}{2} F_{xx}^K(m_t^K, \tilde{\mathcal{X}}_t) v_t^K, \\ v_{t+1}^K &\approx G^K(m_t^K, \tilde{\mathcal{X}}_t) + \frac{1}{2} \left[G_{xx}^K + (F^{K2})_{xx} - 2F^K F_{xx}^K \right]_{(m_t^K, \tilde{\mathcal{X}}_t)} v_t^K, \end{aligned} \quad (3.6.11)$$

for $K \in \{k, h\}$. The two habitat classes are coupled only through the global mean $\tilde{\mathcal{X}}_t$.

Fixed points (m^{K*}, v^{K*}) satisfy Eq. (3.6.11) with $m_{t+1}^K = m_t^K$ and $v_{t+1}^K = v_t^K$. Their explicit expressions are reported in Appendix 3.F. These variance-corrected equilibria provide an effective description of the stochastic dynamics and allow us to assess how heterogeneity in local population size reshapes selection on dispersal.

3.6.4 Exploratory numerical results

Figure 3.5 illustrates the qualitative impact of environmental heterogeneity on dispersal outcomes. The key effect is that heterogeneity can strongly suppress dispersal by introducing asymmetries in habitat quality. Although the results presented here are exploratory, they already reveal clear and interpretable trends that differ markedly from the homogeneous case.

We begin with the homogeneous environment ($k = h = 25$), where all patches have identical quality. In this case, dispersal entails no ecological risk: individuals that leave a patch are guaranteed to arrive in an environment with the same carrying capacity. This symmetry favors comparatively high dispersal rates, consistent with the absence of systematic fitness losses associated with movement.

We next consider heterogeneous environments. The two cases $(h, k) = (25, 1)$ and $(h, k) = (50, 25)$ illustrate how differences in patch quality reshape selection on dispersal.

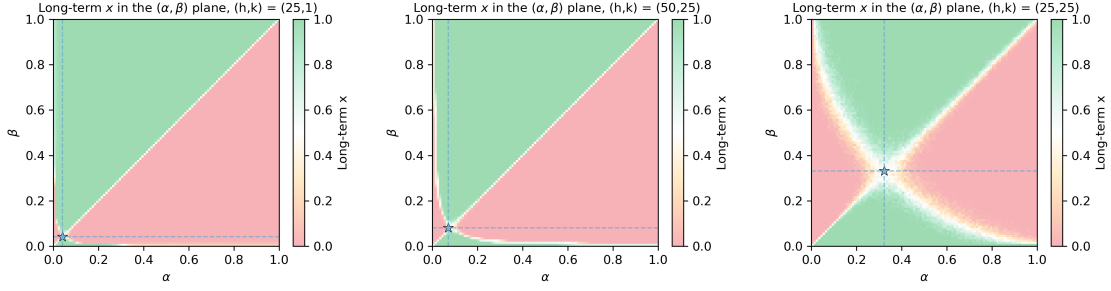


FIG. 3.5. Long-term frequency of the focal type X as a function of the dispersal parameters α and β under three carrying-capacity configurations. Each heatmap reports the long-term average fraction of type X across the metapopulation. Green regions indicate fixation of x ($x \approx 1$) while pink regions represent fixation of y ($x \approx 0$). The blue star marks the evolutionarily stable strategy (ESS). **Left:** heterogeneous environment with capacities $(h, k) = (25, 1)$. **Centre:** heterogeneous environment with $(h, k) = (50, 25)$. **Right:** homogeneous environment with $h = k = 25$. Diagrams are obtained by simulating the full stochastic dynamics of the model (Section 3.2) from uniformly distributed initial conditions and averaging over 10^3 realizations. Fixed parameters are $\mu = 1000$, $p = 0.95$, $\gamma = 0.5$, and $N = 100$.

In the strongly asymmetric environment $(25, 1)$, dispersal frequently transfers individuals from productive patches ($K = 25$) into near-sink habitats ($K = 1$), strongly reducing their long-term contribution to the metapopulation. This generates strong selection against dispersal, leading to very low optimal values of α and β .

By contrast, the environment $(50, 25)$ has weaker heterogeneity. Dispersal can still move individuals from high-quality patches ($K = 50$) into lower-quality ones ($K = 25$), but the difference between patch types is relatively small compared to the $(25, 1)$ case. Dispersal therefore remains costly, though not prohibitively so, and the resulting favored dispersal rates are intermediate between the near-zero values in the strongly heterogeneous case and the much higher values in the homogeneous environment. Notably, despite having a larger mean carrying capacity, the environment $(50, 25)$ exhibits higher ESS than $(25, 1)$, contrary to the expectation from the homogeneous case. This difference is driven by the stronger heterogeneity of the $(25, 1)$ environment. This shows that environmental heterogeneity can dominate over mean habitat quality in shaping dispersal evolution, strongly suppressing dispersal when asymmetries in patch quality are sufficiently pronounced.

While the present results are intended as a qualitative illustration, we have verified that increasing environmental heterogeneity consistently shifts the evolutionarily stable strategy towards lower dispersal rates across a broader range of parameter values. This suggests that the behavior shown in Figure 3.5 is robust rather than fine-tuned. Additional exploratory scans of the long-term outcome as a function of the habitat-size asymmetry and dispersal-strategy asymmetry are reported in Figure 3.7 in the Appendix. Overall, these results show that dispersal evolution is controlled by the interplay between mean habitat quality and environmental heterogeneity. Strong heterogeneity suppresses dispersal, while sufficiently large increases in mean carrying capacity can counteract this effect. A more systematic characterization of this interplay, including a phase-diagram analysis as a function of the statistics of environmental heterogeneity, is left for future work.

3.7 Conclusions

In this work we investigated the evolution of dispersal strategies in discrete-time stochastic metapopulations, focusing on the interplay between finite population size, demographic fluctuations and nonlinear population updates. The model isolates a minimal set of ingredients—density-regulated resampling, type-dependent dispersal, and demographic noise— and shows that finite-population variability can systematically bias the balance between local exploitation and competitive escape.

In the homogeneous setting, naive mean-field descriptions capture the asymptotic behavior only in the limit of large local population sizes, but can fail qualitatively when populations are finite. We derived an effective variance-corrected description that accounts for this breakdown via a systematic noise-induced drift generated by the curvature of the update rule. The resulting reduced framework reproduces long-run simulation outcomes and yields explicit invasion boundaries, demonstrating that the finite-size transition in the evolutionarily favored dispersal effort is a genuinely stochastic effect arising from the interaction between noise and nonlinearity.

We further explored how environmental heterogeneity can be incorporated within the same framework by allowing patch-to-patch variability in local carrying capacity. Although this analysis remains exploratory, the results indicate that heterogeneity can strongly modulate dispersal evolution and interact nontrivially with finite-size effects. In particular, pronounced asymmetries in habitat quality can substantially suppress dispersal, in line with previous results obtained with different approaches [9, 17]. These findings suggest that dispersal is shaped not only by mean conditions but also by variability in the conditions experienced.

In conclusion, both demographic stochasticity and environmental heterogeneity act as sources of variability that can systematically renormalize effective growth and selection in nonlinear metapopulation models. A natural next step is to map the heterogeneous phase diagram more systematically – including extensions beyond two patch classes – to clarify how heterogeneity statistics interact with finite-size noise in setting invasion thresholds and ESS values. More generally, the variance-corrected approach developed here provides a minimal and tractable route from microscopic stochasticity to macroscopic dispersal outcomes, and may be transferable to other “leave-or-stay” settings in which nonlinear updates filter demographic or environmental variability into effective selection pressures.

Appendix

3.A Recruitment fluctuations in the large- k limit

In this appendix we sketch the large- k scaling of stochastic fluctuations arising from the recruitment step, where k is the fixed number of adult individuals per patch, corresponding to the local carrying capacity.

From the hypergeometric sampling described in (3.2.6), the conditional variance of the updated frequency reads

$$\text{Var}\left(x_i^{t+1} \mid x_i^t, \bar{x}^t\right) = \frac{1}{k} F(x_i^t, \bar{x}^t) \left[1 - F(x_i^t, \bar{x}^t)\right] \frac{T_i^t - k}{T_i^t - 1}. \quad (3.A.1)$$

Since the total pool size satisfies $T_i^t = k + \mathcal{O}(k\mu) \geq k$, it follows that $T_i^t \gg 1$ whenever the adult population size k is large. Thus for large pool size T_i^t , we have

$$\frac{T_i^t - k}{T_i^t - 1} = 1 - \frac{k}{T_i^t} + \mathcal{O}\left(\frac{1}{T_i^t}\right). \quad (3.A.2)$$

Since $F(x_i^t, \bar{x}^t) \in [0, 1]$, the factor $F(x_i^t, \bar{x}^t) [1 - F(x_i^t, \bar{x}^t)]$ is bounded between 0 and 1/4, independently of k . As a result, the variance scales as k^{-1} , namely

$$\text{Var}\left(x_i^{t+1} \mid x_i^t, \bar{x}^t\right) \sim \frac{1}{k} \left[1 - \frac{k}{T_i^t} + \mathcal{O}\left(\frac{1}{T_i^t}\right)\right] = \mathcal{O}\left(\frac{1}{k}\right), \quad (3.A.3)$$

showing that fluctuations vanish as the local population size k increases.

3.B Mean-field fixed points and stability

Here we provide the details of the mean-field (MF) analysis summarized in Section 3.3. Under the MF assumption all patches are identical and equal to the spatial mean,

$$x_i^t \equiv \bar{x}^t = m_t, \quad (3.B.1)$$

so that the one-step map for a focal patch reduces to a one-dimensional recursion for m_t .

Starting from the single-patch update rule in Eq. (3.3.2),

$$F(x, \bar{x}) = \frac{x[1 + \mu(1 - \alpha)] + \mu p \alpha \bar{x}}{1 + \mu[1 - \beta(1 - p) + (\beta - \alpha)x]}, \quad (3.B.2)$$

and imposing $x = \bar{x} = m_t$, we obtain

$$m_{t+1} = F(m_t, m_t) = \frac{m_t a}{b + c m_t}, \quad (3.B.3)$$

where we have defined

$$a = 1 + \mu(1 - \alpha(1 - p)), \quad b = 1 + \mu(1 - \beta(1 - p)), \quad c = \mu(\beta - \alpha)(1 - p). \quad (3.B.4)$$

Fixed points m^* satisfy $m^* = F_{MF}(m^*)$. Either $m^* = 0$ or, if $m^* \neq 0$, we can divide both sides by m^* and obtain

$$m^* = \frac{a - b}{c} = 1. \quad (3.B.5)$$

Thus, the fixed points of the MF map are the boundary equilibria

$$m^* = 0 \quad \text{and} \quad m^* = 1. \quad (3.B.6)$$

To characterize their stability we consider the increment

$$\Delta m_t = m_{t+1} - m_t = \frac{c m_t (1 - m_t)}{b + c m_t}. \quad (3.B.7)$$

Because $b + c m_t > 0$ for all $m_t \in [0, 1]$:

$$\text{sign}(\Delta m_t) = \text{sign}(c) = \text{sign}[(\beta - \alpha)(1 - p)]. \quad (3.B.8)$$

If dispersal is costly ($p < 1$) and the strategies differ ($\beta \neq \alpha$), two cases arise:

- If $\beta > \alpha$, then $c > 0$ and $\Delta m_t > 0$ for all $m_t \in (0, 1)$. Thus $m^* = 1$ is globally attracting and $m^* = 0$ is unstable: the higher-dispersal strategy x fixes.
- If $\beta < \alpha$, then $c < 0$ and $\Delta m_t < 0$ for all $m_t \in (0, 1)$. In this case $m^* = 0$ is globally attracting and $m^* = 1$ unstable: the lower-dispersal strategy y fixes.

If instead $\beta = \alpha$ or $p = 1$, then $c = 0$ and Eq. (3.B.7) gives $\Delta m_t = 0$ for all $m_t \in [0, 1]$, corresponding to a continuum of neutrally stable fixed points.

In summary, the naive MF approximation predicts that, in a homogeneous environment with costly dispersal, the type with lower dispersal probability always wins. As shown in the main text, this prediction breaks down at finite local population sizes, where fluctuation-induced corrections (Jensen's force) can reverse the direction of selection on dispersal.

3.C Derivation of the exact moment equations

This appendix reports the detailed derivation of the exact (but unclosed) cumulant recursions (3.4.8) and (3.4.9), starting from the master equation:

$$P_{t+1}(\mathbf{x}') = \sum_{\mathbf{x}} K(\mathbf{x}' | \mathbf{x}) P_t(\mathbf{x}). \quad (3.C.1)$$

This equation encodes the exact evolution of the probability distribution $P_t(\mathbf{x})$, where $\mathbf{x}^t = (x_1^t, \dots, x_N^t)$ is the state of the full metapopulation at time t . Conditioned on the current configuration

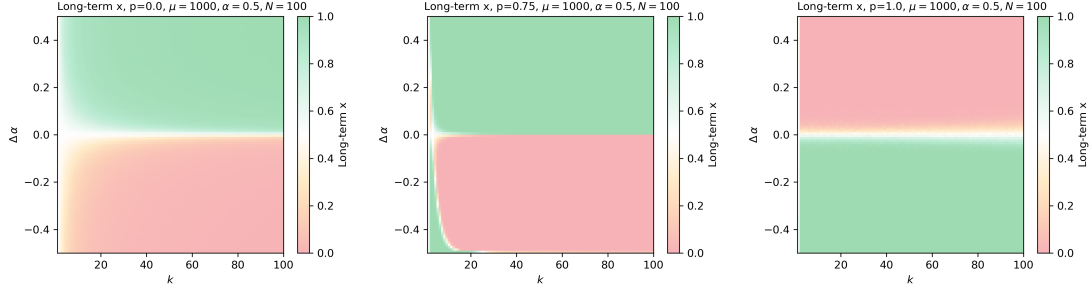


FIG. 3.6. Phase diagrams of the long-term value of x in the $(k, \Delta\alpha)$ plane, illustrating the role of dispersal cost p . The three panels correspond to increasing values of p from 0 to 1, which shifts the dynamics from a dispersal-disfavored to a dispersal-favored regime. The remaining parameters remain fixed at $\alpha = 0.5$, $\mu = 1000$ and $N = 100$. The diagram is obtained by simulating the full stochastic dynamics of the model (Section 3.2) from uniformly distributed initial conditions and averaging over 10^3 realizations. **Left:** In the limit case $p = 0$, where seedlings do not survive dispersal, the lower dispersal strategy systematically wins. **Center:** At intermediate dispersal cost $p = 0.75$, the winning strategy depends on local carrying capacity k . **Right:** In the limit case $p = 1$, where dispersal has no cost, the higher dispersal strategy automatically wins across all system sizes.

$\mathbf{x}^t$, patches update independently according to the single-patch kernel (3.2.6). As a result, the full transition kernel factorizes as

$$K(\mathbf{x}' | \mathbf{x}) = \prod_{i=1}^N \mathbb{P}(x_i^{t+1} = x'_i | x_i^t, \bar{x}(\mathbf{x})), \quad (3.C.2)$$

where $\bar{x}(\mathbf{x}) = N^{-1} \sum_{j=1}^N x_j$ denotes the spatial mean of the configuration $\mathbf{x}$. To obtain a reduced description, we consider the evolution of low-order moments of the distribution. Let

$$m_t = \mathbb{E}[x_i^t], \quad q_t = \mathbb{E}[(x_i^t)^2], \quad v_t = q_t - m_t^2, \quad (3.C.3)$$

denote, respectively, the ensemble mean, second moment, and variance of the type- x frequency at a focal patch i (exchangeability implies that these quantities are independent of i). Using the master equation (3.C.1) and the conditional cumulants in Eq. (3.2.7), one obtains the exact recursions for the first and second moments.

First moment. Starting from the definition of $m_{t+1} = \mathbb{E}[x_i^{t+1}]$ and using the master equation,

$$\begin{aligned} m_{t+1} &= \sum_{\mathbf{x}'} x'_i P_{t+1}(\mathbf{x}') = \sum_{\mathbf{x}'} x'_i \sum_{\mathbf{x}} K(\mathbf{x}' | \mathbf{x}) P_t(\mathbf{x}) \\ &= \sum_{\mathbf{x}} P_t(\mathbf{x}) \sum_{\mathbf{x}'} x'_i K(\mathbf{x}' | \mathbf{x}) \\ &= \sum_{\mathbf{x}} P_t(\mathbf{x}) \mathbb{E}(x_i^{t+1} | \mathbf{x}^t = \mathbf{x}). \end{aligned} \quad (3.C.4)$$

By definition of the single-patch conditional mean in (3.2.7),

$$\mathbb{E}(x_i^{t+1} | \mathbf{x}^t = \mathbf{x}) = F(x_i^t, \bar{x}(\mathbf{x})), \quad (3.C.5)$$

so that (3.C.4) becomes

$$m_{t+1} = \sum_{\mathbf{x}} P_t(\mathbf{x}) F(x_i^t, \bar{x}(\mathbf{x})) = \langle F(x_i^t, \bar{x}^t) \rangle, \quad (3.C.6)$$

which is Eq. (3.4.8).

Second moment. Similarly,

$$\begin{aligned}
 q_{t+1} &= \mathbb{E}[(x_i^{t+1})^2] = \sum_{\mathbf{x}'} x_i'^2 P_{t+1}(\mathbf{x}') \\
 &= \sum_{\mathbf{x}} P_t(\mathbf{x}) \sum_{\mathbf{x}'} x_i'^2 K(\mathbf{x}' | \mathbf{x}) \\
 &= \sum_{\mathbf{x}} P_t(\mathbf{x}) \mathbb{E}[(x_i^{t+1})^2 | \mathbf{x}^t = \mathbf{x}].
 \end{aligned} \tag{3.C.7}$$

Using $\mathbb{E}[Z^2] = \text{Var}(Z) + \mathbb{E}[Z]^2$ with the conditional cumulants in Eq. (3.2.7) gives

$$\mathbb{E}[(x_i^{t+1})^2 | \mathbf{x}^t = \mathbf{x}] = G(x_i^t, \bar{x}(\mathbf{x})) + F(x_i^t, \bar{x}(\mathbf{x}))^2. \tag{3.C.8}$$

Substituting into (3.C.7) yields

$$q_{t+1} = \sum_{\mathbf{x}} P_t(\mathbf{x}) \left[G(x_i^t, \bar{x}(\mathbf{x})) + F(x_i^t, \bar{x}(\mathbf{x}))^2 \right] = \langle G(x_i^t, \bar{x}^t) + F(x_i^t, \bar{x}^t)^2 \rangle, \tag{3.C.9}$$

The variance recursion (3.4.9) then follows from $v_{t+1} = q_{t+1} - m_{t+1}^2$.

3.D VCMF equations

This appendix reports the second-order cumulant expansion leading to the VCMF recursions (3.4.11).

Mean recursion. Starting from the exact identity $m_{t+1} = \langle F(x_i^t, \bar{x}^t) \rangle$ in (3.4.8), write

$$x_i^t = m_t + \delta x_i^t, \quad \bar{x}^t = m_t + \delta \bar{x}^t, \tag{3.D.1}$$

with $\mathbb{E}[\delta x_i^t] = \mathbb{E}[\delta \bar{x}^t] = 0$ and $\mathbb{E}[(\delta x_i^t)^2] = v_t$. We Taylor-expand F around (m_t, m_t) up to second-order:

$$\begin{aligned}
 F(x_i^t, \bar{x}^t) &\approx F(m_t, m_t) + F_x(m_t, m_t) \delta x_i^t + F_{\bar{x}}(m_t, m_t) \delta \bar{x}^t \\
 &\quad + \frac{1}{2} F_{xx}(m_t, m_t) (\delta x_i^t)^2 + \frac{1}{2} F_{\bar{x}\bar{x}}(m_t, m_t) (\delta \bar{x}^t)^2 + F_{x\bar{x}}(m_t, m_t) \delta x_i^t \delta \bar{x}^t.
 \end{aligned} \tag{3.D.2}$$

Taking expectations and using $\mathbb{E}[\delta x_i^t] = \mathbb{E}[\delta \bar{x}^t] = 0$ gives

$$\begin{aligned}
 m_{t+1} &\approx F(m_t, m_t) + \frac{1}{2} F_{xx}(m_t, m_t) v_t + \frac{1}{2} F_{\bar{x}\bar{x}}(m_t, m_t) \text{Var}(\bar{x}^t) \\
 &\quad + F_{x\bar{x}}(m_t, m_t) \text{Cov}(x_i^t, \bar{x}^t).
 \end{aligned} \tag{3.D.3}$$

For exchangeable initial conditions and weak spatial correlations

$$\text{Var}(\bar{x}^t) = O(v_t/N), \quad \text{Cov}(x_i^t, \bar{x}^t) = O(v_t/N), \tag{3.D.4}$$

so that in the large- N limit the leading correction is the Jensen term $\frac{1}{2} F_{xx} v_t$, yielding

$$m_{t+1} \approx F(m_t, m_t) + \frac{1}{2} F_{xx}(m_t, m_t) v_t. \tag{3.D.5}$$

Variance recursion. Starting from (3.4.9) and performing an analogous second-order expansion of $G(x_i^t, \bar{x}^t)$ and $F(x_i^t, \bar{x}^t)^2$ about (m_t, m_t) , while retaining only the leading $O(v_t)$ contributions (and neglecting $O(v_t/N)$ terms as above), one obtains

$$v_{t+1} \approx G(m_t, m_t) + \frac{1}{2} \left[G_{xx}(m_t, m_t) + (F^2)_{xx}(m_t, m_t) - 2F(m_t, m_t)F_{xx}(m_t, m_t) \right] v_t. \quad (3.D.6)$$

Variance-corrected fixed points. Fixed points (m^*, v^*) of the VCMF dynamics satisfy

$$\begin{aligned} m^* &= F(m^*, m^*) + \frac{F_{xx}(m^*, m^*)G(m^*, m^*)}{2 - \{G_{xx}(m^*, m^*) + (F^2)_{xx}(m^*, m^*) - 2F(m^*, m^*)F_{xx}(m^*, m^*)\}}, \\ v^* &= \frac{G(m^*, m^*)}{1 - \frac{1}{2} \{G_{xx}(m^*, m^*) + (F^2)_{xx}(m^*, m^*) - 2F(m^*, m^*)F_{xx}(m^*, m^*)\}}. \end{aligned} \quad (3.D.7)$$

and These equations can be solved exactly in the Binomial approximation, and provide effective equilibria for the full stochastic metapopulation dynamics.

