

# A METAPOPOPULATION MODEL WITH DISCRETE SIZE STRUCTURE

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**ABSTRACT.** We consider a discrete size-structured metapopulation model with the proportions of patches occupied by  $n$  individuals as dependent variables. Adults are territorial and stay on a certain patch. The juveniles may emigrate to enter a dispersers' pool from which they can settle on another patch and become adults. Absence of colonization and absence of emigration lead to extinction of the metapopulation. We define the basic reproduction number  $\mathcal{R}_0$  of the metapopulation as a measure for its strength of persistence. The metapopulation is uniformly weakly persistent if  $\mathcal{R}_0 > 1$ . We identify subcritical bifurcation of persistence equilibria from the extinction equilibrium as a source of multiple persistence equilibria: it occurs, e.g., when the immigration rate (into occupied patches) exceeds the colonization rate (of empty patches). We determine that the persistence-optimal dispersal strategy which maximizes the basic reproduction number is of bang-bang type: If the number of adults on a patch is below carrying capacity all the juveniles should stay, if it is above the carrying capacity all the juveniles should leave.

## 1. INTRODUCTION

A metapopulation is a group of populations of the same species which occupy separate areas (patches) and are connected by dispersal. Each separate population in the metapopulation is referred to as a local population. Metapopulations occur naturally or by human activity as a result of habitat loss and fragmentation. An overview of the empirical evidence for the existence of metapopulation dynamics can be found in [31]. Further ecological examples of Levins-type metapopulations are also discussed in [23].

The metapopulation concept has gained acceptance in the last fifteen years and has become a major theoretical tool in population biology. The rapid increase of citations of “metapopulation” [27], the number of recent books on the subject [15, 28, 22, 26] and the frequent use of the concept in genetics, evolutionary biology, conservation biology [41], landscape ecology and others testify to the rising importance of metapopulation theory.

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*Metapopulation Models with Discrete Size-Structure.* Spatially implicit metapopulation models as the one considered here allow for the extinction and recolonization of patches, but ignore the location of patches. Though patch area could be incorporated as an independent variable, it is neglected here for mathematical tractability. As an extension of the classical Levins framework [37, 38], our model structures the fraction of occupied patches by the local population size taken as a discrete variable. We assume a finite though large number of patches,  $N$ . Furthermore, all patches are assumed equal and capable of supporting very large population sizes while the actual number of occupants may be very small. The vital rates of the local population depend on the number of individuals living on a patch. Metapopulation models with discrete patch-size are obtained as approximations of stochastic mean field metapopulation models [1]. They are indeed generalizations of the Levins model in the sense that the Levins model can be recovered as a reasonable approximation [3].

Differently from [1, 2, 3, 5, 45] where all occupants of a patch can emigrate with the same probability, we assume that only juveniles emigrate, while adults stay on their patch [42]. We explicitly model the dispersing individuals [6, 7, 42]. Dispersing individuals do not reproduce because the resources necessary for reproduction are only available on patches. If the dispersal period were very short, the dispersers could be eliminated as an explicit variable as it has been done in [1, 2, 3, 5, 45].

In both cases, dispersal is modeled under the assumption that all patches freely exchange individuals and immigration and emigration depend only on the local population size but not on the distance between the patches or their area.

From a mathematical point of view, metapopulation models with discrete patch-size structure as well as host-macroparasite models which differentiate the hosts by their discrete parasite loads [21, 51, 52] represent a specific class of infinite systems of ordinary differential equations. We discuss a general theory of such systems in [40] and derive many properties of the model here as special cases, including its well-posedness.

Metapopulation models with discrete size structure have continuous analogs in which the local population size is a continuous variable. A procedure for transition from a discrete to a continuous model is described in [42]. A continuous size-structured metapopulation model was first derived in terms of differential equations [16] and then recast in the setting of general deterministic structured population models [17, 12, 13]. Another type of models which are concerned with patch occupancy, rather than number of individuals, are stochastic patch occupancy models (SPOMs) [47]. SPOMs represent the core of the spatially realistic metapopulation theory.