3.E Adaptive-dynamics analysis of dispersal strategies

In this appendix we provide the technical details underlying the invasion and evolutionary-stability analysis presented in Section 3.5.

Linearised mutant dynamics and invasion fitness. Within the VCMF framework, the ecological dynamics admits two monomorphic fixed points, corresponding to populations consisting exclusively of either the resident or the mutant type. To evaluate the invasibility of a rare mutant strategy α in a resident population with strategy β , we linearise the mutant-moment dynamics around the resident-only state.

Denoting by (m_t, v_t) the mean and variance of the mutant population across patches, the linearised dynamics takes the form

$$\begin{pmatrix} m_{t+1} \\ v_{t+1} \end{pmatrix} = \mathbb{J} \begin{pmatrix} m_t \\ v_t \end{pmatrix}, \quad (3.E.1)$$

where $\mathbb{J}$ is the Jacobian matrix evaluated at $(m_t, v_t) = (0, 0)$.

Under the binomial approximation, the Jacobian reads

$$\mathbb{J} = \begin{pmatrix} \frac{\alpha p - \alpha + 1}{\beta p - \beta + 1} & -\frac{(\alpha - 1)(\alpha - \beta)}{(\beta p - \beta + 1)^2} \\ \frac{\alpha p - \alpha + 1}{k(\beta p - \beta + 1)} & \frac{(\alpha - 1)(-2\alpha + \beta + k(\alpha - 1) + 1)}{k(\beta p - \beta + 1)^2} \end{pmatrix}. \quad (3.E.2)$$

The invasion fitness $\Lambda^\alpha(\alpha, \beta)$ of the mutant with strategy α in a resident population with strategy β is defined as the dominant eigenvalue $\Lambda^\alpha(\alpha, \beta)$ of this Jacobian. Invasion is possible if $\Lambda^\alpha(\alpha, \beta) > 1$, while $\Lambda^\alpha(\alpha, \beta) < 1$ implies extinction of the mutant.

Conversely, invasion of strategy β into a resident population with strategy α is obtained by exchanging the roles of mutant and resident, and evaluating the corresponding Jacobian at $(m, v) = (0, 0)$ in the resident- α environment. This corresponds to linearising the dynamics around the fixed point $x = 1$ and yields the boundary $\Lambda^\beta(\beta, \alpha) = 1$.

Although explicit analytical expressions for the eigenvalues of the Jacobian Eq. (3.E.2) can be obtained, they are not reported here due to their length.

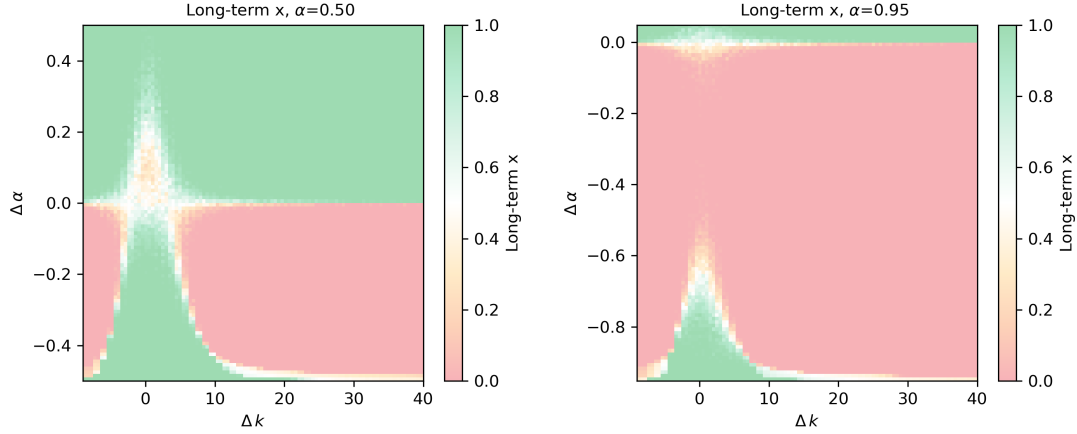


FIG. 3.7. Exploratory numerical phase diagram of the long-term value of $x = \langle f \rangle / k$, obtained by simulating the full stochastic dynamics of the model (Section 3.2) from uniformly distributed initial conditions and averaging over 60 stochastic realizations. The control parameters are the difference between dispersal strategies, $\Delta\alpha = \beta - \alpha$ (vertical axis), and the habitat-size asymmetry $\delta k = k - h$ (horizontal axis). The left panel fixes $\alpha = 0.5$, whereas the right panel fixes $\alpha = 0.95$. Other parameters are held fixed at $h = 10$, $\mu = 1000$, $p = 0.95$, $N = 100$, and $\gamma = 0.5$.

Selection gradient and evolutionary stability. The selection gradient at resident strategy β is defined as

$$s(\beta) = \left. \frac{\partial \Lambda^\alpha(\alpha, \beta)}{\partial \alpha} \right|_{\alpha=\beta}. \quad (3.E.3)$$

The sign of $s(\beta)$ determines the local direction of selection: if $s(\beta) > 0$, selection favors an increase in dispersal probability, whereas if $s(\beta) < 0$, it favors reduced dispersal. Points where $s(\beta) = 0$ mark changes in the selection direction and define *evolutionary singular strategies*,

$$s(\beta^*) = 0. \quad (3.E.4)$$

To assess evolutionary stability, we examine the second derivative of the invasion fitness with respect to the mutant trait,

$$\left. \frac{\partial^2 \Lambda^\alpha(\alpha, \beta)}{\partial \alpha^2} \right|_{\alpha=\beta=\beta^*}. \quad (3.E.5)$$

A negative value indicates that nearby mutant strategies cannot invade, identifying β^* as an evolutionarily stable strategy (ESS).

All singular strategies reported in the main text were obtained by numerically solving $s(\beta) = 0$ for $\beta \in [0, 1]$ and verifying the stability condition Eq. (3.E.5).

3.F Heterogeneity in local population size

In this Appendix we report the full microscopic definition of the stochastic dynamics in the presence of spatial heterogeneity in local carrying capacity, together with the exact transition kernel and the detailed derivation of the variance-corrected mean-field (VCMF) equations presented in Section 3.6 of the main text.

Habitat classes and demographic structure. We consider a metapopulation of N patches partitioned into two habitat classes. A fraction γ of the patches has carrying capacity k , while the remaining fraction $1 - \gamma$ has carrying capacity

$$h = k + \Delta k.$$

We denote the carrying capacity of patch i by

$$K_i \in \{k, h\}, \quad i = 1, \dots, N, \quad (3.F.1)$$

with exactly γN patches such that $K_i = k$ and $(1 - \gamma)N$ such that $K_i = h$.

At time t , patch i contains X_i^t individuals of type x and $Y_i^t = K_i - X_i^t$ individuals of type y . The global abundances are

$$\mathcal{X}^t = \sum_{i=1}^N X_i^t, \quad \mathcal{Y}^t = \sum_{i=1}^N Y_i^t, \quad (3.F.2)$$

with total adult population

$$\mathcal{K} = \sum_{i=1}^N K_i = \gamma N k + (1 - \gamma) N h.$$

Offspring production and global dispersal. Reproduction and dispersal follow the same rules as in the homogeneous model. In patch i at time t , the expected numbers of offspring of each type are

$$\text{Off}_{X,i}^t = \mu \left[(1 - \alpha) X_i^t + p \alpha \frac{\mathcal{X}^t}{N} \right], \quad (3.F.3)$$

$$\text{Off}_{Y,i}^t = \mu \left[(1 - \beta) Y_i^t + p \beta \frac{\mathcal{Y}^t}{N} \right]. \quad (3.F.4)$$

The first term in each expression corresponds to locally retained offspring, whereas the second corresponds to immigrants drawn from the global dispersal pool.

The pool of potential recruits in patch i is therefore

$$A_i^t = X_i^t + \text{Off}_{X,i}^t, \quad B_i^t = Y_i^t + \text{Off}_{Y,i}^t, \quad (3.F.5)$$

with total size

$$T_i^t = A_i^t + B_i^t = K_i + \text{Off}_{X,i}^t + \text{Off}_{Y,i}^t. \quad (3.F.6)$$

At each time step, K_i individuals are sampled without replacement from this pool to form the adult population at time $t + 1$.

Exact transition kernel. Conditioned on $(X_i^t, \mathcal{X}^t)$, the transition probability for patch i is hypergeometric with patch-specific sample size K_i :

$$\mathbb{P}(X_i^{t+1} = n \mid X_i^t, \mathcal{X}^t) = \frac{\binom{A_i^t}{n} \binom{B_i^t}{K_i - n}}{\binom{T_i^t}{K_i}}, \quad n = 0, 1, \dots, K_i. \quad (3.F.7)$$

The conditional expectation and variance of X_i^{t+1} are

$$\mathbb{E}(X_i^{t+1} \mid X_i^t, \mathcal{X}^t) = K_i \frac{A_i^t}{T_i^t} \equiv \mathcal{F}^{K_i}(X_i^t, \mathcal{X}^t), \quad (3.F.8)$$

$$\text{Var}(X_i^{t+1} \mid X_i^t, \mathcal{X}^t) = K_i \frac{A_i^t}{T_i^t} \left(1 - \frac{A_i^t}{T_i^t} \right) \frac{T_i^t - K_i}{T_i^t - 1} \equiv \mathcal{G}^{K_i}(X_i^t, \mathcal{X}^t). \quad (3.F.9)$$

Frequency formulation. Defining the local frequency

$$x_i^t = \frac{X_i^t}{K_i}, \quad K_i \in \{k, h\}, \quad (3.F.10)$$

the conditional moments of x_i^{t+1} are

$$\mathbb{E}(x_i^{t+1} | x_i^t, \mathcal{X}^t) = \frac{A_i^t}{T_i^t} \equiv F_{K_i}(x_i^t, \mathcal{X}^t), \quad (3.F.11)$$

$$\text{Var}(x_i^{t+1} | x_i^t, \mathcal{X}^t) = \frac{1}{K_i} F_{K_i}(x_i^t, \mathcal{X}^t) [1 - F_{K_i}(x_i^t, \mathcal{X}^t)] \frac{T_i^t - K_i}{T_i^t - 1} \equiv G_{K_i}(x_i^t, \mathcal{X}^t). \quad (3.F.12)$$

In the limit $\mu \gg k, h$, the hypergeometric sampling can be approximated by binomial sampling with success probability $p_i^t = A_i^t/T_i^t$. Under this approximation,

$$\mathbb{E}(x_i^{t+1} | x_i^t, \mathcal{X}^t) \approx F_{K_i}(x_i^t, \mathcal{X}^t), \quad (3.F.13)$$

$$\text{Var}(x_i^{t+1} | x_i^t, \mathcal{X}^t) \approx \frac{1}{K_i} F_{K_i}(x_i^t, \mathcal{X}^t) [1 - F_{K_i}(x_i^t, \mathcal{X}^t)]. \quad (3.F.14)$$

Exact class-specific moment equations. We now derive approximate evolution equations for the first two cumulants of the local frequency in each habitat class. Within each habitat class $K \in \{k, h\}$, we define the class-specific first and second moments of the local frequency

$$m_t^K = \mathbb{E}[x_i^t | K_i = K], \quad q_t^K = \mathbb{E}[(x_i^t)^2 | K_i = K], \quad v_t^K = q_t^K - (m_t^K)^2. \quad (3.F.15)$$

Because patches update independently given the global adult pool, the transition kernel factorizes as in the homogeneous case. Focusing on a focal site i in class K (i.e. $K_i = K$), the exact update of the class-specific mean is

$$m_{t+1}^K = \mathbb{E}[x_i^{t+1} | K_i = K] = \mathbb{E}[\mathbb{E}(x_i^{t+1} | x_i^t, \mathcal{X}^t, K_i = K)] \quad (3.F.16)$$

$$= \langle F^K(x_i^t, \mathcal{X}^t) \rangle, \quad (3.F.17)$$

where $\langle \cdot \rangle_K$ denotes the expectation over the distribution of $(x_i^t, \mathcal{X}^t)$ conditional on $K_i = K$. Analogously, the class-specific second moment evolves according to

$$q_{t+1}^K = \mathbb{E}[(x_i^{t+1})^2 | K_i = K] = \mathbb{E}[\mathbb{E}((x_i^{t+1})^2 | x_i^t, \mathcal{X}^t, K_i = K)] \quad (3.F.18)$$

$$= \langle G^K(x_i^t, \mathcal{X}^t) + F^K(x_i^t, \mathcal{X}^t)^2 \rangle, \quad (3.F.19)$$

and hence the class-specific variance satisfies

$$v_{t+1}^K = q_{t+1}^K - (m_{t+1}^K)^2 = \langle G^K(x_i^t, \mathcal{X}^t) + F^K(x_i^t, \mathcal{X}^t)^2 \rangle - \langle F^K(x_i^t, \mathcal{X}^t) \rangle^2. \quad (3.F.20)$$

Equations (3.F.17) and (3.F.20) are exact but not closed, because the expectations involve the full distribution of x_i^t .

Variance-corrected mean-field closure. To obtain a closed deterministic description we again perform a cumulant expansion in each habitat class. We first neglect fluctuations of the global adult pool and replace $\mathcal{X}^t$ by its deterministic mean, i.e.

$$\mathcal{X}^t \simeq \tilde{\mathcal{X}}_t = \gamma N k m_t^k + (1 - \gamma) N h m_t^h.$$

Expanding F^K and G^K to second order in $\delta x_i^t = x_i^t - m_t^K$ and retaining only terms up to $O(v_t^K)$ yields

$$m_{t+1}^K \approx F^K(m_t^K, \tilde{\mathcal{X}}_t) + \frac{1}{2} F_{xx}^K(m_t^K, \tilde{\mathcal{X}}_t) v_t^K, \quad (3.F.21)$$

$$v_{t+1}^K \approx G^K(m_t^K, \tilde{\mathcal{X}}_t) + \frac{1}{2} \left[G_{xx}^K + (F^{K2})_{xx} - 2F^K F_{xx}^K \right]_{(m_t^K, \tilde{\mathcal{X}}_t)} v_t^K. \quad (3.F.22)$$

These equations constitute the class-specific VCMF dynamics reported in the main text.

Class-specific fixed points. Fixed points (m^{K*}, v^{K*}) satisfy

$$m^{K*} = F^K(m^{K*}, \tilde{\mathcal{X}}^*) + \frac{F_{xx}^K(m^{K*}, \tilde{\mathcal{X}}^*) G^K(m^{K*}, \tilde{\mathcal{X}}^*)}{2 - \left[G_{xx}^K + (F^{K2})_{xx} - 2F^K F_{xx}^K \right]_{(m^{K*}, \tilde{\mathcal{X}}^*)}}, \quad (3.F.23)$$

$$v^{K*} = \frac{G^K(m^{K*}, \tilde{\mathcal{X}}^*)}{1 - \frac{1}{2} \left[G_{xx}^K + (F^{K2})_{xx} - 2F^K F_{xx}^K \right]_{(m^{K*}, \tilde{\mathcal{X}}^*)}}, \quad (3.F.24)$$

for $K \in \{k, h\}$, with

$$\tilde{\mathcal{X}}^* = \gamma N k m^{k*} + (1 - \gamma) N h m^{h*}. \quad (3.F.25)$$

3.G Heterogeneity in growth rates

We first consider a landscape composed of two types of habitat, differing in their local growth rate. A fraction γ of the patches has growth rate μ , while the remaining fraction $1 - \gamma$ has growth rate $\nu = \mu + \Delta\mu$. We define the spatial means

$$\bar{x}^{\mu,t} = \frac{1}{\gamma N} \sum_{i=1}^{\gamma N} x_i^t, \quad \bar{x}^{\nu,t} = \frac{1}{(1 - \gamma) N} \sum_{i=\gamma N+1}^N x_i^t, \quad (3.G.1)$$

over habitats with growth rate μ and ν , respectively.

The expected numbers of offspring contributing to a patch of type μ become

$$\text{offs}_{x,i}^{\mu,t} = k \left[\mu(1 - \alpha) x_i^t + p\alpha(\gamma\mu\bar{x}^{\mu,t} + (1 - \gamma)\nu\bar{x}^{\nu,t}) \right], \quad (3.G.2)$$

$$\text{offs}_{y,i}^{\mu,t} = k \left[\mu(1 - \beta)(1 - x_i^t) + p\beta(\gamma\mu(1 - \bar{x}^{\mu,t}) + (1 - \gamma)\nu(1 - \bar{x}^{\nu,t})) \right], \quad (3.G.3)$$

with analogous expressions for patches of type ν obtained by exchanging $\mu \leftrightarrow \nu$. The corresponding pools of potential recruits are

$$A_i^{\mu,t} = k x_i^t + \text{offs}_{x,i}^{\mu,t}, \quad B_i^{\mu,t} = k(1 - x_i^t) + \text{offs}_{y,i}^{\mu,t}, \quad (3.G.4)$$

$$A_i^{\nu,t} = k x_i^t + \text{offs}_{x,i}^{\nu,t}, \quad B_i^{\nu,t} = k(1 - x_i^t) + \text{offs}_{y,i}^{\nu,t}, \quad (3.G.5)$$

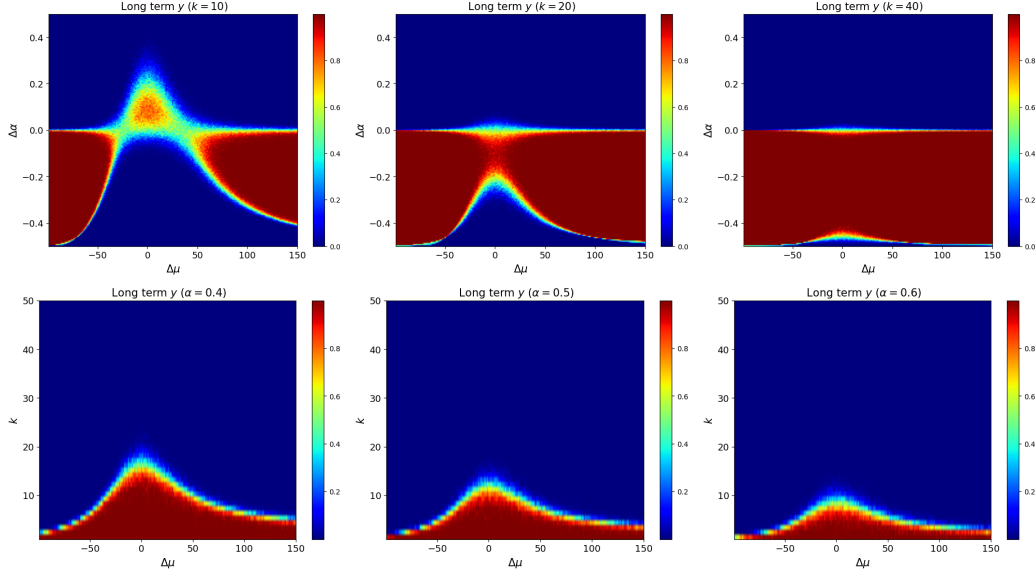


FIG. 3.8. Top: Phase diagram of the long-run frequency of type Y as a function of $\Delta\mu$ and $\Delta\alpha$ across different carrying capacities k . The parameters $\alpha = 0.5$ and $p = 0.95$ are fixed. For large k , the dynamics approaches a near-mean-field regime and the effect of environmental heterogeneity become less noticeable. **Bottom:** Phase diagram of the long-run frequency of type Y as a function of $\Delta\mu$ and k , across different values of α , for fixed $\Delta\alpha = 0.1$ and $p = 0.95$.

with total sizes $T_i^{\mu,t} = A_i^{\mu,t} + B_i^{\mu,t}$ and $T_i^{\nu,t} = A_i^{\nu,t} + B_i^{\nu,t}$.

Proceeding as in the homogeneous case, we can derive exact equations for the first two cumulants in each habitat class. After a second-order expansion around the class-specific mean frequencies and a mean-field approximation for spatial correlations, we obtain a system of four weakly coupled VCMF equations:

$$\left\{ \begin{array}{l} m_{t+1}^{\mu} \approx F^{\mu}(m_t^{\mu}, m_t^{\mu}, m_t^{\nu}) + \frac{1}{2} F_{xx}^{\mu}(m_t^{\mu}, m_t^{\mu}, m_t^{\nu}) v_t^{\mu}, \\ v_{t+1}^{\mu} \approx G^{\mu}(m_t^{\mu}, m_t^{\mu}, m_t^{\nu}) + \frac{1}{2} \left[G_{xx}^{\mu}(m_t^{\mu}, m_t^{\mu}, m_t^{\nu}) + (F^{\mu})_{xx}^2(m_t^{\mu}, m_t^{\mu}, m_t^{\nu}) \right. \\ \quad \left. - 2F^{\mu}(m_t^{\mu}, m_t^{\mu}, m_t^{\nu}) F_{xx}^{\mu}(m_t^{\mu}, m_t^{\mu}, m_t^{\nu}) \right] v_t^{\mu}, \\ m_{t+1}^{\nu} \approx F^{\nu}(m_t^{\nu}, m_t^{\mu}, m_t^{\nu}) + \frac{1}{2} F_{xx}^{\nu}(m_t^{\nu}, m_t^{\mu}, m_t^{\nu}) v_t^{\nu}, \\ v_{t+1}^{\nu} \approx G^{\nu}(m_t^{\nu}, m_t^{\mu}, m_t^{\nu}) + \frac{1}{2} \left[G_{xx}^{\nu}(m_t^{\nu}, m_t^{\mu}, m_t^{\nu}) + (F^{\nu})_{xx}^2(m_t^{\nu}, m_t^{\mu}, m_t^{\nu}) \right. \\ \quad \left. - 2F^{\nu}(m_t^{\nu}, m_t^{\mu}, m_t^{\nu}) F_{xx}^{\nu}(m_t^{\nu}, m_t^{\mu}, m_t^{\nu}) \right] v_t^{\nu}. \end{array} \right. \quad (3.G.6)$$

Numerical simulations of the full stochastic model in heterogeneous environments (Figure 3.8) show that increasing the difference in growth rates $|\Delta\mu|$ has an effect qualitatively similar to increasing the local population size k : lower-dispersal invaders become more likely to succeed, and the critical population size k_c at which the system transitions from a fluctuation-dominated to a mean-field-like regime decreases. The VCMF equations Eq. (3.G.6) capture these trends and clarify how demographic and environmental heterogeneity combine to modulate the strength and direction of Jensen's force.

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4

Minimal model of Norway spruce–bark beetle outbreak dynamics

Abstract. Bark beetles pose a growing threat to coniferous forests worldwide, with outbreaks increasingly linked to environmental stress and host vulnerability. Most mechanistic models focus on equilibrium states, neglecting the dynamical nature of outbreaks triggered by environmental perturbations. Using *Ips typographus* as focal species, we present a minimal model capturing key processes such as threshold-driven mass attacks, with parameters adaptable to different environmental conditions. Under current conditions, the model predicts a stable endemic state that is reactive, meaning environmental shocks trigger isolated, transient outbreaks. Under altered conditions, reflecting potential climate change scenarios, the system undergoes a regime shift, producing recurrent outbreaks that arise spontaneously from insect–host feedback. Finally, we examine repeated environmental disturbances and forest management, showing that the effectiveness of outbreak mitigation depends on the interplay between management frequency and intensity. Overall, we provide a mechanistic framework for understanding outbreak dynamics and guiding management strategies under changing environmental conditions.

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Structure. Section 4.1 introduces the ecological context and motivation. Sections 4.2.1–4.2.2 present the well-mixed model and parameter estimates. In Sections 4.2.3–4.3.3 we analyze equilibrium behavior, reactivity, and the emergence of recurrent outbreaks. Section 4.3.4 examines repeated environmental perturbations, and Section 4.3.5 explores management strategies. Section 4.9 outlines a spatial extension of the model and presents preliminary results on emerging spatial patterns.

4.1 Introduction

Conifer-dominated forests constitute a significant component of the boreal and temperate ecosystems throughout Europe and North America [1,2]. These forests provide essential services such as carbon sequestration, biodiversity preservation, and renewable raw material for economic activities. Within forest environments, biotic agents such as insects and fungi play key ecological roles, influencing

nutrient cycling, succession, and structural complexity. Among these biotic agents, bark beetles (Coleoptera Curculionidae Scolytinae) are particularly important due to their capacity to profoundly shape forest structure and successional pathways [3,4]. Under endemic conditions, bark beetles typically attack and kill weakened or overmature trees, thus contributing to forest regeneration and improving spatial heterogeneity [5,6]. When population outbreaks occur, tree mortality increases to the point that affected stands may be severely depleted [7–10]. Under certain triggering conditions, bark beetle populations erupt into epidemics that cause severe ecological upheaval. Widespread tree mortality leads to severe forest loss and substantial economic repercussions, impacting timber production and necessitating costly management interventions [11].

Over the past several decades, a variety of modeling approaches has been developed to understand the drivers and dynamics of bark beetle infestations [12,13]. These modeling approaches can be broadly grouped into two complementary categories. Detail-rich models [14], along with conceptual models that incorporate specific ecological mechanisms at varying levels of abstraction [15], successfully reproduce outbreak dynamics through explicit processes, providing detailed, system-specific representations and valuable insight into the ecological mechanisms underlying specific systems. However, they typically rely on system-specific structure and parameterization, limiting their generality and the identification of common dynamical mechanisms across systems. They are primarily explored through numerical simulations, with dynamical interpretations tied to specific model formulations rather than general analytical principles. In contrast, more minimal and analytically tractable models [16,17] provide general insights into system behavior, yet often focus on equilibrium properties and thus offer limited understanding of the full transient dynamics of outbreaks, including their initiation, evolution, decay, and recurrence. In many documented cases, however, large-scale epidemics do not arise solely from gradual, internal processes operating near equilibrium. Instead, they are often triggered by abrupt external shocks that rapidly alter system conditions. Prominent examples are windstorms, which caused extensive treefall and dramatically increased the availability of vulnerable hosts, leading to a surge in beetle attacks [18–20], and heat waves or drought events that can strongly affect host tree defences [21–23]. Such episodes underscore the fact that outbreaks frequently emerge as transient responses to perturbations, rather than arising naturally from long-term ecological balance, even though climate modification might lead to persistent disturbance regime regionally [24].

These observations highlight a gap in our understanding of the dynamical mechanisms underlying empirically observed outbreak patterns. While current models emphasize either mechanistic realism or analytical generality, a simple and ecologically plausible dynamical explanation of outbreak temporal patterns in terms of minimal and general dynamical mechanisms remains elusive, limiting our ability to interpret outbreak dynamics and inform mitigation strategies – especially as climate change increases the likelihood of disruptive environmental events [25–27]. Here, we address this gap by identifying reactivity—i.e., the transient amplification of environmental perturbations — as a minimal dynamical property governing the emergence of outbreaks, while abstracting from system-specific mechanisms. To this end, we develop a minimal dynamical model of bark beetle–tree interactions, using the *Ips typographus* (European spruce bark beetle, ESBB) –*Picea abies* system as a case study. Our goal is to explain the outbreak phenomenology of the ESBB through a simple mechanistic framework that captures key ecological processes, while remaining analytically tractable. Our analysis builds on two complementary perspectives: first, we investigate the stability of typical forest conditions and their reactivity — i.e., whether small perturbations are initially amplified or suppressed; second, we explore the emergence of regularly-recurrent outbreaks arising from ecological feedbacks.

4.2 Methods

4.2.1 Model

We develop a compartmental deterministic model to describe the temporal dynamics of ESBB populations and their interactions with Norway spruce trees within a sufficiently large forest patch, such that spatial heterogeneity and finite-size effects are neglected. The model tracks three state variables over time: the density of bark beetles, denoted by $x(t)$, and the densities of trees in two distinct physiological states, *healthy* $y(t)$ and *vulnerable* $z(t)$, the latter signifying immediate susceptibility to beetle attack. Vulnerable trees are intended as those with impaired defenses, typically due to aging, drought/pathogens stress, or mechanical damage (e.g. wind-throw). These individuals are highly susceptible to colonization even at low beetle densities and serve as the primary resource for reproduction. Such distinction is critical for capturing outbreak dynamics, as the presence and abundance of vulnerable hosts strongly influence the potential for beetle population growth and the onset of epidemic phases. The bark beetle population follows consumer–resource dynamics, with individuals dying at rate δ and reproducing at a rate βz , reflecting the dependence of successful reproduction on access to vulnerable host trees. In addition, beetles arrive via a constant immigration term λ , representing an influx of bark beetles from surrounding areas. In real ecosystems, bark beetles disperse through active flight, wind-assisted transport, or anthropogenic movement (e.g., infested wood), giving rise to an immigration pressure from neighboring populations. From a modeling perspective, this term reflects the assumption that the focal system is part of a larger, spatially connected landscape, and prevents unrealistic extinction due to transient local declines, ensuring beetle persistence even under temporarily unfavorable conditions. In the absence of bark beetles, the tree population follows logistic growth with rate η and a normalized carrying capacity set to 1. Healthy trees enter the vulnerable state at a baseline rate ϵ , representing the effects of aging or moderate environmental stress. Episodic shocks, such as major windstorms or heat waves, are not included as they will be treated as external perturbations (Section 4.3.1, Section 4.3.4). Vulnerable trees die and are removed from the system at rate ρ . The balance between ϵ and ρ serves as a proxy for forest condition: when trees shift more quickly into vulnerability (high ϵ) and are removed more slowly (low ρ), the ϵ/ρ ratio increases, indicating a more degraded or stressed ecosystem. We model bark beetle–host interactions by incorporating a density threshold mechanism that governs attacks on healthy trees. In the absence of an outbreak, healthy trees become vulnerable at the baseline rate ϵ , as described earlier. However, when the beetle density exceeds a critical threshold σ , coordinated mass attacks lead to an accelerated conversion of healthy trees into vulnerable ones at rate κx . Vulnerable trees, in turn, are depleted as part of the beetle reproductive cycle, with a removal rate $\gamma x z$ that reflects their role as the primary substrate for brood development. While beetle aggregation behavior is not explicitly modeled, its effects are implicitly incorporated into the definition of the threshold σ , consistent with our mean-field approach [28] as discussed in Appendix 4.B.1. The system can thus be described at the deterministic level by the following set of coupled differential equations:

$$\begin{cases} \dot{x} = \lambda + x(\beta z - \delta) \\ \dot{y} = -F(x, y) + \eta(y + z)(1 - y - z) \\ \dot{z} = F(x, y) - \rho z - \gamma x z \end{cases} \quad (4.2.1)$$

where the function $F(x, y) = \epsilon y + \kappa \Theta(x - \sigma)xy$ represents the conversion rate from healthy to vulnerable trees, comprising both *background* and *outbreak-induced* conversion from healthy to vulnerable trees, the latter being represented through the Heaviside step function $\Theta(x - \sigma)$. A schematic representation of the model compartments and transitions is presented in Figure 4.1.

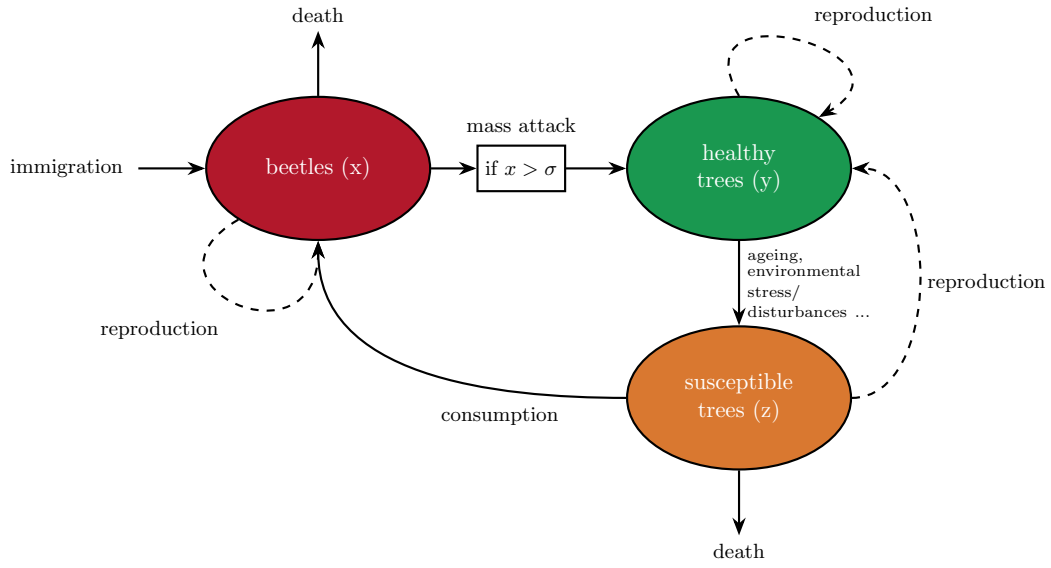


FIG. 4.1. Schematic representation of the compartmental model describing interactions between spruce bark beetles (ESBB) and host trees. Solid arrows represent transitions between states: immigration and mortality for beetles (x), transitions from healthy (y) to susceptible (z) trees due to aging or stress, ESBB-induced mass attacks above a density threshold σ , and mortality of susceptible trees. The reproductive role of each compartment is shown with dashed arrows. Vulnerable trees serve as the primary resource for beetle reproduction and are depleted through consumption.

The detailed derivation of Eq. (4.2.1) from minimal ecological key processes is described in Appendix 4.A.

While the model is simple, capturing only the essential features of bark beetle–host interactions, its core ingredients are sufficient to reproduce key nonlinearities and feedback loops that characterize bark beetle–host dynamics. This balance enables rich ecological phenomenology while retaining analytical tractability. Moreover, the model is flexible, as parameters can be adapted to reflect different forest health conditions or climate scenarios.

4.2.2 Parameter assumptions and estimation

We adopt a set of simplifying assumptions that specify how beetle and tree processes are represented. These abstractions are coarse but crucial for tractability. In particular, although bark beetles reproduce in discrete generations and are largely inactive during winter, we model processes by averaging seasonal dynamics over the year. Since reproduction depends on ovipositing females, we track only the adult female population. Accordingly, we model recruitment as half of the total brood size, assuming a 1:1 sex ratio, while juvenile stages are not explicitly represented. Trees smaller than the minimum size required for successful attack by ESBB are not explicitly tracked. Tree population growth is modeled with a logistic function, reproducing both host replenishment and stand saturation. Mass attacks on healthy trees require a critical number $\tilde{\sigma}$ of insects per tree. ESBB are known to aggregate via pheromone chemical signaling over a finite spatial range. As a result, each tree is exposed to ESBB within its neighborhood, and we accordingly assume that mass attacks are triggered when the number of insects within this aggregation area exceeds $\tilde{\sigma}$. While the threshold σ captures the resistance limit of trees, the colonization rate κ describes how efficiently

Parameter	Description	Reference value	Variability range
L^2	Area of the forest patch	1 ha	fixed
M	Maximum number of trees per patch	500	300 – 700
ρ	Death rate of vulnerable trees	0.001 day^{-1}	$[6 \cdot 10^{-4}, 5 \cdot 10^{-3}] \text{ day}^{-1}$
ϵ	Conversion rate (healthy $\rightarrow$ vulnerable)	$1 \cdot 10^{-5} \text{ day}^{-1}$	$[7 \cdot 10^{-6}, 3 \cdot 10^{-5}] \text{ day}^{-1}$
η	Birth rate of healthy trees	$1.3 \cdot 10^{-2} \text{ day}^{-1}$	$[4 \cdot 10^{-3}, 3 \cdot 10^{-2}] \text{ day}^{-1}$
δ	Death rate of ESBB	0.5 day^{-1}	$[0.3, 1.0] \text{ day}^{-1}$
n	Number of insects per brood (females)	25	20 – 30
β	Reproduction rate of ESBB	18 day^{-1}	$[5, 40] \text{ day}^{-1}$
γ	Tree death rate due to beetles	0.4 day^{-1}	$[0.1, 0.7] \text{ day}^{-1}$
σ	ESBB density threshold for mass attack	10	3 – 85
κ	Colonization rate of healthy trees	Free	–
λ	ESBB immigration rate	Free	–

TAB. 4.1. Reference values and variability ranges for the model’s parameters, representative of generic present-day environmental conditions. We estimate reference values for the model’s parameters based on available ecological and entomological literature [4, 29–34]. These estimates reflect current typical conditions in managed European spruce forests, while also accounting for known sources of variability, derived from ecological heterogeneity or uncertainty in empirical measurements. Where precise data are lacking, we use informed assumptions to define plausible orders of magnitude or leave parameters free for exploration. All details on parameter meaning and estimation are provided in Appendix 4.B, together with the references to the literature.

insects exploit that vulnerability under outbreak conditions. Since no direct empirical estimates are available, κ is treated as a free parameter in our scenario analysis.

Based on these assumptions, we estimate order-of-magnitude values for all parameters from the ecological and entomological literature. These values are not tuned to any specific local ecosystem but are intended to reflect typical conditions of Norway spruce forests in Europe. This level of approximation is sufficient to investigate the model’s qualitative dynamics, such as the emergence of equilibria or recurrent outbreaks. However, more precise estimates—tailored to specific ecosystems—would be required for reliable quantitative predictions (e.g. outbreak duration or magnitude). Table 4.1 summarizes the adopted reference values and plausible variability ranges. The latter reflect both ecological heterogeneity (e.g., altitude, forest density) and measurement uncertainty, and they define what we refer to as the ecologically plausible region of parameter space. Further details on parameter estimation are provided in Appendix 4.B. While the values presented here provide a consistent reference framework for analyzing the model’s behavior, they can readily be adjusted to reflect different ecological or forest structural conditions.

4.2.3 Equilibria

The first step in analyzing dynamical models is to identify their stable equilibria — population levels at which ESBB and trees remain approximately constant over time. Ecologically, these represent long-term configurations of population stability, without rapid growth or collapse, maintained by a balance among interacting biological processes. These states are stable, meaning that if an environmental disturbance briefly perturbs the system, populations will eventually return to their

previous levels.

The following theoretical classification outlines the types of steady states that the system can, in principle, sustain under different climatic scenarios, based on the identification of fixed points and the analysis of their linear stability (Appendix 4.C). Depending on parameter values, the model admits qualitatively distinct equilibria:

- (i) The *trivial equilibrium* describes a forest in which healthy and vulnerable trees are absent, and the ESBB population persists only through external immigration. Without suitable hosts, beetles cannot reproduce, and in the absence of immigration ($\lambda = 0$) they decline to extinction. This state is ecologically meaningless, as neither trees nor a self-sustaining beetle population can persist.
- (ii) The *endemic equilibrium* is a state where both trees and ESBB persist, but beetle density remains too low to trigger mass attacks on healthy trees, representing a forest that is not inherently prone to outbreaks. The existence of this stable state requires immigration ($\lambda > 0$): without it, beetles would go extinct, yet even minimal influx is sufficient to maintain a low-density population.
- (iii) The *epidemic equilibrium* is characterised by an ESBB abundance high enough to mount mass attacks on healthy trees. In this state, the ESBB remains permanently above the mass-attack threshold, corresponding to an indefinitely sustained outbreak.
- (iv) Lastly, *out-of-equilibrium regimes* occur under climatic conditions where no stable equilibrium exists. In this case, ESBB and tree populations fluctuate persistently, with outbreak and forest recovery phases that never settle into a steady state.

Although identifying stable equilibria provides insight into the long-term baseline behavior of the ecosystem, it is not sufficient to capture outbreak dynamics. Within this equilibrium framework, the system can only display three idealized behaviors: a complete absence of outbreaks (endemic state), a permanently sustained outbreak (epidemic state), or endless collapse and recovery (out-of-equilibrium regime). None of these configurations reflects the typical forest dynamics observed in reality, where outbreaks are transient events triggered by environmental disturbances. To address this limitation, we extend the analysis to dynamical properties beyond equilibrium stability and we examine *reactivity*, which quantifies the system’s short-term response to perturbations.

4.2.4 Reactivity

To characterize outbreak dynamics beyond long-term equilibria, we analyze the system’s reactivity [35], which quantifies the short-term response of a system in a stable equilibrium state, when it is perturbed e.g. by environmental disturbances. Unlike classical equilibrium stability analysis, which assesses only whether small perturbations eventually decay, reactivity captures whether they temporarily grow before decaying. This transient amplification leads to short-lived outbreaks, even though the system ultimately returns to equilibrium.

Mathematically, reactivity is assessed via the symmetric part of the Jacobian matrix $\mathbb{J}$ evaluated at the equilibrium:

$$\mathbb{J}_{\text{symm}} = \frac{1}{2} (\mathbb{J} + \mathbb{J}^T), \quad (4.2.2)$$

Letting $\lambda_1, \lambda_2, \lambda_3$ be the eigenvalues of $\mathbb{J}_{\text{symm}}$, we define reactivity as:

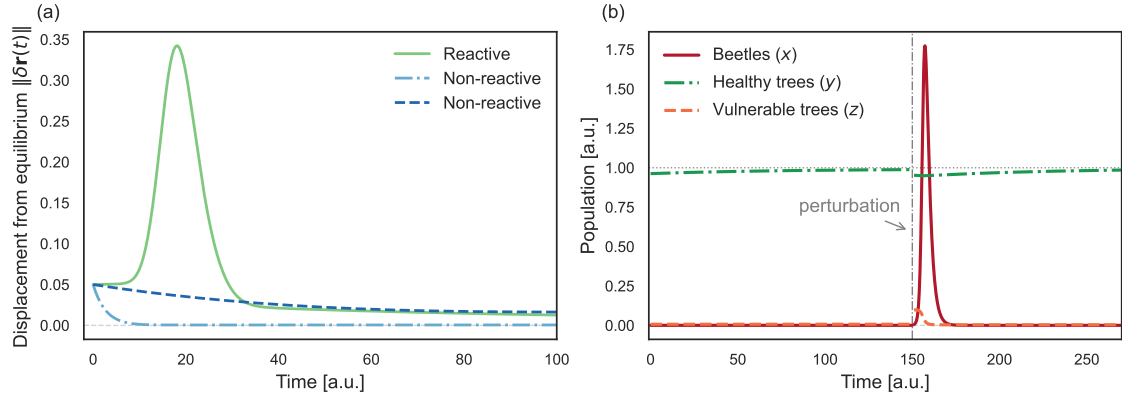


FIG. 4.2. Reactive dynamics in the ESBB model. (a) System response to small perturbations applied at $t = 0$ along different directions defined by the eigenvectors of the symmetrized Jacobian at equilibrium. A perturbation along the most reactive direction (green) causes transient amplification of the distance from equilibrium before decay — characteristic of a reactive system. In contrast, a perturbation along non-reactive directions (blue) decays monotonically. (b) Time evolution of the full system. After reaching equilibrium, a small perturbation is applied at $t = 20$ along a direction close to $\mathbf{v}_1$ ($\varepsilon = 0.1$, $\delta \mathbf{r}(t) \cdot \mathbf{v}_1 \sim 0.89$). This causes a sharp, temporary increase in beetle population (red), before the system returns to equilibrium. Healthy trees (green) decline slightly, while vulnerable trees (orange) show a brief increase. The system's strong transient response reflects its reactivity. All quantities are given in arbitrary units (a.u.). The dashed horizontal line in panel (b) marks $y = 1$, as a visual guide to the carrying capacity condition $y + z = 1$ when $z \ll 1$.

$$R = \max\{\lambda_1, \lambda_2, \lambda_3\} \quad (4.2.3)$$

The system is reactive if $R > 0$, meaning disturbances temporarily grow before decaying, causing an outbreak; otherwise ($R < 0$) it is non-reactive and perturbations decay monotonically. Importantly, when positive, R provides an intrinsic measure of outbreak propensity: the larger its value, the stronger the amplification of a given environmental disturbance, leading to more intense transient outbreaks.

4.3 Results

Our analysis builds on two complementary dynamical aspects introduced earlier: (i) reactivity, which characterizes the system's transient response to small perturbations near equilibrium, and (ii) intrinsic regularly recurring outbreaks emerging from nonlinear ecological interactions.