Size-structured metapopulation models are notably well adept for the investigation of questions related to the influence of migration and dispersal on the dynamics of the metapopulation.

*Persistence-extinction dynamics: the impact of colonization.* Extinction occurs on two scales in the metapopulation dynamics: local extinction and extinction of the entire metapopulation [25]. Small local populations are particularly prone to local extinction. In reality, local extinction can be a result of demographic stochasticity (e.g. too many individuals die before reproduction), genetic stochasticity (e.g. loss of fitness due to inbreeding), environmental stochasticity (sudden drought or freeze) [35, 36, 14], or human destruction of natural habitats. In our model, local extinction can occur through a series of deaths or by a “catastrophe” which abruptly turns a patch occupied by  $n$  individuals into an empty patch. Catastrophes are a result of extreme environmental stochasticity. We assume that they occur at a rate which depends on the local population size,  $\kappa_n$ .

Local extinctions may be common without leading to extinction of the entire metapopulation because patches that have become vacant are often quickly recolonized. The transfer of individuals from one patch to another is a key process in metapopulations [34]. The components of the transfer process are emigration/immigration, dispersal and colonization which are all incorporated in our model. Dispersing individuals  $D(t)$  are modeled through a separate equation with all relevant vital dynamics. In this respect, our model is similar to the one discussed in [6] as well as the continuous size-structured models [16]. We assume that only the juveniles are subject to emigration: a proportion  $1 - q_n$  which depends on the local population size  $n$  emigrates and enters the dispersal pool  $D(t)$ . Dispersers settle on a patch with  $n$  adults with immigration rate  $\sigma_n$ ,  $n \geq 1$ , or colonize an empty patch at a colonization rate  $\sigma_0$ .

Concerning the interplay between local extinction and migration/colonization, our main result shows that the metapopulation eventually goes extinct if there is no colonization of empty patches,  $\sigma_0 = 0$ . This is independent of whether or not dispersers settle on already occupied patches and even holds when the effect of local catastrophes is ignored,  $\kappa_n = 0$ . Two other scenarios lead to obligatory extinction of the metapopulation as well: the case when all juveniles stay in the patch where they were born,  $q_n = 1$  for all  $n \geq 1$ , and the case when for all local populations the birth rate,  $\beta_n$ , is strictly smaller than the death rate,  $\mu_n$ .

In analogy with epidemiology and single-population dynamics, we determine a basic reproduction number of the metapopulation,  $\mathcal{R}_0$ , in the case with no catastrophes,  $\kappa_n = 0$ . In the context of our model,  $\mathcal{R}_0$  gives the number of secondary dispersing individuals that one dispersing individual will produce if all patches are empty initially. The immigration rates into occupied patches,  $\sigma_n$ ,  $n \geq 1$ , have no impact on the basic reproduction number.

$\mathcal{R}_0$  may have different interpretations in other metapopulation models; some can be found in [25, 33]. In our case, as well as in the continuous size-structured models, the basic reproduction number is a measure for the strength of persistence of the metapopulation. If  $\mathcal{R}_0 > 1$ , under reasonable

extra assumptions, the total population size remains bounded away from zero for all initial configurations (except the one where the metapopulation is extinct). If  $\mathcal{R}_0 < 1$ , the metapopulation necessarily dies out if its total populations size is sufficiently small.

Dispersal is a key element of metapopulation dynamics and is one of the central concepts in ecology and evolutionary biology [9]. The evolution of dispersal in metapopulations has received significant attention in the literature recently [32] and particularly in the setting of structured metapopulation models (see [46, 48, 49, 18, 50] and the references therein). In this paper, we investigate which dispersal strategies maximize the basic reproduction number, and therefore, the strength of persistence of the metapopulation. We call those *persistence-optimal dispersal strategies*. It turns out that there always are persistence-optimal strategies of bang-bang type: If the number of adults on a patch is below carrying capacity all juveniles should stay, if it is above the carrying capacity all juveniles should leave.

Analogous considerations in epidemics teach that a persistence-optimal strategy may [4] or may not [10] be an evolutionarily stable strategy. The basic reproduction number only measures how a metapopulation performs in an almost empty habitat. It does neither a priori indicate whether or not a mutant strain can invade a well-established existing strain which has a lower basic reproduction number, nor whether or not a well-established strain can be invaded by a strain which has a higher basic reproduction number. Invasion studies for this model have been done in [42], but while it is shown that evolutionarily stable strategies are of bang-bang type, indeed, for continuously structured metapopulations, this question seems to be still open for discrete structure.

*Subcritical bifurcation and multiple equilibria.* There are scenarios in which the basic reproduction number satisfies  $\mathcal{R}_0 < 1$  but the metapopulation can survive provided that it starts out from a sufficiently large size. This can occur as a result of subcritical bifurcation of persistence equilibria from the extinction equilibrium. The phenomenon of subcritical bifurcation with multiple equilibria of alternating stability was first discovered in a metapopulation model in the setting of continuous size-structured models [16]. It was also observed in a much simpler model of Levins type [29] with spatial variation in the patch size. The simple model consists of a single equation and exhibits subcritical bifurcation if a “rescue effect” is introduced in the form of a decreasing rate of extinction of local populations. The observation that the rescue effect leads to multiple stable equilibria was used to form a core-satellite hypothesis - a hypothesis that provides a possible metapopulation dynamic explanation of the bimodal distribution of site occupancy frequencies which has been observed for plants or animals in nature [29]. A rescue effect was also found to lead to multiple stable equilibria (see [22], section 4.3) in a model with a small and a large population first introduced in [24]. The theoretical predictions of the mathematical models were tested

against the extensive data on the butterfly *Melitaea cinxia* where a striking bimodal distribution of the fraction of occupied patches was found [30].

Subcritical bifurcation and multiple stable equilibria have caused significant interest in the mathematical epidemiology literature, too, in the last ten years (see [39] and the references therein), despite the fact that their practical confirmation in that setting remains elusive. Models of macro-parasitic diseases share with the metapopulation models not only the general mathematical structure [40] but also the presence of multiple equilibria [20].

The possibility that discrete size-structured metapopulation models may be able to support multiple persistence equilibria was conjectured in [42]. We establish this fact rigorously here by providing a necessary and sufficient condition for subcritical bifurcation of persistence equilibria from the extinction equilibrium. Conditions for the existence and global stability of a unique nontrivial equilibrium is established in [2] for a model without explicit dispersal. We also show that in the case of multiple persistence equilibria, every other equilibrium is unstable.

It has been established in size-structured metapopulation models [17] that subcritical bifurcation occurs if the impact of migration on local dynamics is sufficiently large. In this paper we confirm this observation in the framework of discrete size-structured models. Furthermore, in the special case of obligatory juvenile emigration, we show that this phenomenon occurs if and only if the immigration rate is sufficiently larger than the colonization rate  $\sigma_0 < \sigma_n$ ,  $n \geq 1$ .

The paper is structured as follows:

2. The model and its well-posedness
3. Extinction and persistence equilibria
4. Subcritical bifurcation and multiple persistence equilibria
5. Obligatory juvenile emigration
6. Conditions for persistence and extinction of the metapopulation
7. A bang-bang principle of persistence-optimal emigration
- A. Proofs of the results in Section 7

## 2. THE MODEL AND ITS WELL-POSEDNESS

We consider a population living in a patchy habitat. We ignore gender and genetics. Adult individuals are territorial and live on a fixed patch. Juvenile individuals may leave the patch on which they are born, disperse between patches and finally settle on a new patch (from which moment they are also considered adults). Rather than considering the population sizes on the various patches, we consider the proportion of patches which have a certain population size.