4.3.1 Transient outbreaks triggered by disturbances

We assess the reactivity of the endemic equilibrium state, representing the most ecologically plausible scenario under typical conditions (Table 4.1) for managed European spruce forests. This equilibrium is consistent with observations from undisturbed stands where beetles persist at low-densities, insufficient to trigger mass attacks. Despite the structural stability of the endemic equilibrium, outbreaks commonly occur in real forests. This apparent contradiction is explained by the reactivity of the endemic equilibrium under realistic conditions. As explained in Section 4.2.4, a positive eigenvalue of the symmetrized Jacobian $\mathbb{J}_{\text{symm}}$ indicates reactivity, i.e. small perturbations of the equilibrium state of the forest ecosystem initially grow, before eventually decaying. In

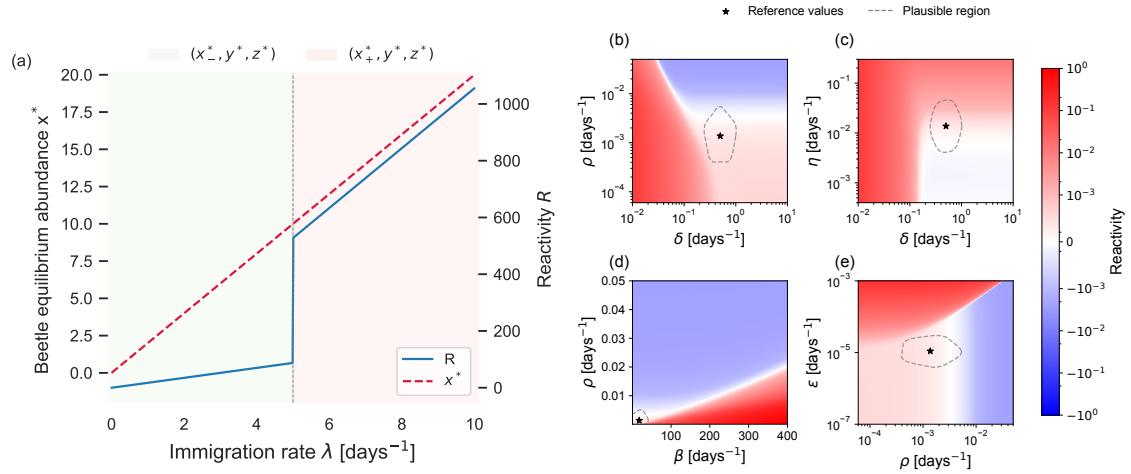


FIG. 4.3. (left) Reactivity and beetle equilibrium abundance as a function of the immigration rate parameter λ . As λ increases, the beetle equilibrium abundance grows linearly. When x^* crosses the mass attack threshold $\sigma = 10$, the system transitions from a regime characterized by the stable endemic equilibrium (x^*, y^*, z^*) to a regime where the above-threshold fixed point (x_+, y^*, z^*) becomes stable. Both regimes are reactive and display a linear increase of reactivity with λ , indicating growing sensitivity to perturbations at higher immigration rates. Notably, at the critical immigration rate ($\lambda = 5$), reactivity undergoes a discontinuous jump in value, accompanied by a sharp change in slope, reflecting a fundamental shift in system dynamics upon crossing the outbreak threshold. The remaining parameters are kept fixed at the values reported in Table 4.1. **(right) Reactivity landscape.** Reactivity over a region of parameter space centered on the reference values given in Table 4.1. The star marks the reference parameter set, at which the reactivity is $R \approx 0.002$. As one moves into the ecologically plausible regime surrounding the reference point, which represents approximate but realistic ranges for model parameters, the system becomes consistently reactive. Thus, despite uncertainties in precise parameter values, the system is generally expected to exhibit reactive dynamics under realistic ecological conditions, suggesting inherent susceptibility to transient outbreaks following perturbations.

contrast, if all eigenvalues are negative, the equilibrium is non-reactive, and all perturbations decay monotonically.

As shown in Figure 4.2(a), the most reactive perturbation (along the eigenvector of the positive eigenvalue) leads to a transient spike away from equilibrium, whereas the two non-reactive ones (related to negative eigenvalues) yield monotonic relaxation. The structure of the eigenvectors (Appendix 4.D) reveals that this transient growth is primarily driven by changes in the susceptible tree population. In contrast, perturbations along non-reactive eigenvectors are dominated by changes in healthy trees or beetles alone, and do not produce significant transient growth. This suggests that reactivity in the ESBB model is mainly driven by perturbations that abruptly increase the abundance of vulnerable trees, such as extreme windstorms or heat waves. To illustrate reactive behavior, Figure 4.2(b) shows population trajectories following a perturbation strongly aligned with the reactive eigenvector. The ESBB population exhibits a sharp but temporary increase before returning to equilibrium, capturing the hallmark of a transient outbreak. The duration of the outbreak and the height of the ESBB peak depend on two factors: first, the reactivity index R , which reflects the background environmental conditions within the typical parameter range (Table 4.1); second, the strength of the perturbation, representing the environmental shock.

We emphasize that, although the ESBB population may temporarily exceed the mass-attack threshold

during the transient growth phase, this increase is short-lived because the conditions required to sustain epidemic activity are not met, and the system eventually relaxes back to the sub-threshold endemic state. If epidemic conditions were fulfilled, by contrast, the system would settle into an epidemic equilibrium, where ESBB abundance would remain permanently above the mass-attack threshold, corresponding to a persistent outbreak state. Figure 4.3(left) shows that reactivity exhibits a dramatic, discontinuous jump as the system transitions from the endemic to the epidemic equilibrium, and reveals a link between equilibrium beetle density and outbreak propensity.

4.3.2 Phenomenology of dynamical behaviors across ecological conditions

We use *phase diagrams* to explore how ecological parameters shape ecosystem dynamics. These diagrams show which equilibria arise under different conditions, capturing long-term system behavior. Complementarily, we map the reactivity of each equilibrium to assess short-term sensitivity to perturbations. Here, two parameters are varied along the axes, while color coding indicates equilibrium type, providing a compact view of how ecological conditions can shift the system from endemic stability to more outbreak-prone or unstable regimes.

Figure 4.4(a) illustrates the model's dynamical richness when parameters are broadly varied beyond ecologically grounded values reflecting current forest conditions (Table 4.1). Figure 4.4(c) shows representative time trajectories illustrating the range of possible behaviors under different parameter combinations. These trajectories are not intended to reproduce realistic time series for specific ecosystems, nor to predict the exact timing, duration, or magnitude of real outbreaks. Rather, they illustrate possible outcomes under different ecological scenarios, represented here by varying the underlying parameters. We observe: (i) monostable regimes (green, blue, and red) where populations approach unique equilibria, potentially after transient oscillations; (ii) bistable regimes (yellow and violet) where the attained state sensitively depends on initial conditions, resulting in alternative stable attractors; and (iii) regions lacking stable equilibria (grey), where populations exhibit regularly recurrent, self-sustained outbreaks. The latter regime is examined in depth in Section 4.3.3. Importantly, in highly reactive endemic equilibria with complex eigenvalues (as in the blue panel), oscillations that cross the mass-attack threshold σ can trap the system in recurrent outbreak dynamics, even though the equilibrium is formally stable.

Figure 4.4(b) focuses on ecologically plausible parameter ranges for managed European spruce forests (Table 4.1). Within this region, the system robustly settles into a reactive endemic equilibrium (with non-complex eigenvalues), discussed in Section 4.3.1. Notably, the endemic equilibrium remains robust across a broad parameter region, suggesting resilience beyond finely tuned ecological conditions.

The right panel of Figure 4.3 illustrates the dependence of reactivity on ecological parameters. Outside realistic parameter ranges (Table 4.1), the endemic equilibrium is typically non-reactive (blue), meaning disturbances decay directly without causing outbreaks. Within ecologically grounded values, the system becomes consistently reactive (red), indicating high sensitivity to small shocks that result in outbreaks. As expected, reactivity increases with longer adult beetle flight period δ (panels a-b) or higher ESBB reproductive rate β (panel c), while faster removal of vulnerable trees (higher ρ in panels c-d) reduces it. An elevated tree susceptibility ϵ also raises reactivity (panel d), linking increased environmental stress to higher transient outbreak risk. Additional reactivity maps for other parameter pairs are shown in Figure 4.7.

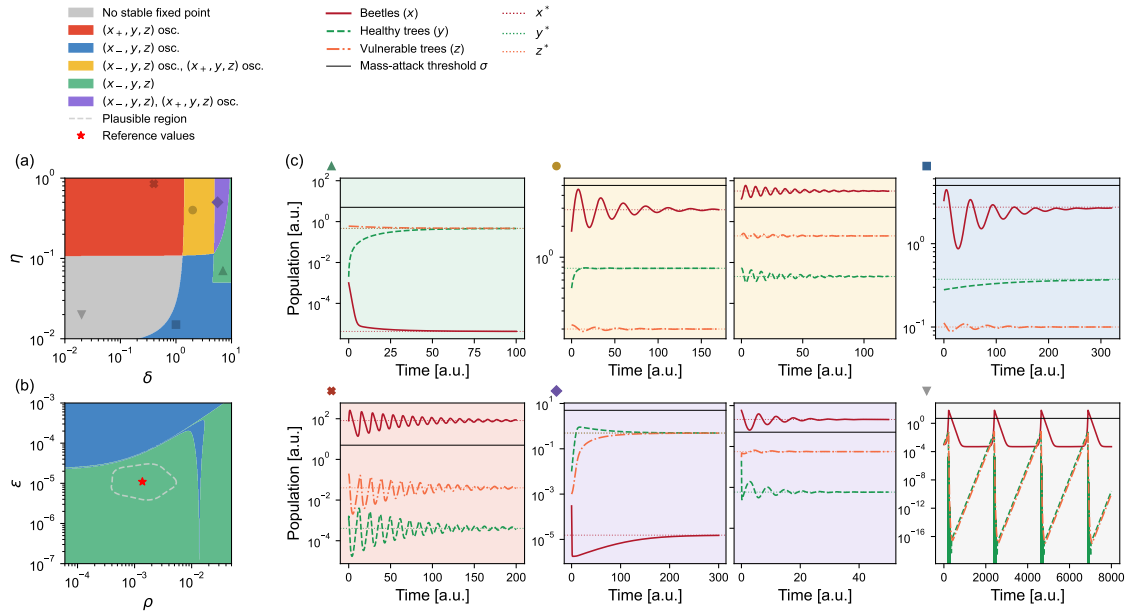


FIG. 4.4. Phenomenology of the model. (a) Phase diagram computed over a wide, arbitrary parameter range to illustrate the diversity of possible dynamical behaviors supported by the model, including stable coexistence, oscillations, and instability. These values are not ecologically grounded but demonstrate the system’s inherent dynamical richness. Parameters ϵ and κ are varied, while all others are held fixed at the values reported in Appendix 4.H. (b) Phase diagram restricted to broad parameter ranges centered around the ecologically grounded reference values reported in Table 4.1. The highlighted region approximately denotes an plausible ecological regime, representative of managed European spruce forests. Even well beyond this region, the system consistently converges to a stable endemic equilibrium characterized by sub-threshold beetle densities. (c) Trajectories of beetle, healthy, and vulnerable tree populations for parameter values sampled from distinct regions of the phase diagram in Figure 4.4(a), where the corresponding points are marked with diamond symbols. Each panel corresponds to a qualitatively different dynamical regime, that is not intended as a realistic scenario, but rather as a qualitative exploration of the different possible behaviors of the system over time. In bistable regions (yellow and violet), the system can converge to different stable fixed points depending on the initial conditions. Notably, in regions where no stable fixed point exists (grey phase), we consistently observe sustained oscillations, indicative of limit cycles, which will be analyzed in detail in Section 4.3.3. The labels x^* , y^* , z^* indicate the equilibrium values for ESBB, healthy and vulnerable tree populations, respectively. We remark that population abundances and timescales are given in arbitrary units (a.u.).

4.3.3 Recurrent outbreak dynamics

As noted in Section 4.2.3, for some parameter choices outside the reference range representing current environmental conditions, the model does not admit any stable equilibrium. In such cases, there are in principle three possibilities: populations may diverge, fluctuate chaotically, or oscillate regularly. In our model, we observe only the latter. Such oscillations are known as *limit cycles* in dynamical systems theory, but for simplicity we refer to them here as recurrent outbreaks. Interestingly, such regularly-recurring outbreaks also emerge in parameter regions where a stable equilibrium exists but is effectively inaccessible due to extreme reactivity: even minimal increases in the number of susceptible trees can push the system away from equilibrium and trigger recurrent outbreaks (Figure 4.5(a)).

Recurrent outbreak dynamics arise intrinsically from internal ecological feedbacks and interactions.

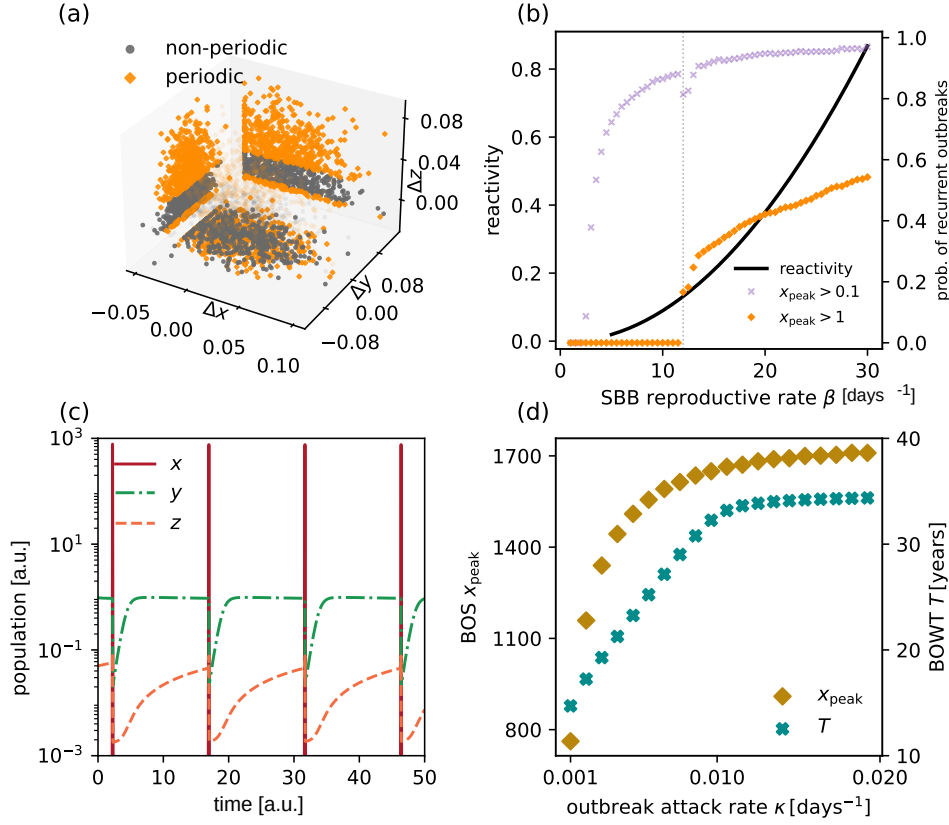


FIG. 4.5. Emergence of recurrent outbreaks with increasing reactivity. (a) For a fixed set of parameters, we perturb equilibrium with a Gaussian vector. We project the ensemble of 10^4 sampled perturbations, $(\Delta x, \Delta y, \Delta z)$, on the coordinate planes. (b) Varying β causes reactivity of the endemic equilibrium to grow continuously (solid line). Instead, the probability of observing recurrent outbreaks ($x_{\text{peak}} > x_{\text{thr}}$ with $x_{\text{thr}} \approx 1$) increases sharply at $\beta \approx 12$ (dotted vertical line), indicating a new dynamical phase. Detecting recurrent dynamics with a smaller threshold ($x_{\text{peak}} > x_{\text{thr}} = 0.1$) gives qualitatively consistent results over a broad range of values for the threshold, while also counting small decaying oscillations. As in panel (a), outbreak probability has been computed by sampling initial conditions for Eq. (4.2.1) from a Gaussian neighborhood of the stable equilibrium value and automatically detecting recurrent outbreak dynamics. (c) Population dynamics for ESBB x , healthy trees y and susceptible trees z (densities). The peaks of ESBB population $x(t)$ define the baseline outbreak size (BOS), while their temporal spacing defines the baseline outbreak waiting time (BOWT). Population abundances and timescales are given in arbitrary units (a.u.). (d) Outbreaks observables: baseline outbreak size x_{peak} and baseline outbreak waiting time T for different values of κ . Note that the period and intensity of outbreaks are sensitive to parameter choices; since ecological parameters are not precisely constrained, these results should be interpreted as a phenomenological investigation of the model's dynamical behavior rather than quantitative predictions of BOS and BOWT. Full parameter values and numerical details are reported in Appendix 4.H.

In the time interval between outbreaks, the ESBB population remains close to zero, and healthy and susceptible trees tend towards a steady balance. As susceptible trees accumulate, the insect population starts growing exponentially, even from very low densities, provided it is not exactly zero. Once they exceed the density threshold σ , insects begin attacking healthy trees, which further accelerates their growth. As host trees are quickly depleted, insect population soon recedes to endemic levels, allowing the forest stand to recover through tree regrowth and the cycle to begin again (Figure 4.5(c)).

To study the recurrent outbreak regime, we select parameter values that lie outside the ecologically plausible range representing current forest conditions (Table 4.1), but still preserve a realistic balance between ecological rates. This parameter region is not intended to reflect present-day dynamics, but rather a potential future state of the system under increased ecological stress — for example due to climate change or other long-term disturbances. In particular, we increase the ϵ/ρ ratio with respect to the current reference condition (Table 4.1), implying that trees remain vulnerable for longer on average, thereby reflecting increased forest stress. More details are available in Appendix 4.E.

We characterize recurrent outbreaks using two key observables: the maximum population size during an outbreak (*baseline outbreak size* BOS), and the period between successive outbreaks (*baseline outbreak waiting time* BOWT). These observables allow us to investigate how outbreak intensity and frequency respond to changes in ecological parameters.

As shown in Figure 4.5b, boom-and-bust dynamics become more likely as reactivity increases — for instance when the ESBB reproduction rate β is higher. Another key parameter is the attack efficiency on healthy trees, κ , which remains unconstrained by available data. We find that both BOS and BOWT increase with κ up to a saturation point (Figure 4.5(d)). However, recurrent outbreaks are sustained only within an intermediate range of κ values: if κ is too low, beetles can’t attack healthy hosts; if too high, host trees are depleted during the first outbreak, preventing long-term persistence of the insect population. Despite the uncertainty in its estimation, recurrent outbreaks emerge robustly across a broad range of κ values, highlighting the intrinsic capacity of the system to generate recurrent outbreaks through internal ecological feedbacks alone.

4.3.4 Repeated environmental disturbances

We investigate repeated disturbances under the recurrent outbreak regime, which we adopt as a plausible climate-change scenario where forests become intrinsically more vulnerable to pest outbreaks. In addition, we include extrinsic disturbance events — such as heat waves, droughts and windstorms [36] — modeled as sequences of shocks that temporarily increase forest susceptibility to ESBB attacks. While Section 4.3.1 focused on the endemic state, which reflects current conditions, and examined the effect of a single isolated disturbance, the analysis here reflects a stylized scenario of increased forest vulnerability, which may be qualitatively consistent with some expected effects of climate change. In this setting, environmental shocks are no longer isolated events, but occur more frequently. Each disturbance converts a fraction of healthy trees into susceptible trees, representing the weakening of host defenses. In practice, disturbances are numerically implemented as instantaneous state updates at discrete times (Dirac-delta perturbations), $z \rightarrow z + \Delta z$, $y \rightarrow y - \Delta z$, with continuous evolution governed by Eq. (4.2.1) between events. Importantly, we do not model isolated shocks, but a repeated sequence of disturbances over time, mimicking the recurrent stress episodes that forests may experience under changing environmental conditions. Disturbances occur at random intervals of time and with varying intensity, allowing us to explore a broad range of environmental scenarios. Higher frequency represents increasingly unstable climate conditions, while greater severity corresponds to more intense stress events, such as severe droughts. The effect of these disturbances is to modify the otherwise regular dynamics of recurrent outbreaks by introducing variability in both their timing (BOWT) and size (BOS). As shown in Figure 4.6a-f, more frequent or severe disturbances lead to smaller but more frequent outbreaks, although rare large outbreaks still occur. Mathematical details of the disturbance implementation are provided in Appendix 4.F.

4.3.5 Management strategies

We adopt the recurrent outbreak regime as a future scenario to investigate how forest management strategies might mitigate outbreak dynamics. In this context, we represent management as discrete removal events that reduce the density of susceptible trees at regular intervals — an idealized approximation of management practices aimed at lowering stand vulnerability. Although forest operations typically remove both vulnerable and healthy trees, in the model only susceptible trees are removed. This simplification is justified because our analysis shows that system reactivity — and thus outbreak response — depends almost exclusively on the density of susceptible hosts. As a result, selective removal in the model effectively reproduces the ecological outcome of unselective thinning, while allowing a more transparent mechanistic interpretation.

Specifically, we model management as the removal of a fixed fraction Δ_m of susceptible trees every τ_m time units, as detailed in Appendix 4.G. As for disturbances, these interventions are numerically implemented as instantaneous updates of the system state, with the system evolving according to Eq. (4.2.1) between successive events. We then explore how the frequency and intensity of removal influence outbreak dynamics. If interventions are too frequent, each action removes only a very small fraction of vulnerable trees, making it ineffective unless the removal rate is unrealistically high. Conversely, if interventions are too rare, the ESBB population may already reach outbreak levels before the next removal event takes place. Crucially, we find that outbreaks can be reliably suppressed when management intervals are tuned to be slightly longer than the system’s natural recurrence timescale (Figure 4.6).

4.4 Discussion and conclusions

Bark beetles such as *Ips typographus* play a key role in forest ecosystems, by removing vulnerable trees and accelerating decomposition processes, thereby enhancing the overall heterogeneity [37, 38]. However, under certain conditions, their activity can shift from background ecological function to large-scale disturbances, leading to widespread tree mortality.

Mechanistic descriptions of beetle–forest interactions [16, 17] have so far been restricted to static endemic or epidemic states, thus neglecting the dynamical nature of outbreaks triggered by ecological perturbations. In contrast, process-based, detail-rich models (e.g. [33, 36, 39, 40]) have examined outbreak drivers in depth, but often at the expense of analytical tractability. By reducing the system to its essential components, minimal models clarify the conditions under which forests shift between stability, outbreaks, or collapse. Rather than replicating site-specific details, such models highlight general principles, offering insights that complement more detailed approaches and serving as a foundation for ecological theory and the anticipation of future outcomes. Yet a comprehensive understanding of beetle–forest outbreaks as dynamical events within a mechanistic framework is still lacking.

In this study we address these limitations by adopting a dynamical systems perspective, treating outbreaks as transient phenomena driven by ecological feedbacks. Our minimal mechanistic model of beetle–host interactions captures how isolated or regularly-recurring outbreaks can emerge from the interplay of ecological rates such as reproduction, mortality, and host susceptibility. It is important to clarify the interpretative scope of our results. We do not aim to precisely reproduce the exact timing or amplitude of observed outbreaks in a given forest, which would require detailed empirical data and site-specific calibration. Rather, our goal is to identify general dynamical regimes that forest systems may enter under different environmental conditions, represented by varying

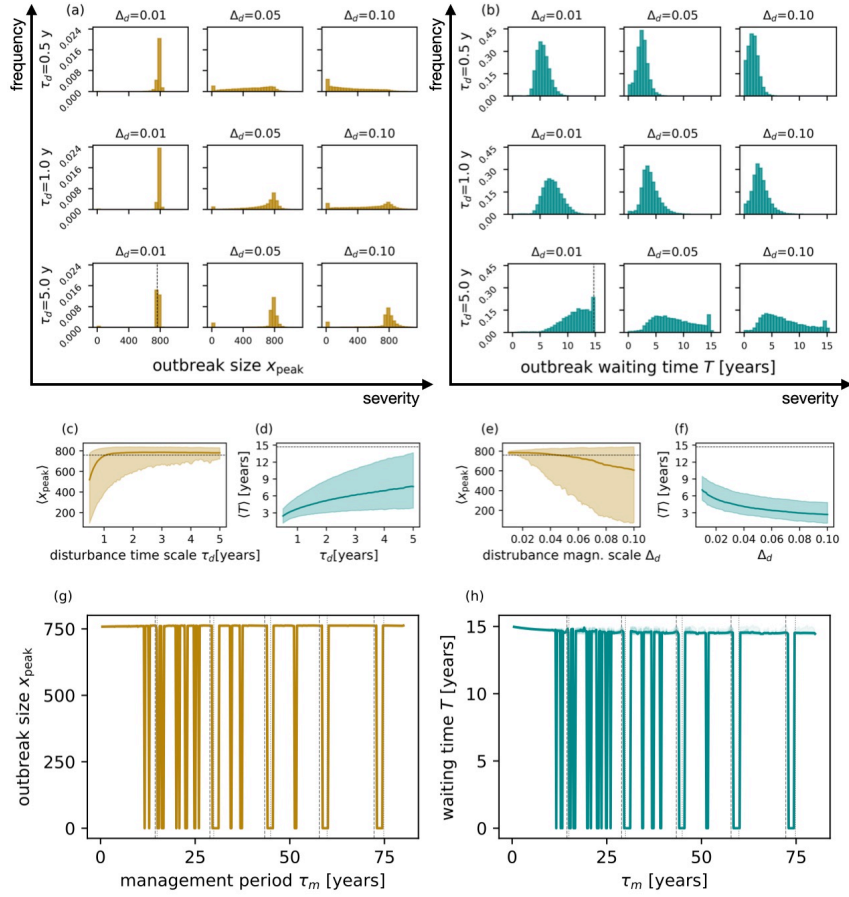


FIG. 4.6. Outbreaks' size and waiting times change under different disturbance and management regimes. (Top) Empirical distribution of outbreak size x_{peak} and waiting time T for different disturbance parameters τ_d and Δ_d , defining the scales of the exponential distributions of the random size and time of the disturbances. (a-b) Distributions of outbreak size x_{peak} (a) and waiting time T (b) for different choices of perturbation time scale τ_d and magnitude scale Δ_d . (c-e) Mode (solid line) and 10-90 quantiles (envelope) for x_{peak} and T , for fixed $\Delta_d = 0.05$ and different values of τ_d (c-d), and for fixed $\tau_d = 1$ year and different values of Δ_d (e-f). All dashed lines represent BOS and BOWT of the corresponding unperturbed dynamics. (Bottom) Outbreak size x_{peak} (g) and waiting time T (h) as functions of the management periodicity τ_m , in a regime of mild disturbances for which $\langle x_{\text{peak}} \rangle \approx 750$ and $\langle T \rangle \approx 14.97$ without management; in the presence of management, when outbreaks are not avoided, their mean waiting time decreases significantly, with $\langle T' \rangle \approx 14.45$ at $\tau_m = 80$. Only $x_{\text{peak}} > \sigma$ have been counted, with $T = 0$ corresponding to absence of outbreaks. Solid lines are means and envelopes are 10-90 and 20-80 quantiles. Dashed and dotted vertical lines mark values of τ_m which are integer multiples of $\langle T' \rangle$ and $\langle T \rangle$, respectively; we note that the former values consistently signal effective management timing. Results are obtained with interdependent Δ_m and τ_m , $\Delta_m = \frac{\hat{\Delta} \tau_m}{\tau_0 + \tau_m}$. Statistics are accumulated over 1000 realizations for each value of τ_m . Timescales and peaks are given in arbitrary units (a.u.). Further details are reported in Appendix 4.H.

ecological parameters.

Under current ecological conditions, parameterized using empirically grounded values from spruce–beetle ecology, our model predicts a reactive endemic equilibrium: the bark beetle population remains at low levels, but perturbations can trigger transient outbreaks before the system eventually returns to equilibrium. This behavior is consistent with the available literature, which indicates a low population density during endemic phases and high density and tree mortality

during the outbreak phases [4, 41]. Outbreak propensity, captured by the reactivity index, quantifies how strongly a system amplifies small perturbations. Outbreak intensity varies with background environmental conditions and with the strength of the triggering shock. Notably, changes in the abundance of susceptible trees emerge as the primary driver of reactive dynamics. Again, our model captures the effect of the most common triggering factors, such as windstorms and heat waves, which suddenly increase the amount of vulnerable trees [42, 43], facilitating the beetle reproduction and thus sustaining the build-up of the epidemic phase.

We next investigate the model's predictions when ecological parameters are shifted from present-day conditions to represent increased and sustained forest vulnerability — for instance, under extended droughts or other climate-driven stressors. In the model, this corresponds to increasing the average time that trees remain in the vulnerable state. Under such conditions, the system becomes more reactive and transitions into a new regime dominated by regularly recurring outbreaks. In this regime, the endemic equilibrium becomes either inaccessible or unstable, and the system exhibits recurrent boom-and-bust dynamics, which arise dynamically from the underlying feedbacks among beetle population growth, host depletion, and forest recovery. Altogether, our findings suggest that forest systems under persistent stress might become increasingly prone to self-sustained outbreak dynamics, a scenario consistent with projected impacts of climate change, foreseeing expected increases in both frequency and magnitude of extreme events [10]. Secondary spruce forests, often under suboptimal climatic conditions, have been suggested to be unsustainable in the long term due to climate warming [24].

We adopt the recurrent outbreak regime as a future scenario to investigate how external environmental shocks and management might affect or mitigate outbreak dynamics. Environmental disturbances are modeled as the conversion of a random fraction of healthy trees into susceptible ones at randomly occurring times, representing punctuated events such as storms and droughts. More frequent and intense disturbances lead to smaller but more frequent ESBB outbreaks, consistent with empirical observations of increased beetle activity during epidemic phases [44] and with evidence that repeated stressors increase forest susceptibility [26, 38]. This pattern aligns with recent recurrent outbreaks driven by rising temperatures and drought, which enhance the conversion of healthy trees into susceptible ones. In Central Europe, the combination of recurrent extreme events has increased overall forest vulnerability, leading to a prolonged, continental-scale outbreak [20, 45]. Overall, this analysis highlights the effect of the interplay between external repeated environmental stressors and internal forest dynamics.

Scheduled forest maintenance is modeled as the discrete removal of a fixed fraction of trees at regular intervals of time. Our results indicate that, in the model-predicted regime of recurrent outbreaks under increased ecological stress, management effectiveness depends not only on the removal intensity but also on timing: outbreaks can be reliably suppressed when the management removal frequency matches the system's natural recurrence timescale. Moderately intensive but well-timed management can thus outperform frequent, low-intensity interventions. This timing sensitivity, rooted in the model's dynamical nature, captures the interplay between internal ecological feedbacks and external interventions. Our insights complement findings from more detailed models [46], providing a mechanistic understanding of forest–management interactions and emphasizing the importance of timing-aware strategies.

Future steps include calibrating and testing the model against empirical outbreak data to infer site-specific parameters and improve predictive accuracy. Such applications require long-term data, which are not yet widely available but are increasingly being collected (D. Nardi, pers. comm.).

Moreover, the framework could be extended by incorporating spatial structure — for example, through explicit modeling of beetle movement and forest heterogeneity — to investigate outbreak propagation and the effectiveness of spatially targeted interventions. Integrating spatial dynamics would enable the exploitation of geophysical and remote-sensing data, and help to predict spatial patterns of ESBB outbreaks under different environmental scenarios [47–49]. This could support the design of spatially targeted management strategies, such as optimizing trap tree deployment, evaluating passive management strategies, or exploring how mixed-species stands mitigate outbreak severity under changing disturbance regimes [50, 51].

Appendix

4.A From individual-level processes to system-level rates

We define the model parameters starting from a set of basic ecological processes, represented as effective reactions between individual agents. These include tree recruitment, natural weakening and death, as well as beetle-driven attacks and reproduction. The individual-level processes are listed in Table 4.2, where B denotes a reproductive female beetle, T a healthy tree (not susceptible to colonization under endemic conditions), and W a vulnerable tree. The W compartment includes structurally compromised or fallen individuals typically attacked during endemic phases, as well as trees that have undergone mass beetle attacks and become vulnerable to colonization. The symbols $\emptyset$ and 0 represent, respectively, an unoccupied vegetation site and an empty site in the beetle compartment.

We assume a finite carrying capacity for the tree population, such that $n_T + n_W + n_\emptyset = M$, where M is the maximum number of tree sites in the forest patch. In contrast, we do not impose a saturation limit on the beetle population.

Our model assumes a well-mixed forest patch, i.e. individuals are assumed to be homogeneously distributed across the patch, implying that the probability of interaction does not depend on spatial location. This is a common simplifying assumption in compartmental ecological models [52, 53], allowing to focus primarily on the temporal dynamics. Because insects are thus uniformly distributed across the M tree sites, it is natural to define the densities with respect to the number of tree sites:

$$x = n_B/M, \quad y = n_T/M, \quad z = n_W/M. \quad (4.A.1)$$

$T(W) + \emptyset \xrightarrow{\tilde{\eta}} T + T$	birth of healthy tree from seed dispersal of both healthy & vulnerable trees
$T \xrightarrow{\epsilon} W$	healthy tree spontaneously becomes vulnerable
$W \xrightarrow{\rho} 0$	vulnerable tree death
$B \xrightarrow{\delta} 0$	ESBB death
$B + T \xrightarrow{\tilde{\kappa}\Theta(n_B - \tilde{\sigma})} B + W$	ESBB attacks and weakens a healthy tree (mass attack)
$B + W \xrightarrow{\tilde{\beta}} B + n B + \emptyset$	ESBB reproduces (n offspring) in a colonized susceptible tree, killing it
$0 \xrightarrow{\lambda M} B$	bark beetle immigration

TAB. 4.2. Reaction rules for the Norway spruce–bark beetle model.

A schematic of the model compartments and transitions is presented in Figure 4.1.

Deterministic dynamical equations. From these individual-level processes, we derive deterministic equations for the expected population densities. This is obtained following a standard approach in stochastic population dynamics [54].

Let $\mathbf{n} = (n_B, n_T, n_W)$ denote the microscopic state of the system. The probability distribution $P(\mathbf{n}, t)$ evolves according to the master equation

$$\frac{d}{dt}P(\mathbf{n}, t) = \sum_{\mathbf{n}' \neq \mathbf{n}} [T(\mathbf{n}|\mathbf{n}') P(\mathbf{n}', t) - T(\mathbf{n}'|\mathbf{n}) P(\mathbf{n}, t)] , \quad (4.A.2)$$

where the transition kernel $T(\mathbf{n}|\mathbf{n}')$ is nonzero only for configurations differing by a single elementary reaction listed in Table 4.2. Explicitly:

$$\begin{aligned} T(n_B, n_T + 1, n_W | \mathbf{n}) &= \tilde{\eta} (n_T + n_W)(M - n_T - n_W), \\ T(n_B, n_T - 1, n_W + 1 | \mathbf{n}) &= \epsilon n_T + \tilde{\kappa} \Theta(n_B - \tilde{\sigma}) n_B n_T, \\ T(n_B, n_T, n_W - 1 | \mathbf{n}) &= \rho n_W, \\ T(n_B - 1, n_T, n_W | \mathbf{n}) &= \delta n_B, \\ T(n_B + n, n_T, n_W - 1 | \mathbf{n}) &= \tilde{\beta} n_B n_W \\ T(n_B + 1, n_T, n_W | \mathbf{n}) &= \lambda M. \end{aligned} \quad (4.A.3)$$

From the master equation 4.A.2, one derives evolution equations for the first moments of the densities 4.A.1 by multiplying by the relevant variables and summing over all states. These equations generally involve higher-order moments (e.g. $\langle x^2 \rangle$ and $\langle xz \rangle$) and are therefore not closed. To obtain a closed system, we adopt a mean-field approximation valid for sufficiently large system size M , neglecting correlations and finite-size terms of order $1/M$. In practice, this corresponds to approximating higher-order moments as products of first moments, for instance

$$\langle x^2 \rangle \approx \langle x \rangle^2, \quad \langle xz \rangle \approx \langle x \rangle \langle z \rangle. \quad (4.A.4)$$

Under this closure, each reaction in Table 4.2 contributes a corresponding term to the deterministic equations. For example, beetle reproduction through colonization of vulnerable trees ($B + W \xrightarrow{\tilde{\beta}} nB$) yields the term βxz , while spontaneous tree weakening ($T \xrightarrow{\epsilon} W$) contributes ϵy , and density-dependent tree recruitment generates the logistic term $\eta(1 - y - z)(y + z)$. This procedure yields the following deterministic evolution equations for the average population densities:

$$\begin{cases} \dot{x} = \lambda - \delta x + \beta xz \\ \dot{y} = -\epsilon y - \kappa \Theta(x - \sigma)xy + \eta(1 - y - z)(y + z) \\ \dot{z} = \epsilon y - \rho z + \kappa \Theta(x - \sigma)xy - \gamma xz \end{cases} \quad (4.A.5)$$

The parameters $\tilde{\eta}$, $\tilde{\kappa}$, and $\tilde{\beta}$ are defined at the individual-tree level. When expressing the dynamics in terms of normalized densities, the corresponding effective rates are rescaled with the system size M as $\beta = nM\tilde{\beta}$, $\gamma = M\tilde{\gamma}$, $\kappa = \tilde{\kappa}$, $\eta = \tilde{\eta}M$. Notice that γ and β need not be equal, depending on the choice of scales of the model; in particular, if the dynamical variables represent individual densities, one typically has $\beta \gg \gamma$. The immigration rate λ represents an external input and is therefore defined directly at the population level. The scaling of σ with M is instead discussed in detail in Appendix 4.B.1, where we adopt a biologically motivated formulation in which the effective threshold remains finite at the density level. Empirical estimates for these parameters are discussed in Appendix 4.B.

4.B Reference parameters estimation

To calibrate the model, we estimate reference values for the parameters based on available ecological and entomological literature. These estimates reflect typical conditions in managed European spruce forests, while also accounting for known sources of variability. Where precise data are lacking, we use informed assumptions to define plausible orders of magnitude or leave parameters free for exploration. Table 4.1 of the main text summarizes the final reference values adopted in the model, along with estimated variability ranges. These ranges are derived from ecological heterogeneity (e.g., altitude, forest density) or uncertainty in empirical measurements.

Several simplifying assumptions have been made for tractability. First, although bark beetles are largely inactive during winter, we model processes as if they occur continuously throughout the year, effectively averaging over seasonal dynamics. Second, we assume two generations per year, reflecting average life cycle patterns observed across altitudes and typical annual temperatures. Third, since only female beetles contribute to reproduction, we track uniquely female individuals; consequently, parameters involving reproduction (notably β) are adjusted by assuming a 1:1 sex ratio and halving the brood size accordingly. Tree recruitment, modeled by a logistic curve, provides a mechanism for host replenishment and stand saturation effect. Healthy trees are assumed to transition through a vulnerable state before dying, thus the typical lifetime of an individual tree, t_{life} , can be approximated as the sum of the average durations spent in each compartment, i.e., $t_{life} \approx \epsilon^{-1} + \rho^{-1}$.

Tree demographic parameters

Maximum number of trees per patch (M)

We normalize the system to a forest patch of 1 hectare, assuming a typical total number of $M \sim 500$ spruce trees per patch [29]. Observed values usually vary from 300 in high-altitude or sparse stands to 700 in dense, low-altitude forests (G. Petit, pers. comm.). Where relevant, we explicitly relate individual-level processes (e.g., fecundity) to system-level rates via rescaling to a forest patch of area 1 ha, as explained in Appendix 4.A. This should not be taken to mean that our model represents a forest patch of 1 ha: as we are making the assumption of spatial homogeneity, the results can in principle be scaled up to a forest in any size. Indeed, it is rather the assumption of homogeneity that restricts our model by neglecting spatial dynamics at all scales.

Death rate of susceptible trees (ρ)

Susceptible trees represent vulnerable individuals that include both structurally compromised trees, such as those heavily damaged or uprooted by wind (but we may include senescent, severely drought-stressed or pathogen-stressed trees as well) and otherwise healthy trees that have undergone mass beetle attacks. Wind-fell trees are typically expected to degrade and die mostly within a few years [30]. Based on this, we assume an average viability of about 1 to 4 years following the onset of weakening, yielding a plausible range of $6 \cdot 10^{-4}$ to $5 \cdot 10^{-3} \text{ day}^{-1}$, which reflects variability in environmental conditions.

Conversion rate from healthy to susceptible trees (ϵ)

Assuming that trees typically pass through a vulnerable state before dying, we estimate ϵ based on typical lifespans. For a typical lifespan of 250 years, within a conservative range of 100–400 years [31, 32], this yields $\epsilon = 1 \cdot 10^{-5} \text{ day}^{-1}$. The plausible range from $7 \cdot 10^{-6}$ to $3 \cdot 10^{-5} \text{ day}^{-1}$ reflects such variation in tree longevity and site-specific factors.

Birth rate of healthy trees (η)

Tree recruitment rates depend on forest age structure and site productivity. We assume that the growth of the tree population can be modeled as a logistic curve, with growth rate $\tilde{\eta} = 1/(100 \text{ years})$, and scale by M to obtain $\eta = 1.3 \cdot 10^{-2} \text{ day}^{-1}$. This parameter reflects the rate at which new trees reach a proper size such that they can be attacked by ESBB. Based on regeneration times ranging from about 60 years in low-altitude stands to over 200 years in high-altitude forests (G. Petit, pers. comm.), we define a plausible range between $4 \cdot 10^{-3}$ and $3 \cdot 10^{-2} \text{ day}^{-1}$.

Beetle demographic parameters

Death rate of beetles (δ)

We assume a typical adult flight of 1–3 days during the dispersal phase, leading to $\delta = 1/(2 \text{ days}) \approx 0.5$ as the reference value. This corresponds to a plausible range between 0.3 and 1.0 day^{-1} .

Beetles per brood (n)

Each female typically lays around 80 eggs [4]. Since only a fraction of individuals survive the winter and successfully emerge as adults, we account for an estimated winter mortality of 30% to 50% [4] (D. Nardi, pers. comm. from field observations). Additionally, assuming a 1:1 sex ratio, we consider only the female offspring contributing to reproduction, effectively dividing the brood size by two. This yields an average of $n \approx 25$ viable female offspring. We allow for a range from 20 to 30 to reflect variability in survival due to environmental conditions.

Reproduction rate of beetles (β)

We assume two generations per year. As detailed in Appendix 4.B.2, we compute the growth rate by matching the population growth resulting from two successive cohorts in a single year with a continuous time growth, obtaining $\beta \approx 18 \text{ day}^{-1}$. We consider a range from 5 to 40 day^{-1} to account for variation in brood size, survival, and generation time. We remark that here we assumed conditions which are favorable to the growth of beetle population, neglecting interspecific competition.

Beetle-tree interaction parameters

Tree death rate due to beetle attack (γ)

This rate is linked to β via $\gamma = \beta/n$. Given variability in β and n , we define a range of 0.1 to 0.7 day^{-1} , with a reference value of 0.4 day^{-1} .

Threshold for mass attack (σ)

Mass attacks on healthy trees require a critical number of insects, typically estimated at around $\tilde{\sigma} \sim 5000$ individuals per tree [33]. In the model, this threshold is expressed as a condition on beetle density, using a scaling argument that accounts for local aggregation behavior. Due to pheromone-mediated chemical signaling, ESBB are known to aggregate over a finite spatial scale. Lacking data on natural aggregation distances, we use artificial chemical signaling [34] as a broad estimate of aggregation radius; where the effective pheromone attraction range is estimated to lie in the range $R \sim 19\text{--}97 \text{ m}$. As a result, each tree is not exposed to the entire beetle population in the forest, but only to those within an aggregation area $A \sim \pi R^2$ out of the total area L^2 . Accordingly, we assume that mass attacks are triggered when the number of insects within this aggregation area exceeds $\tilde{\sigma}$. This leads to an effective density threshold $\sigma = \tilde{\sigma}/m$, where m is the number of trees within the aggregation area: $m = M \cdot A/L^2$. Based on empirical attraction ranges, we estimate that σ lies between approximately 3.3 and 83. Thus, given this uncertainty, we set as a conservative reference value $\sigma = 10$. A detailed derivation of this scaling and its implications is provided in Appendix 4.B.1.

Colonization rate of healthy trees (κ)

This parameter reflects the efficiency with which ESBB successfully colonizes and weakens healthy trees once mass attacks are triggered. This is distinct from the threshold parameter σ , which controls the number of insects required to initiate an attack. Both κ and σ can be modified to reflect the health state of the forest, drought, and prior damage: while σ captures the resistance threshold of trees, κ describes how effectively insects exploit that vulnerability under outbreak conditions. Due to the lack of direct empirical estimates, we treat κ as a free parameter in our scenario analysis.

4.B.1 Density threshold for mass attacks and scalability of the model

Mass attacks on healthy trees typically require around $\tilde{\sigma} \sim 5000$ beetles per tree. In the model, this threshold must be expressed in terms of beetle density $x = B/M$. Different assumptions about aggregation lead to different scalings of the Heaviside function used to trigger mass attacks.

A) *Global aggregation*: we assume that all beetles in the forest patch can potentially attack a single tree. Then:

- $\#B$ = total number of beetles in the forest patch,
- $\tilde{\sigma}$ = number of beetles needed to colonize a healthy tree,

leading to the condition: $\Theta(\#B - \tilde{\sigma}) \propto \Theta(x - \frac{\tilde{\sigma}}{M})$.

B) *Local density threshold*: we assume that each tree is only affected by the local beetle density in its immediate vicinity:

- $x = \#B/M$ = average number of beetles per tree site,
- $\tilde{\sigma}$ = beetle threshold per tree,

resulting in the simpler form: $\Theta(x - \tilde{\sigma})$. This implies beetles do not aggregate and each tree interacts with the local beetle density only.

C) *Intermediate aggregation scale*: a more realistic scenario accounts for beetle aggregation over a finite spatial range. Beetles are known to attract mates via pheromone-mediated chemical signaling over a certain spatial length-scale, which we denote by R . This leads to an effective aggregation area $A = \pi R^2$, which defines a fraction $f = A/L^2$ of the total forest patch corresponding to $m = f \cdot M = AM/L^2$ tree sites. Hence, we compare:

- $xm = \#Bm/M$ = average number of beetles within the aggregation area,
- $\tilde{\sigma}$ = per-tree attack threshold,

yielding: $\Theta(xm - \tilde{\sigma}) \propto \Theta(x - \frac{\tilde{\sigma}}{m})$. Since m is determined by the aggregation area A and not the total patch size L^2 , this formulation captures beetle spatial behavior while preserving scalability with forest patch size.

Among these possibilities, we adopt the intermediate aggregation scenario (C), which assumes that beetles aggregate over a finite spatial scale. This choice is biologically motivated and leads to a density threshold that remains independent of the total system size M , ensuring a well-defined and scalable formulation of the model.

4.B.2 Continuous-time consistency in determining β and γ

We wish to estimate β from empirical observations, and consequently derive γ . However, a considerable difficulty is given by the fact that β is not merely a birth rate for ESBBs; instead, the dynamical birth rate at time t is given by $\beta z(t)$, which depends on the availability of susceptible

trees. As such, empirical estimates on biological grounds are not readily available, and we must root our analysis in population dynamics.

Our starting point is the observation that each female ESBB entering a susceptible tree reproduces, yielding a net increase in ESBB population. Furthermore, in each year, a succession of N cohorts will be observed, with $1 \leq N \leq 3$. In the following we will neglect all other processes, and work under the assumption that, through successive reproductive cycles, each offspring will reproduce with similar success. Under these assumptions, if N cohorts emerge in a time T , with each individual generating n offspring, we expect that during this time the population of ESBB will increase by a factor $\mu \approx n^N$. Hence, by tracking the growth rate of successive cohorts and matching the resulting population growth, we are able to link expected populations levels to likely values of β .

For the sake of conceptual clarity, we first estimate β by assuming the continuous time evolution for ESBB density, and assuming that the density of susceptible trees does not change over time, namely:

$$\dot{x} = \beta x z, \quad z = \text{const.} \quad (4.B.1)$$

In the time interval $[0, T]$, the population of ESBB increases of a factor μ , where

$$\mu = \frac{x(T)}{x(0)} = e^{\beta z T} \quad (4.B.2)$$

Thus, knowing the parameters μ and T , we can estimate

$$\beta = \frac{\log(\mu)}{z T}. \quad (4.B.3)$$

The use of estimate (4.B.3) in a continuous time model leads to the requested growth of ESBB population over a given time T . However, this estimate is obtained under the assumption that z is constant, it is not clear what value of z one should utilize; yet, this value will directly affect our estimation of β . Both these difficulties are addressed by taking into account the dynamic nature of z , as obtained by the following differential equations:

$$\begin{cases} \dot{x} = \beta x z \\ \dot{z} = -\gamma x z \end{cases} \quad \text{with } \gamma = \beta/n \quad (4.B.4)$$

Through eqs. (4.B.4), we manifestly tie together the dependence of β on n and the non-reciprocity of x – z interaction; however, we note that this does not reduce the number of independent parameters. The ESBB relative growth, $\mu = x(T)/x(0)$, can be obtained from Eq. (4.B.4) by noting that the quantity $C = x + nz$ is conserved: indeed, using $\gamma = \beta/n$, one finds $\dot{C} = 0$. The resulting expression is

$$\mu = x(T)/x(0) = \frac{C/x(0)}{1 + \frac{nz(0)}{x(0)} e^{-(\beta C/n)T}}. \quad (4.B.5)$$

From this, β can be extracted in terms of $x(0)$, $z(0)$, T , n and μ : we find

$$\beta = \frac{n}{CT} \log \left(\frac{C/x_0 - 1}{C/(x_0\mu) - 1} \right). \quad (4.B.6)$$

In the limit of $x(0) \rightarrow 0$, we recover the result in Eq. (4.B.3) (which is independent of n), provided we identify $z \equiv z(0)$. Here, the assumption of constant density of vulnerable trees is substituted with the assumption of small initial ESBB density, consistent with an endemic state. Therefore, $z(0)$ should reflect a low density of susceptible trees in standard conditions, namely (see Table 4.2) $z(0) = \frac{\text{few susceptible trees}}{L} / \frac{M \text{ trees}}{L} \propto M^{-1}$. As it is impossible — and perhaps not meaningful — to assign a fixed value to $z(0)$, we will consider a rather broad range of values for β comprising the estimates obtained in this section.

4.C Equilibrium states

Mathematically, equilibria (or *fixed points*) are defined as the solutions of the dynamical equations such that their time derivatives vanish [52]. To determine the equilibria of the system, therefore, we have to calculate the solutions of the equations Eq. (4.A.5) where the left-hand side is equal to zero. We denote an equilibrium as (x^*, y^*, z^*) , corresponding to the stable densities of ESBB, vulnerable trees, and healthy trees, respectively. We classify them according to whether the ESBB abundance lies below or above the outbreak threshold σ .

In the sub-threshold regime ($x^* < \sigma$), two possible equilibria exist.

1. The trivial, ecologically unrealistic equilibrium is:

$$(x^*, y^*, z^*) = (\delta/\lambda, 0, 0) . \quad (4.C.1)$$

2. The endemic coexistence equilibrium, where beetles and trees persist, is found by solving the following equation in the beetle population x^* :

$$f_<(x^*) = 0, \quad f_<(x) = a_3x^3 + a_2x^2 + a_1x + a_0. \quad (4.C.2)$$

where $f_<(x)$ is a 3-rd order polynomial in the ESBB density x , whose coefficients depend on the model's ecological parameters as follows:

$$\begin{aligned} a_3 &= \gamma^2 \delta \eta \\ a_2 &= \gamma [\beta\epsilon(\epsilon - \eta) - \gamma\eta\lambda + 2\delta\eta(\rho + \epsilon)] \\ a_1 &= \eta(\rho + \epsilon)(\delta(\rho + \epsilon) - 2\gamma\lambda) - \beta\epsilon(\eta(\rho + \epsilon) - \rho\epsilon) \\ a_0 &= -\eta\lambda(\rho + \epsilon)^2 \end{aligned} \quad (4.C.3)$$

The corresponding tree densities of this endemic equilibrium are given by:

$$z^* = \frac{\delta x^* - \lambda}{\beta x^*}, \quad y^* = z^* \frac{\rho + \gamma x^*}{\epsilon}. \quad (4.C.4)$$

Above the outbreak threshold ($x^* > \sigma$), mass attacks on trees alter the system dynamics, leading to a modified fixed point. ESBB equilibrium abundance is given by the solution x^* of $f_>(x^*) = 0$, where $f_>(x)$ is a quartic polynomial incorporating the additional effects of beetle-induced tree mortality through the attack rate κ :

$$f_>(x^*) = 0, \quad f_>(x) = b_4x^4 + b_3x^3 + b_2x^2 + b_1x + b_0. \quad (4.C.5)$$

with coefficients:

$$\begin{aligned} b_4 &= \beta\gamma\kappa^2 \\ b_3 &= \gamma\kappa(-\beta\eta + 2\beta\epsilon + 2\delta\eta) + \kappa^2(\beta(\rho - \eta) + \delta\eta) + \gamma^2\delta\eta \\ b_2 &= \beta\epsilon(\gamma(\epsilon - \eta) - 2\eta\kappa) + \beta\kappa\rho(2\epsilon - \eta) - \eta(\gamma + \kappa)(\lambda(\gamma + \kappa) - 2\delta(\rho + \epsilon)) \\ b_1 &= \eta(\rho + \epsilon)(\delta(\rho + \epsilon) - 2\lambda(\gamma + \kappa)) - \beta\epsilon(\eta(\rho + \epsilon) - \rho\epsilon) \\ b_0 &= -\eta\lambda(\rho + \epsilon)^2 \end{aligned}$$

In this regime, tree densities are correspondingly given by:

$$z^* = \frac{\delta x^* - \lambda}{\beta x^*}, \quad y^* = z^* \frac{\rho + \gamma x^*}{\kappa x^* + \epsilon} \quad (4.C.6)$$

Given the full expression of the coefficients, Eq. (4.C.2) and Eq. (4.C.5) can be solved numerically, yielding the fixed points (x^*, y^*, z^*) . To analyze their stability, we compute the Jacobian matrix $\mathbb{J}(x^*, y^*, z^*)$, which describes the local linearization of the system around equilibrium points. The explicit expression for $\mathbb{J}(x, y, z)$ is given by:

$$\mathbb{J}(x, y, z) = \begin{pmatrix} \beta z - \delta & 0 & \beta x \\ -\kappa y [x\delta(x - \sigma) + \theta(x - \sigma)] & \eta [1 - 2(y + z)] - \kappa x \theta(x - \sigma) - \epsilon & \eta [1 - 2(y + z)] \\ -\gamma z + \kappa y [x\delta(x - \sigma) + \theta(x - \sigma)] & \epsilon + \kappa x \theta(x - \sigma) & -(\gamma x + \rho) \end{pmatrix} \quad (4.C.7)$$

where $\delta(x - \sigma)$ denotes the Dirac delta function, and $\theta(x - \sigma)$ is the Heaviside step function. The eigenvalues of $\mathbb{J}(x, y, z)$ determine the local stability properties of each fixed point. While we have obtained analytical expressions for the eigenvalues, their complexity makes them impractical to present explicitly. There are three possible scenarios. In the first scenario there is at least one eigenvalue with positive real part, which corresponds to an unstable equilibrium. In the second scenario all the eigenvalues are real and negative, which corresponds to a stable equilibrium that is reached monotonically exponentially at large times. In the third scenario all eigenvalues have negative real part, but a couple of them have nonzero imaginary part. The latter scenario corresponds to a stable equilibrium that is reached with a damped oscillation at large times.

4.D Reactivity

Reactivity assesses a system's transient response to perturbations. It is determined by the largest eigenvalue of the symmetric part of the Jacobian matrix:

$$\begin{aligned} \mathbb{J}_{\text{symm}} &= \frac{1}{2}(\mathbb{J} + \mathbb{J}^T) = \\ &= \frac{1}{2} \begin{pmatrix} 2(\beta z - \delta) & -\kappa y [x\delta(s - x) + \theta(x - s)] & \beta x - \gamma z + \kappa y [x\delta(s - x) + \theta(x - s)] \\ -\kappa y [x\delta(s - x) + \theta(x - s)] & -2[\epsilon + 2\eta(y + z - 1) + \kappa x \theta(x - s)] & \epsilon - 2\eta(y + z - 1) + \kappa x \theta(x - s) \\ \beta x - \gamma z + \kappa y [x\delta(s - x) + \theta(x - s)] & \epsilon + \eta[1 - 2(y + z)] + \kappa x \theta(x - s) & -2(\gamma x + \rho) \end{pmatrix} \end{aligned} \quad (4.D.1)$$

While we have obtained analytical expressions for the eigenvalues of $\mathbb{J}_{\text{symm}}$, they are too complex to be presented explicitly. Instead, we focus on numerical evaluations to analyze their dependence on key parameters and to identify conditions under which transient growth is maximized.

We proceed to analyze the reactivity of the endemic coexistence equilibrium, which represents the most ecologically plausible scenario under typical conditions. We start by evaluating Eq. (4.D.1) at the reference parameter values reported in Table 4.1 of the main text. The eigenvalues of $\mathbb{J}_{\text{symm}}$ at the reference endemic equilibrium are approximately

$$\lambda_1 \sim 0.002, \lambda_2 \sim -0.02, \text{ and } \lambda_3 \sim -0.4. \quad (4.D.2)$$

The positive value of λ_1 indicates that such equilibrium is reactive. To illustrate the reactive behavior, we numerically integrate the system after applying small perturbations (of magnitude $\epsilon = 0.05$) along each eigenvector of $\mathbb{J}_{\text{symm}}$. The most reactive direction (associated with λ_1) leads to a transient spike in the perturbation norm $\|\delta r(t)\|$, while non-reactive directions, i.e. all the ones perpendicular to the reactive direction, result in monotonic relaxation (Figure 4.2a of the main text). The dominant eigenvector is approximately

$$\mathbf{v}_1 \sim \begin{bmatrix} 0.05 \\ -0.40 \\ 0.91 \end{bmatrix}, \quad (4.D.3)$$

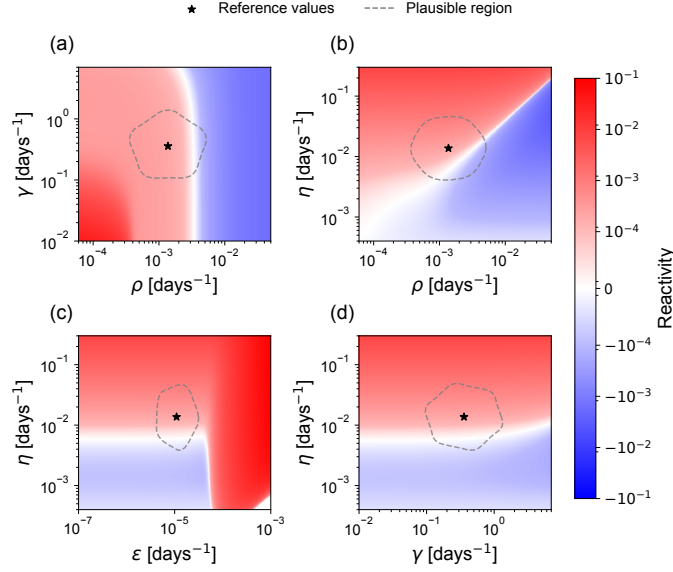


FIG. 4.7. Reactivity landscape over a region of parameter space centered around the reference values given in Table 4.1 of the main text. The star indicates the reference parameter set, for which the reactivity is $R \approx 0.002$. Within the ecologically plausible region, reactivity is predominantly positive. Therefore, despite parameter values and ranges being approximate, the system is generally expected to exhibit reactive dynamics under realistic ecological conditions, indicating an inherent vulnerability to transient outbreaks triggered by perturbations.

indicating that transient growth is primarily driven by shifts in the weakened tree population. In contrast, directions in the plane spanned by

$$\mathbf{v}_2 = \begin{bmatrix} 0.02 \\ 0.9 \\ 0.4 \end{bmatrix} \quad \text{and} \quad \mathbf{v}_3 = \begin{bmatrix} -0.9987 \\ 0.0008 \\ 0.0504 \end{bmatrix} \quad (4.D.4)$$

are dominated by changes in healthy trees or beetles alone and do not produce significant transient growth. This indicates that reactivity in the endemic equilibrium is mainly driven by perturbations involving the abundance of vulnerable trees. To further illustrate ecological relevance, Figure 4.2b of the main text shows the full system trajectory following a perturbation with a strong projection along $\mathbf{v}_1$, (with $\epsilon = 0.1$).

We report below additional reactivity maps visualizing reactivity's dependence on ecological parameters.

4.E Recurrent outbreaks

To study the recurrent outbreak regime, we choose parameter values that give rise to this particular dynamical behavior. These values are outside the ecologically plausible range representing current forest conditions (Table 4.1 of the main text), but we focus on the case in which they still preserve a realistic balance between key ecological rates. In the selected parameters case, an equilibrium exists but it is only weakly stable due to its high reactivity, making it effectively inaccessible without fine-tuning of the initial conditions: even minimal increases in the number of susceptible trees can push the system away from equilibrium and trigger outbreaks.

Because the insect population periodically collapses, allowing susceptible trees to accumulate during intervals when it is effectively absent, we consider a regime of weak immigration by setting $\lambda \gtrsim 0$. After recurrent outbreaks begin, λ plays no further role. Here, the stability properties of the system are effectively unaltered with respect to the case $\lambda = 0$. Thus, we will start from initial conditions for trees' population in proximity of the ESBB-free stationary values, obtained from Eq. (4.A.5) for $\lambda = 0 = x^*$, finding

$$x(0) = x^* = 0, \quad y(0) = y^* = \frac{\rho[\epsilon(1 - \frac{\rho}{\eta}) + \rho]}{(\epsilon + \rho)^2}, \quad z(0) = z^* = \frac{\epsilon}{\rho}y(0). \quad (4.E.1)$$

This fixed point is feasible, i.e. $y^* > 0$, if $\eta > (\epsilon^{-1} + \rho^{-1})^{-1}$. Moreover, the insect population can successfully invade, i.e. has positive growth at low density, if the following condition is satisfied:

$$\beta > \frac{\delta\eta(\epsilon + \rho)^2}{\epsilon[\epsilon(\eta - \rho) + \eta\rho]}. \quad (4.E.2)$$

Notably, the denominator in Eq. (4.E.2) is proportional to y^* and z^* , implying that invasion becomes increasingly difficult as the equilibrium number of host trees declines. Moreover, even when condition (4.E.2) holds, it does not guarantee the emergence of recurrent outbreaks. These require additional dynamical conditions — in particular, sufficiently high reactivity — as pointed out in Section 4.3.3 of the main text.

The observables used to characterize the recurrent outbreak regime are defined as the maximum population size during an outbreak x_{peak} (BOS), and the time between successive outbreaks T (BWT). In such regime, the dynamics is regularly repeating, therefore they are linked by the periodicity condition :

$$x(t) = x(t + T) \equiv x_{\text{peak}} \quad (4.E.3)$$

We underline that in this section we analyze stressors as encoded by static parameters, hence the exact periodic dynamics are to be intended as describing the overall susceptibility of the system to ESBB outbreaks, in a mean sense. Stressor anomalies, described by dynamical noise, are considered in the next section.

4.F Environmental disturbances

Each disturbance is incorporated in our model as an external force that occurs at random times and with random magnitude, and converts a fraction of healthy trees into susceptible trees. A *temporal series of disturbances* is described by the sequence of random pairs

$$\{(\Delta_{(n)}, t_{(n)})\}_n. \quad (4.F.1)$$

Here, $t_{(n)}$ denotes the time of the n -th disturbance, and $\Delta_{(n)} \in (0, 1)$ its magnitude — i.e., the fraction of healthy trees converted into susceptible ones. In practice, disturbances are numerically implemented as instantaneous state updates $z \rightarrow z + \Delta_{(n)}z$, $y \rightarrow y - \Delta_{(n)}z$ at discrete times $t_{(n)}$, with continuous evolution governed by Eq. (4.2.1) between events.

Each $\Delta_{(n)}$ is independently drawn from a probability distribution with support in $(0, 1)$, whose shape is controlled by the parameter Δ_d . The occurrence times $t_{(n)}$ are obtained as cumulative sums of independent waiting times, $t_{(n)} = \sum_{m=1}^n \tau_{(m)}$, where each $\tau_{(n)}$ is independently drawn from an exponential distribution with mean τ_d

$$\tau_{(n)} \sim \frac{1}{\tau_d} e^{-\tau_{(n)}/\tau_d}. \quad (4.F.2)$$

For mathematical consistency, we require that as $\tau_d \rightarrow 0$, $\Delta_d \rightarrow 0$ as well, so that the average contribution of disturbances per unit time remains finite [55]. For simplicity, we do not consider the general case of statistically dependent $\Delta_{(n)}$ and $t_{(n)}$, although this possibility could better characterize realistic disturbance [56, 57]. Nonetheless, this framework allows us to explore how shifts in environmental conditions affect outbreak dynamics: specifically, we decrease τ_d to model more frequent disturbances, while we increase Δ_d to enhance severity.

Under this stochastic forcing, the system no longer follows strictly periodic dynamics as in the unperturbed case: both x_{peak} and T become random variables whose distributions depend on the disturbance parameters. Intuitively, more frequent or severe disturbances are expected to reduce the average waiting time T with respect to the baseline (BOWT). However, the effect on the outbreak size x_{peak} is less obvious. As shown in Figure 4.6 (top) of the main text, the distribution of T is upper-bounded by the BOWT observed in unperturbed recurrent outbreak dynamics, shifting towards smaller waiting times as τ_d decreases and Δ_d increases. Simultaneously, the distribution of x_{peak} becomes broader: most outbreaks become smaller than in the baseline case, though occasional extreme events may still exceed the baseline size. Taken together, these results suggest that more frequent and severe disturbances lead to smaller but more frequent outbreaks, a shift consistent with the increased overall severity of ESBB activity during epidemic phases [44].

4.G Management strategies

We now consider how periodic management can reduce the risk of ESBB outbreaks. We define a *management strategy* $\mathcal{M}_{\Delta_m, \tau_m}$ as a periodic forcing that instantaneously reduces the density of susceptible trees, $z \rightarrow z - \Delta_m z$, at regular time intervals τ_m .

In practice, this is implemented as instantaneous state updates at discrete times, with the system evolving according to Eq. (4.2.1) between interventions. For completeness, this can be formally represented by a Dirac-delta forcing,

$$\dot{z}(t) = \cdots - \mathcal{M}_{\Delta_m, \tau_m}(t)z(t), \quad \mathcal{M}_{\Delta_m, \tau_m}(t) \equiv \Delta_m \sum_{n=0}^{+\infty} \delta(t - n\tau_m) \quad (4.G.1)$$

where $0 < \Delta_m < 1$ and $\tau_m > 0$.

The management strategy seeks to limit ESBB population growth by reducing the density of available susceptible trees. Without considering constraints on management, if this reduction is frequent and thorough enough, i.e. if τ_m and Δ_m are respectively small and large enough, the insect density will remain below the threshold for mass attacks on healthy trees, thus preventing outbreaks altogether. However, as we will argue next, τ_m and Δ_m may not be chosen independently from each other. To formalize this, we first examine the limit $\tau_m \rightarrow 0$, corresponding to continuous management. This limit is well-defined if $\Delta_m = \bar{\Delta} \tau_m + O(\tau_m^2)$, in which case the forcing converges to a constant rate $\mathcal{M}_{\bar{\Delta}\tau_m, \tau_m}(t) \rightarrow \bar{\Delta}$. The susceptible-tree equation becomes: $\dot{z} = \cdots - (\rho + \bar{\Delta})z$ and outbreaks are avoided if the invasion condition from Eq. (4.E.2) is violated under the substitution $\rho \rightarrow \rho + \bar{\Delta}$. From a practical standpoint, this scaling is also realistic: high-frequency interventions can only remove a small fraction of susceptible trees at a time. To account for the previous mathematical and practical considerations, we choose

$$\Delta_m = \frac{\hat{\Delta} \tau_m}{\tau_0 + \tau_m}, \quad (4.G.2)$$

where $\hat{\Delta} < 1$ and the constant τ_0 defines the time scale past which waiting for the next intervention

has reduced marginal utility. In this case, $\Delta_m < \hat{\Delta}$ for any finite τ_m , while for $\tau_m \sim 0$ we may approximate $\Delta_m = (\hat{\Delta}/\tau_0) \tau_m + O(\tau_m^2)$. Then, the previous case of linear scaling is recovered for $\tau \ll \tau_0$ with the identification $\bar{\Delta} = \hat{\Delta}/\tau_0$. While $\bar{\Delta}$ has the dimension of an inverse time, since τ_0 is a time scale, $\hat{\Delta}$ is a dimensionless quantity.

We now examine the effectiveness of such strategies in the presence of small and frequent disturbances (Figure 4.6 (bottom) of the main text). In the absence of management, outbreak observables x_{peak} and T remain tightly distributed around the baseline values (BOS and BOWT). In the limit $\tau_m \rightarrow 0$, where vulnerable trees are continuously removed, management is ineffective unless $\hat{\Delta}/\tau_0$ is very large. More realistically, when $\hat{\Delta}/\tau_0$ is small, outbreaks can only be prevented if $\tau_m \gtrsim \text{BOWT}$. Beyond this threshold, the ecological response to management becomes irregular: both x_{peak} and T switch between non-outbreak conditions (where $T = 0$) and their maximum value, as τ_m increases together with Δ_m (Eq. (4.G.2)). However, we find invariably that management is reliably effective when τ_m is slightly larger than $\langle T' \rangle$, which represents the average outbreak waiting under management. Therefore, in this regime of large τ_m , the success of a management strategy depends not only on the magnitude of intervention, but also on the timing which must align with the system's intrinsic response timescale.

4.H Parameters and other details on Figures

General information. Unless specified otherwise, Eq. (4.2.1) has been integrated using a fourth-order Runge-Kutta scheme. Whenever necessary, peaks have been automatically detected using the function `scipy.signal.find_peaks`.

Figure 4.2. Trajectories are obtained by integrating Eq. (4.2.1) using the Euler scheme. The parameter values used are reported in Table 4.1, and the reactivity associated to the stable fixed point (x^-, y, z) , representing the endemic state, is $\lambda \simeq 2 \cdot 10^{-3}$.

Figure 4.3. (b) For each stable fixed point across parameter space, determined analytically as explained in Section 4.2.3 and Appendix 4.C, we calculate reactivity (Section 4.2.4) as detailed in Appendix 4.D. The parameter values kept fixed in these diagrams are reported in Table 4.1.

Figure 4.4. The phase diagrams here presented are analytical. The fixed points displayed are obtained by studying the existence and stability of the stationary solutions presented in Section 4.2.3 and detailed in Appendix 4.C. (a) The parameter values kept fixed in this diagram are: $\delta = 5, \beta = 10, \sigma = 5, \kappa = 1, \epsilon = 10^{-2}, \gamma = 10^{-2}, \rho = 10^{-2}, \eta = 0.5, \lambda = 10^{-5}$. (b) The parameter values used in these diagrams are reported in Table 4.1. (c) Trajectories have been numerically integrated using the Euler scheme or the fourth-order Runge-Kutta scheme (in the case of oscillatory trajectories).

Figure 4.5 For both panels (a) and (b), $\lambda = 10^{-200}, \delta = 0.5, \eta = 5 \times 10^{-3}, \epsilon = \rho = 10^{-5}, \gamma = 10^{-2}, \kappa = 10^{-3}, \sigma = 10; dt = 0.1, t_{\text{max}} = 365 \times 100$. (a) $\beta = 20$; (b) β varies over the interval $[5, 30]$. Initial conditions are sampled ((a): 5×10^3 samples; (b): 10^3 samples) by perturbing the endemic fixed point found numerically (see Section 4.2.3) with a Gaussian array with independent components of zero mean, and variance equal to 10^{-3} . Negative components of initial conditions, whenever found, have been set equal to zero. Periodic solutions have been detected by counting peaks of $x(t)$ exceeding a given density threshold (σ for both (a) and (b), with also smaller thresholds for (b)). (c) Parameters are as in Figure 4.5 (a-b), with fixed $\beta = 20$, whereas initial conditions are given by Eq. (4.E.1). (d) Same parameters and initial conditions as panel (c), but with varying $\kappa \in [10^{-3}, 2 \times 10^{-2}]$.

Figure 4.6. Top: disturbances. Models' parameters are identical as in Figure 4.5 (c-d); $dt = 0.05$, $t_{\max} = 365 \times 10^3$. Bottom: management. Figures are obtained by the simulations of Eq. (4.2.1), replicated 1000 times, with all model's parameters and initial conditions equal to those of Figure 4.5. The parameters of management $\mathcal{M}_{\Delta, \tau}$ with $\Delta = \frac{\hat{\Delta}\tau}{\tau_0 + \tau}$ are $\hat{\Delta} = 1.8 \times 10^{-4}$ and $\tau_0 = 10$ years.

Figure 4.7. The plots here presented are analytical. The fixed points are obtained by studying the existence and stability of the stationary solutions presented in Section 4.2.3 and detailed in Appendix 4.C, while the associated reactivity (Section 4.2.4) is calculated as explained in Appendix 4.D. The parameter values used are reported in Table 4.1.

Code Availability

All data and code supporting the results of this study are available on Zenodo at link:
<https://doi.org/10.5281/zenodo.17432287>.

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Perspective: spatial extension of the Norway spruce–bark beetle model

A natural extension of the work presented in this thesis is the explicit incorporation of space into the Norway spruce–bark beetle dynamical model. While the well-mixed assumption allows one to clarify the main mechanisms underlying outbreak initiation and its temporal dynamics, many ecological processes—and bark beetle outbreaks in particular—are intrinsically spatial. Local infestation patterns [1], limited beetle dispersal ranges [2], and landscape heterogeneity all suggest that spatial structure may play an essential role in shaping outbreak dynamics [3].

In addition, European spruce bark beetles are known to aggregate via pheromone-mediated chemical signaling acting over finite spatial ranges, where male-produced aggregation pheromones attract conspecifics to host trees and coordinate mass attacks [4]. This biologically well-established mechanism introduces inherently nonlocal effects in dispersal and attack dynamics, and is therefore expected to influence both the spatial organization of infestations and the way outbreaks initiate and propagate across forested landscapes.

From a theoretical perspective, while detail-rich spatial models of bark beetle dynamics already exist [5], spatially explicit models formulated within a minimal dynamical setting may provide a more transparent framework for studying emergent phenomena such as cluster formation and propagating outbreak fronts, and for exploring how local extinction and recolonization processes generate long-lived transient dynamics beyond homogeneous descriptions. Finally, the explicit inclusion of space would enable future studies aimed at the design and assessment of the potential effectiveness of spatially targeted management strategies.

The spatial model introduced below should be regarded as a preliminary and exploratory extension of the ESBB framework. Its purpose is not to provide a detailed quantitative description of bark beetle spread, but rather to investigate how the ecological mechanisms identified in the well-mixed case interact with explicit dispersal and local interactions.

4.9 Spatially discrete model formulation

The analysis presented in Chapter 4 treated the system as spatially homogeneous and well-mixed, an assumption that is appropriate for large and relatively uniform forest patches. However, bark beetle outbreaks are intrinsically spatial phenomena, driven by localized attacks and dispersal across heterogeneous landscapes. To investigate how the same ecological mechanisms operate in space, we introduce a spatially explicit extension of the ESBB model.

We consider a two-dimensional square lattice with periodic boundary conditions, where sites are labeled by the index $i = 1, \dots, N$. At each spatial site, all demographic and interaction processes of the well-mixed model (see Table 4.2) take place locally. In addition, beetles are allowed to disperse between neighboring sites through an explicit migration process.

Specifically, beetle migration is modeled as

$$B_i \rightarrow B_j, \quad j \in \text{nnn}(i), \quad (4.9.1)$$

where $\text{nnn}(i)$ denotes the set of next-nearest neighbors of site i (Moore neighborhood).

The transition rate for migration from site i to site j is taken as

$$T_{i \rightarrow j} = \nu x_i \frac{\max\{\alpha, x_j\}}{S_i}, \quad S_i := \sum_{k \in \text{nnn}(i)} \max\{\alpha, x_k\}, \quad (4.9.2)$$

while all other transition rates coincide with those of the well-mixed model.

This choice of migration rate is designed to capture an aggregation mechanism in beetle dispersal:

- for low beetle densities at the destination site ($x_j < \alpha$), the weight associated with site j is constant and equal to α , ensuring a nonzero baseline probability of migration;
- for high beetle densities ($x_j > \alpha$), the weight increases linearly with x_j , favoring migration toward already infested sites;
- the normalization factor S_i ensures that the total migration probability out of site i is properly normalized.

Under a deterministic mean-field approximation, the resulting spatially extended model reads

$$\begin{cases} \dot{x}_i = \beta z_i x_i - \delta x_i + \lambda + \nu M_i(\vec{x}), \\ \dot{y}_i = -\epsilon y_i - \kappa x_i y_i \Theta(x_i - \sigma) + \eta(1 - y_i - z_i)(y_i + z_i), \\ \dot{z}_i = \epsilon y_i + \kappa x_i y_i \Theta(x_i - \sigma) - \rho z_i - \gamma z_i x_i, \end{cases} \quad (4.9.3)$$

where the migration term $M_i(\vec{x})$ is given by

$$M_i(\vec{x}) = \sum_{j \in \text{nnn}(i)} \left[x_j \frac{\max\{\alpha, x_j\}}{S_j} - x_i \frac{\max\{\alpha, x_j\}}{S_i} \right] = \max\{\alpha, x_i\} \sum_{j \in \text{nnn}(i)} \frac{x_j}{S_j} - x_i. \quad (4.9.4)$$

The sharp $\max\{\alpha, x\}$ function modeling the aggregation mechanism and the Heaviside function $\Theta(x - \sigma)$ controlling the mass-attack threshold can alternatively be replaced by smooth approximations.

As in the well-mixed formulation, we retain the constant immigration term $+\lambda$ in the ESBB equation. In the absence of migration ($\nu = 0$), the model reduces to N independent copies of the well-mixed dynamics at each site.

Continuum limit In the limit of vanishing lattice spacing a and under suitable smoothness assumptions, the spatially discrete model Eq. (4.9.3) admits a continuum description. In this formulation, $x(\mathbf{r}, t)$, $y(\mathbf{r}, t)$, and $z(\mathbf{r}, t)$ denote beetle, healthy-tree, and vulnerable-tree abundances at position $\mathbf{r}$ and time t , respectively, and the dynamics reads

$$\begin{cases} \dot{x}(\mathbf{r}, t) = \beta z x - \delta x + \lambda + \nu_c \left[m(x, \alpha) \nabla^2 \left(\frac{x}{m(x, \alpha)} \right) - \frac{x}{m(x, \alpha)} \nabla^2 m(x, \alpha) \right] \\ \dot{y}(\mathbf{r}, t) = -\epsilon y - \kappa x y \Theta(x - \sigma) + \eta(1 - y - z)(y + z), \\ \dot{z}(\mathbf{r}, t) = \epsilon y + \kappa x y \Theta(x - \sigma) - \rho z - \gamma z x, \end{cases} \quad (4.9.5)$$

where $m(x, \alpha)$ denotes a suitably smoothed approximation of the sharp max function, and $\nu_c = \frac{3}{8}a^2\nu$. Equation Eq. (4.9.5) defines a system of nonlinear reaction–diffusion–like equations with density-dependent transport, reflecting the underlying aggregation-biased dispersal mechanism at the discrete level.

In suitably simplified limits and under additional approximations, this continuum formulation may become amenable to systematic analytical investigation, which is left for future work. In the present study, we instead focus on numerical simulations of the spatially discrete model Eq. (4.9.3) as a first step toward characterizing its emergent spatiotemporal phenomenology.

4.10 Numerical exploration

The spatially explicit ESBB model is explored numerically through direct simulations of the discrete lattice dynamics defined in Eq. (4.9.3). The purpose of this numerical exploration is not to provide a systematic or exhaustive characterization of the spatial model across parameter space. Rather, it is intended to illustrate representative behaviors and to qualitatively assess how the dynamical regimes identified in the well-mixed formulation are affected by the inclusion of explicit spatial structure and dispersal.

In particular, the simulations presented below focus on a limited set of parameter choices, chosen to correspond to well-characterized regimes of the well-mixed ESBB model. The resulting spatial patterns and dynamical features should therefore be interpreted as illustrative examples, highlighting possible phenomenological outcomes of the spatial extension, rather than as definitive or comprehensive results.

Key qualitative outcomes (exploratory). In the numerical examples reported below we observe: (i) spontaneous spatial organization (clusters or smooth heterogeneous states) driven by aggregation-biased dispersal in homogeneous landscapes; (ii) long-lived active configurations at $\lambda = 0$ in parameter sets where the well-mixed predicts ESBB extinction; (iii) near well-mixed boundaries, wave-like transients and hotspot dynamics triggered by localized perturbations, with sensitivity to perturbation size.

4.10.1 Baseline endemic regime: the role of ν and α

We first consider parameter values corresponding to the reference endemic state of the well-mixed ESBB model (Table 4.1), characterized by a stable, non-oscillatory fixed point with low reactivity $R \sim 0.002$. The system is initialized by introducing small random heterogeneous perturbations around the homogeneous endemic equilibrium and letting the system evolve on a two-dimensional 100×100 lattice with periodic boundary conditions.

For sufficiently small dispersal rates ν , the spatial system progressively relaxes toward a nearly homogeneous configuration, consistent with the well-mixed equilibrium. In this limit, dispersal primarily acts as a homogenizing mechanism, and the spatial heterogeneity introduced by the initial condition seems to be confined to short-range, uncorrelated fluctuations.

For larger values of ν , however, the system generically develops spatial heterogeneity in the beetle distribution. The nature of this heterogeneity depends sensitively on the aggregation threshold α . When α is much smaller than the ESBB equilibrium abundance of the well-mixed model, the system tends to form localized, high-density patches of ESBB, resulting in dot-like spatial patterns. Conversely, for α comparable to or larger than the equilibrium density, the system settles into

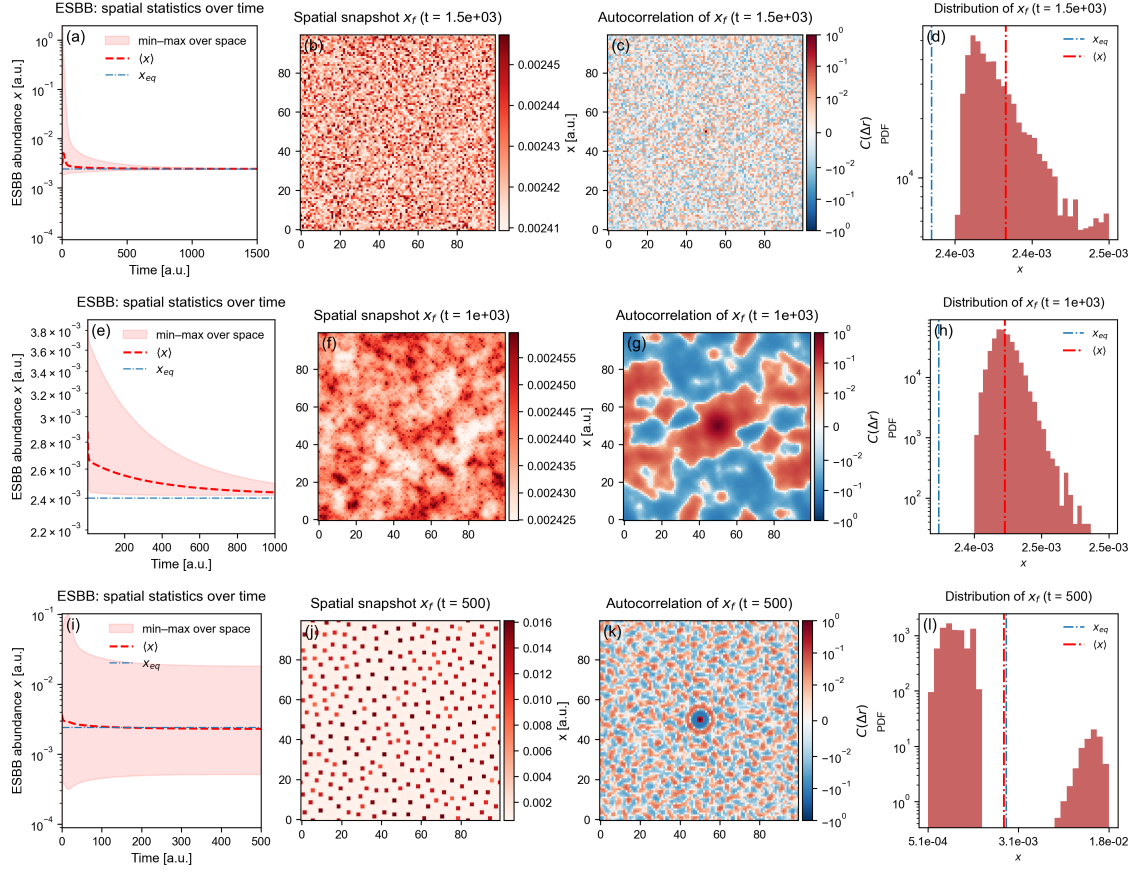


FIG. 4.8. Exploratory illustration of the spatial distributions in the spatially explicit ESBB model in the baseline endemic regime, for different dispersal and aggregation parameters. **First column:** time evolution of the spatial mean $\langle x \rangle$ (red dashed) and spatial min–max band (shaded), compared with the well-mixed equilibrium x_{eq} . **Second column:** long-time snapshots of the beetle density $x(\mathbf{r}, t)$. **Third column:** normalized spatial autocorrelation $C(\Delta r)$ computed from the corresponding snapshot and rescaled so that $C(0) = 1$. **Fourth column:** probability density function (PDF) of the field values x at the same snapshot time, shown on logarithmic scale; vertical lines indicate the spatial mean $\langle x \rangle$ and the well-mixed equilibrium x_{eq} . **(a–d)** small dispersal rate $\nu < 1$ ($\nu = 0.1$ in the case shown), yielding relaxation toward a nearly homogeneous configuration, where spatial heterogeneity is limited to short-range, seemingly uncorrelated fluctuations. **(e–g)** large $\nu > 1$ and small aggregation threshold $\alpha < x_{eq}$, producing dot-like clustered patterns. $\nu = 10$ and $\alpha = 0.0014$ in the case shown. **(i–l)** large $\nu > 1$ and large $\alpha > x_{eq}$, leading to smoother heterogeneous states without sharply localized clusters. $\nu = 10$ and $\alpha = 0.94$ in the case shown.

smoother heterogeneous configurations without sharply localized clusters. Importantly, these patterns emerge despite the absence of any imposed environmental heterogeneity in the lattice sites, suggesting an intrinsic spatial organization driven by ESBB dispersal and local dynamics. Illustrative examples are shown in Figure 4.8, including the distribution $P(\curvearrowright)$ of site abundances (fourth column), which is unimodal in the homogeneous and smooth regimes and becomes bimodal in the clustered case.

4.10.2 Spatial ESBB persistence in the absence of immigration

A qualitative difference between the well-mixed and spatially explicit models emerges when the constant beetle immigration term λ is set to zero. In the well-mixed formulation, $\lambda = 0$ leads to

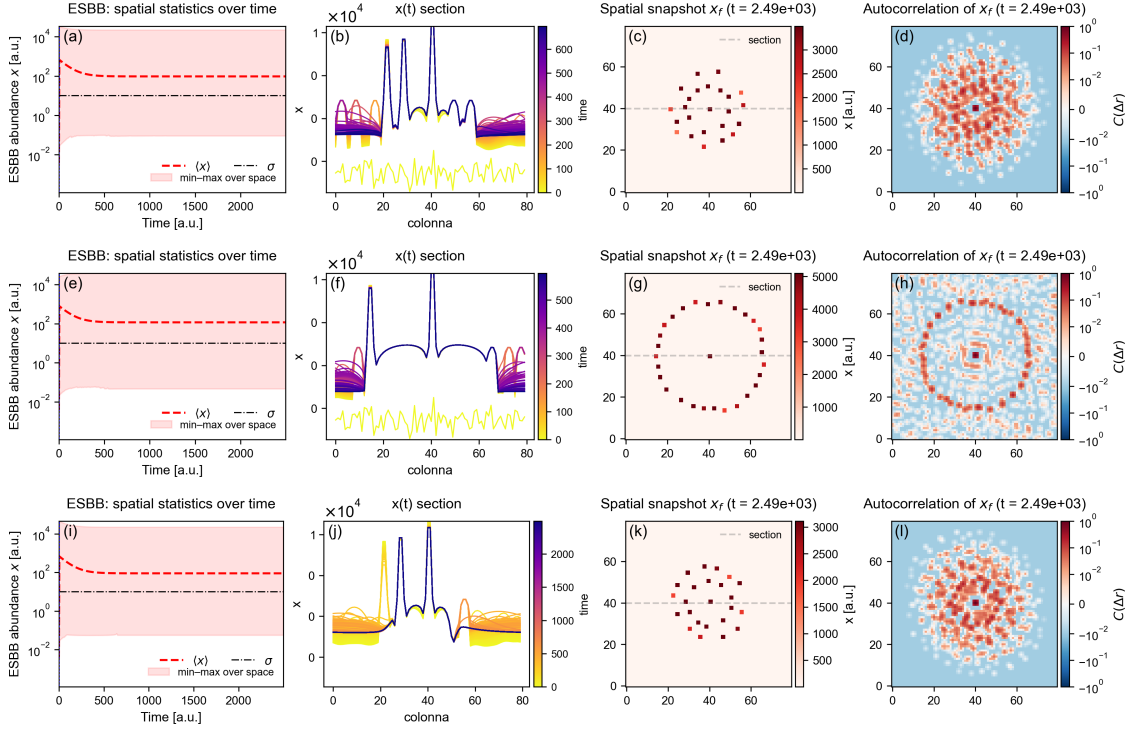


FIG. 4.9. Illustrative examples of long-lived spatial configurations obtained in the spatially explicit ESBB model at $\lambda = 0$ for different choices of tree demographic parameters. **First column:** spatial statistics over time. **Second column:** temporal evolution of a one-dimensional spatial section of the ESBB abundance along a fixed lattice row. **Third column:** final spatial snapshots of the ESBB abundance; the dashed line indicates the lattice row from which the sections shown in the second column are extracted. **Fourth column:** normalized spatial autocorrelation functions computed from the final configurations. After an initial transient characterized by propagating fronts of ESBB activity, the system settles into spatially heterogeneous configurations that remain effectively unchanged over the simulated time scales. The healthy and vulnerable tree populations show analogous trends and distributions. These examples are shown for illustrative purposes and do not imply asymptotic stability or rigorous persistence. Panels (a–d), and (e–h) correspond to different values of tree demographic parameters. **(a–d):** $\varepsilon=1, \rho=0.1, \eta \approx 1.37$. **(e–h):** $\varepsilon=0.1, \rho \approx 0.14, \eta \approx 1.37$. **(i–l):** $\varepsilon=1, \rho \approx 0.14, \eta \approx 1.37$. Simulations are run on a two-dimensional 80×80 lattice with periodic boundary conditions, using as initial condition a localized patch of susceptible trees of finite radius r and fixing $\alpha \equiv \sigma = 10$ and $\nu = 100$.

beetle extinction. In contrast, numerical simulations of the spatial model suggest that long-lived, seemingly stable spatial configurations can persist over extended time scales even in the absence of external influx.

In these simulations, beetles survive by forming localized regions of activity, often following an initial transient similar to traveling waves or moving fronts. The long-term spatial configuration depends on the relative time scales of tree demography and beetle dynamics. Depending on the relative time scales of tree demography and beetle dynamics, the system settles into different spatially heterogeneous configurations, whose representative examples of such configurations are shown in Figure 4.9.

While these results do not establish persistence in a rigorous or asymptotic sense, they indicate that spatial structure and bark-beetle dispersal can substantially enhance insect population persistence

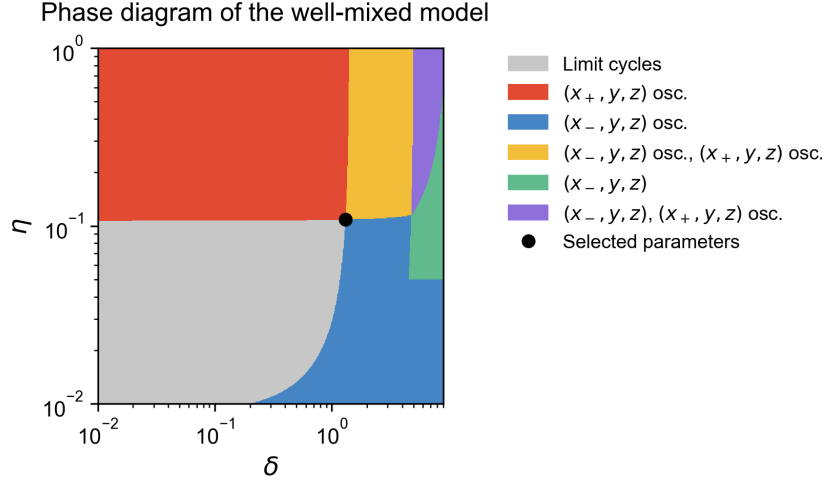


FIG. 4.10. Phase diagram of the well-mixed ESBB model in the (δ, η) parameter plane. Colored regions correspond to qualitatively different dynamical regimes, including stable endemic or epidemic equilibria, damped oscillations, sustained oscillations, and parameter regions with no stable fixed point. The black dot marks a representative point located in the immediate vicinity of the intersection of four distinct phases. In the spatial simulations discussed in this section, parameters are chosen close to this point and approached from within the neighboring phases.

compared to the well-mixed case.

4.10.3 Dynamics near a well-mixed transition

To probe the spatial dynamics in the vicinity of a transition in the well-mixed ESBB model, we perform simulations with parameters chosen close to the phase-boundary point in the well-mixed phase diagram (Figure 4.10). In this set of explorations we keep a small but nonzero uniform input $\lambda = 10^{-5}$, since at $\lambda = 0$ the well-mixed model does not display a stable fixed point and the corresponding phase boundaries cannot be defined in the same way. Simulations are run on a two-dimensional 80×80 lattice with periodic boundary conditions, using as initial condition a localized patch of susceptible trees of finite radius r , representing a localized perturbation of the forest system, and fixing $\alpha \equiv \sigma = 10$ and $\nu = 100$. In the following, localized outbreak *hotspots* are operationally defined as connected clusters of adjacent lattice sites in which the beetle density exceeds the mass-attack threshold σ .

Across the parameter regions considered, a common qualitative feature is the emergence of spatially structured transient dynamics, often involving epidemic waves of ESBB activity propagating through space and the formation of localized hotspots. Depending on the phase from which the transition is approached in the well-mixed model, these transients are followed either by relaxation toward an inactive, homogeneous configuration or by the onset of long-lived oscillatory regimes, corresponding to recurrent outbreak dynamics. In all cases, the transient dynamics depend sensitively on the radius r of the initial susceptible-tree patch.

When parameters lie close to the transition within the gray region of Figure 4.10, where the well-mixed model exhibits limit cycles, the spatial system displays an initial transient in which epidemic activity spreads across the system, followed by sustained oscillations of the mean ESBB abundance $\langle x \rangle$ around the mass-attack threshold (see panels a–d of Figure 4.11). These oscillations

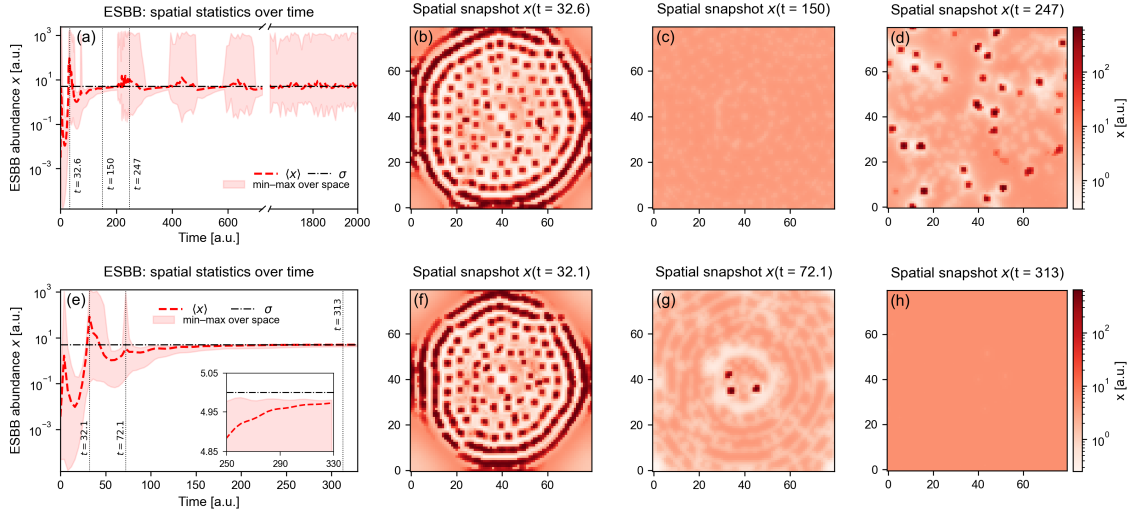


FIG. 4.11. Spatiotemporal dynamics of the spatial ESBB model near the well-mixed transition. **(a–d)** Sustained oscillatory regime, observed within the epidemic oscillatory phase and also occurring within limit cycle region, close to the transition in the well-mixed phase diagram. **(a)** Time evolution of the spatially averaged beetle abundance $\langle x \rangle$ (red dashed), compared with the mass-attack threshold σ and the spatial min–max band (shaded). Vertical dashed lines indicate the times at which spatial snapshots are shown. The extended time window shows that, at long times, the dynamics of the system undergoes changes in temporal regularity, ranging from repeated epidemic waves to more irregular population oscillations, reflecting the variability observed within the oscillatory regimes. **(b)** Snapshot during the initial transient, characterized by a wave of elevated activity propagating across the system and the emergence of multiple localized hotspots. **(c)** Snapshot during a quiescent phase, with low beetle abundance and weak spatial structure. **(d)** Snapshot during an active phase, showing renewed localized outbreak activity, with hotspots that change position and size over time, and may merge, split, or disappear. **(e–h)** Transient epidemic-wave dynamics with relaxation to a homogeneous endemic state, observed close to the transition in the parameter region corresponding to the stable endemic phase of the well-mixed model. **(e)** Time evolution of $\langle x \rangle$, showing an initial transient with epidemic waves followed by relaxation toward a homogeneous endemic state with $\langle x \rangle < \sigma$. At long times, the ESBB population remains below the mass-attack threshold at all spatial sites, as evidenced by the zoomed inset. **(f, g)** Spatial snapshots of active phases during the transient stage, illustrating the propagation of epidemic waves and the temporary formation of localized outbreak hotspots. **(h)** Late-time snapshot after relaxation, characterized by low beetle abundance and the absence of pronounced spatial structure.

correspond to recurrent epidemic waves alternating with quiescent phases, and are associated with the continuous appearance, displacement, and disappearance of localized outbreak hotspots. Depending on the realization, the oscillations may remain relatively regular over long times, progressively become more frequent and lose temporal coherence (see Figure 4.11a), or conversely reorganize from an initially disordered regime into more coherent epidemic waves. The frequency and intensity of these oscillations also appear to be influenced by the initial radius r , although no systematic dependence was established within the present numerical exploration.

Similar dynamical behavior of the spatial system is observed in the red region of Figure 4.10, which corresponds in the well-mixed model to a stable epidemic phase ($x > \sigma, y, z$) with damped oscillations and high reactivity $R \sim 43$.

The blue region of Figure 4.10 represents instead a stable endemic phase ($x < \sigma, y, z$) of the well-mixed model, characterized by damped oscillations and high reactivity $R \sim 25$. In the spatial

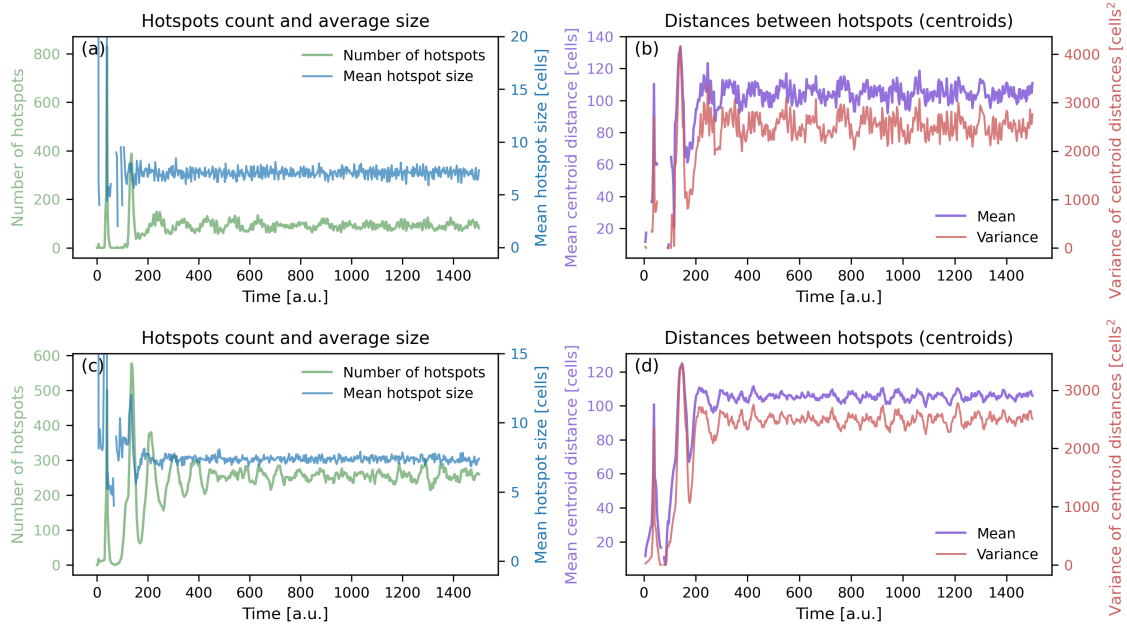


FIG. 4.12. Cluster statistics in the epidemic regime near the well-mixed transition (spatial grid 200×200), for two values of the threshold-smoothing parameter. **Top:** weak threshold smoothing. **Bottom:** strong threshold smoothing. **Left:** Number of detected hotspots (green, left axis) and mean hotspot area (blue, right axis, in cells). **Right:** Mean (purple, left axis) and variance (red, right axis, in cells^2) of pairwise distances between hotspot centroids. After an initial transient, the system reaches a regularly oscillating state in which these observables fluctuate around well-defined plateaus. While the hotspot count is sensitive to the smoothing level (segmentation/merging effect), the characteristic hotspot size and inter-hotspot spacing remain comparatively stable across smoothing choices. Parameters correspond to a regime close to the well-mixed transition, within the oscillatory epidemic phase with reactivity $R \sim 42$.

system, propagating wave-like patterns again develop during a transient stage. However, rather than triggering a sustained oscillatory regime, their amplitude progressively decreases and the system eventually relaxes toward a nearly homogeneous endemic state with $\langle x \rangle < \sigma$ (see panels e–h of Figure 4.11). The number of epidemic waves also appears to be influenced by the radius r of the initial susceptible-tree patch: larger initial perturbations tend to generate a greater number of epidemic waves and longer transient phases before relaxation, although the present numerical exploration does not establish a systematic dependence on r .

4.10.4 Robustness and limitations

A number of numerical checks were performed to assess the robustness of the phenomenology reported above. In particular, replacing the sharp mass-attack and aggregation thresholds with smooth approximations does not qualitatively alter the main dynamical regimes observed. The emergence of epidemic waves, localized hotspots, and long-lived transient phases is preserved across a broad range of smoothness parameters. At the same time, within the explored parameter sets, increasing the threshold smoothness has a noticeable effect on the dynamics, leading to oscillations with reduced high-frequency fluctuations and to spatial structures that appear more continuous and “particle-like”, with localized hotspots that persist longer and show more clearly identifiable spatial drift and merging/splitting events. Similarly, increasing the system size affects the number and duration of transient outbreak phases, but does not modify the qualitative nature of

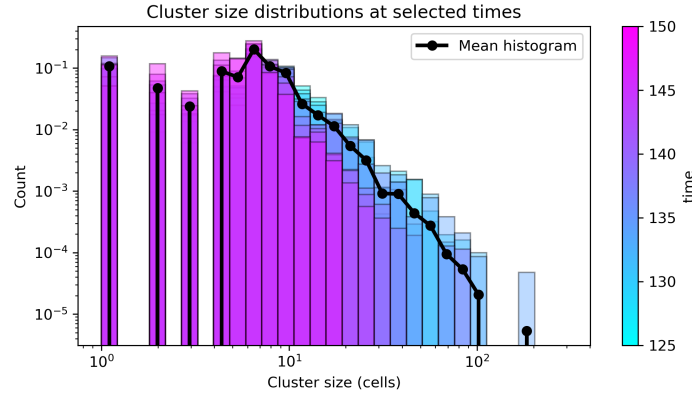


FIG. 4.13. Cluster-size distributions in the epidemic regime near the well-mixed transition (spatial grid 200×200 , same parameter set as Fig. 4.12). Histograms show the probability distribution of hotspot sizes (in number of lattice cells) on logarithmic axes; colors indicate different times, while the black line represents the temporal average distribution. The distributions are computed over a restricted time window to reduce the impact of temporal variability in the dynamics. The distributions display a broad decay over an intermediate range of cluster sizes, without a clear characteristic scale, and exhibit a cutoff at large sizes consistent with the finite system size.

the spatiotemporal dynamics.

As an additional descriptive diagnostic, we also consider simple hotspot statistics; representative examples for two smoothing values are shown in Figure 4.12. An illustrative example of the observed cluster-size distributions is shown in Figure 4.13. While not pursued further here, these cluster-level observables could provide a compact and ecologically interpretable description of spatiotemporal outbreak organization.

Despite these robustness checks, the present numerical exploration remains necessarily incomplete. The spatial ESBB model combines multiple threshold mechanisms, explicit dispersal, and high-dimensional spatial coupling, resulting in a particularly rich and complex dynamical structure. For this reason, numerical simulations alone are not sufficient to provide a systematic or exhaustive characterization of the model behavior across parameter space. A deeper understanding of the observed regimes would require analytical guidance, at least in suitably simplified limits, to identify the mechanisms responsible for localized hotspot formation, long-lived transients, and spatial persistence. Such an analytical treatment has not been developed here and is therefore left for future work. Accordingly, the results presented in this section should be regarded as exploratory evidence highlighting the potential richness of the spatial ESBB model, rather than as definitive or comprehensive conclusions.

4.11 Concluding remarks

Despite the limited scope of the present exploration, the spatial ESBB model provides a concrete and transparent spatial generalization of the well-mixed ESBB framework, in which thresholds, dispersal mechanisms, and local population dynamics are consistently combined.

The preliminary numerical investigations presented here indicate that the explicit inclusion of space can qualitatively enrich the system's dynamics. Even in the absence of imposed environmental heterogeneity, the interaction between nonlinear aggregation in dispersal and local demographic

processes gives rise to spontaneous spatial organization, long-lived transient outbreak dynamics, and localized regions of sustained beetle activity. These exploratory findings suggest that spatial coupling can substantially modify the dynamical regimes predicted by well-mixed formulations, particularly in parameter regions close to phase transitions, offering a promising starting point for future investigation.

A key next step is to turn the exploratory spatial extension into an analytically interpretable framework by working in simplified limits where dominant mechanisms can be isolated. This would enable a principled study of when aggregation emerges, how wave-like transients propagate, and under what conditions spatial coupling can sustain long-lived active configurations.

A central challenge will be to define a small set of robust spatial observables—for instance hotspot lifetimes and sizes, front speeds, and clustering measures—that compress the high-dimensional dynamics into reproducible signatures. These observables would provide common targets for analysis, numerical exploration, and empirical confrontation, and they would make it possible to compare regimes across parameter changes without relying on visually qualitative pattern descriptions. Once such signatures are in place, the spatial model can be linked more directly to spatial outbreak proxies, including products derived from remote sensing [6–8], shifting validation from pointwise time series to spatiotemporal pattern statistics.

Finally, the management analysis in the well-mixed ESBB model motivates framing mitigation as a dynamical control problem, in which timing and spatial targeting may matter as much as overall intervention intensity. Extending this perspective to the spatial setting would provide a principled way to assess when localized actions can suppress, redirect, or fragment outbreak propagation, and to identify intervention strategies that exploit intrinsic outbreak time and length scales.

In conclusion, further development of the spatial extension of the ESBB model would represent a concrete step toward linking individual-level mechanisms with large-scale outbreak dynamics in spatially structured ecological systems.

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5

Conclusions and perspectives

By combining analytically tractable models with exploratory numerical investigations, this thesis investigates how stochasticity, nonlinear interactions, and dispersal shape the dynamics of spatially distributed populations, with particular emphasis on persistence thresholds and transitions between dynamical regimes. Across distinct modeling frameworks, it highlights how population-level outcomes emerge from underlying individual-level processes and how departures from deterministic and mean-field assumptions can qualitatively affect ecological dynamics.

A first set of results concerns finite-size stochasticity in metapopulations (Chapter 2). In parameter regimes where deterministic dynamics predicts long-term persistence, finite local population size makes extinction ultimately unavoidable and turns persistence into a metastable phenomenon, whose ecological relevance is controlled by extinction-time scales rather than by equilibrium states. Within a simplified setting with effectively mean-field dispersal, Section 2.4 characterizes extinction-time statistics near the deterministic persistence threshold and derives finite-size scaling forms for survival probabilities as a function of the distance from criticality, including analytical scaling exponents (Table 2.1). These results translate deterministic persistence criteria into quantitative predictions of stochastic extinction risk and persistence time scales. One interesting direction for future developments is to assess the robustness of these scaling predictions beyond mean-field dispersal by introducing explicit spatial connectivity. More generally, the existence of long-lived metastable states provides a natural setting to study persistence under environmental perturbations, highlighting that demographic noise is not merely a complicating factor but can carry early-warning information about system stability.

A second theme is addressed in Chapter 3, where dispersal evolution is studied in discrete-time stochastic metapopulations with finite local population size. The central outcome is that demographic fluctuations do not merely add noise around mean-field trajectories: when coupled to nonlinear population updates, they generate systematic corrections to effective growth and selection (Section 3.4), so that invasion conditions and competitive outcomes can differ qualitatively from naive deterministic expectations. As a consequence, the evolutionarily favored dispersal effort can undergo a finite-size transition, with thresholds that shift with local population size and can reverse which strategy is selected in the long run, as shown in Section 3.3. An exploratory extension outlined in Section 3.6 further indicates that persistent spatial heterogeneity can interact with these finite-size effects, modulating invasion boundaries and evolutionary outcomes beyond what mean habitat quality alone would predict. These results suggest treating persistent environmental heterogeneity as a first-class driver of dispersal evolution, rather than a secondary refinement. A natural follow-up is to map more systematically how patch-to-patch variability interacts with finite

local population size to shift invasion boundaries and long-run evolutionary outcomes. This would clarify which features of heterogeneity control the heterogeneous phase diagram and motivate broader generalizations beyond discrete patch classes.

Finally, Chapter 4 turns to a biologically motivated forest–insect system and develops a minimal model of Norway spruce–bark beetle outbreak dynamics. By incorporating threshold-driven mass attacks and feedbacks between beetle density and host availability, the model predicts a reactive endemic regime under present-day conditions, in which perturbations trigger transient outbreaks followed by recovery (Section 4.3.1). When parameters are shifted to represent increased and sustained forest vulnerability, the same feedbacks can shift the system into a distinct regime dominated by intrinsically recurrent outbreaks (Section 4.3.3). Sections 4.3.5 and 4.3.4 analyze idealized disturbances and periodic management respectively, revealing a critical timing sensitivity for outbreak suppression.

Within this broader context, the spatially explicit extension of the Norway spruce–bark beetle model (Section 4.9) represents a natural synthesis of the main themes addressed throughout the thesis. Preliminary numerical investigations points to additional dynamical richness when movement and local interactions are made explicit (Section 4.10). A key next step is a systematic characterization of spatial patterns and cluster statistics, together with analytical progress on simplified limits of the continuum formulation. Moreover, the explicitly spatial nature of the model opens the possibility of direct comparisons with spatially resolved outbreak statistics, derived for instance from remote sensing data.

Overall, this thesis shows that variability and nonlinearity in spatial systems can yield important ecological outcomes that are not always captured by deterministic equilibrium intuition. By developing minimal mechanistic models and tractable reduced descriptions, it connects microscopic processes to macroscopic predictions for persistence times, invasion thresholds, and outbreak propensity. This offers a coherent starting point for extending the results to more explicitly structured landscapes and, potentially, for comparisons with empirical observations.

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