*List of symbols**Independent variables*

- $t$  time  
 $n$  number of individuals on a patch

*Dependent variables*

- $D(t)$  number of dispersing individuals at time  $t$   
 $u_n(t)$  proportion of patches with  $n$  individuals at time  $t$

*Parameters and parameter functions*

- $N$  number of patches  
 $\delta$  per capita death rate of a dispersing individual  
 $\rho = \delta/N$   
 $q_n$  probability that a newborn individual stays on its birth patch with  $n$  adult individuals  
 $\beta_n$  rate at which a patch with  $n$  adult individuals produces one offspring  
 $\mu_n$  rate at which an adult dies in a patch with  $n$  adults  
 $\kappa_n$  rate at which catastrophes hit a patch with  $n$  adults  
 $\sigma_n$  rate at which a dispersing individual settles on a patch with  $n$  adults (immigration rate)  
 $\sigma_0$  rate at which a dispersing individual settles on an empty patch (colonization rate)

*Model equations.* We write  $\mathbb{N}$  for the set of natural numbers  $1, 2, 3, \dots$ , and  $\mathbb{Z}_+$  for the set of non-negative integers,  $\mathbb{Z}_+ = \mathbb{N} \cup \{0\}$ . There is a constant number of patches,  $N \in \mathbb{N}$ . The proportion of patches with  $n$  occupants, at time  $t$ , is denoted by  $u_n(t)$ .  $\sum_{j=1}^{\infty} j u_j(t)$  is the average number of occupants per patch,

$$R(t) = N \sum_{j=1}^{\infty} j u_j(t)$$

the total number of patch occupants.  $D(t)$  denotes the average number of dispersing individuals at time  $t$ ,

$$D(t) = \sum_{j=1}^{\infty} j \pi_j(t),$$

where  $\pi_j(t)$  is the probability that  $j$  is the number of dispersing individuals at time  $t$ .  $P = R + D$  is the average total number of individuals. The patch emigration rate is given by

$$E(t) = N \sum_{n=1}^{\infty} (1 - q_n) \beta_n u_n(t),$$

the per capita rate of a disperser to settle on a patch by

$$I(t) = N \sum_{n=0}^{\infty} \sigma_n u_n(t).$$

We obtain the following relations:

$$\begin{aligned} u'_0(t) &= \mu_1 u_1(t) + \sum_{n=1}^{\infty} \kappa_n u_n(t) - \sigma_0 D(t) u_0(t), \\ u'_n(t) &= [q_{n-1} \beta_{n-1} + \sigma_{n-1} D(t)] u_{n-1}(t) + \mu_{n+1} u_{n+1}(t) \\ &\quad - [q_n \beta_n + \sigma_n D(t) + \mu_n + \kappa_n] u_n(t), \quad n = 1, 2, \dots \\ D(t) &= \sum_{j=1}^{\infty} j \pi_j(t), \\ \pi'_0(t) &= (\delta + I(t)) \pi_1(t) - E(t) \pi_0, \\ \pi'_n(t) &= E(t) \pi_{n-1} + (\delta + I(t)) (n+1) \pi_{n+1}(t) \\ &\quad - (E(t) + [\delta + I(t)] n) \pi_n(t), \quad n = 1, 2, \dots \end{aligned}$$

We substitute the differential equations for  $\pi_n$  into  $D$  and obtain

$$D' = N \sum_{n=1}^{\infty} (1 - q_n) \beta_n u_n(t) - \left[ \delta + N \sum_{n=0}^{\infty} \sigma_n u_n(t) \right] D.$$

So the system can be condensed into the following form,

$$(2.1) \quad \begin{cases} u'_0(t) = \mu_1 u_1(t) + \sum_{n=1}^{\infty} \kappa_n u_n(t) - \sigma_0 D(t) u_0(t), \\ u'_n(t) = [q_{n-1} \beta_{n-1} + \sigma_{n-1} D(t)] u_{n-1}(t) + \mu_{n+1} u_{n+1}(t) \\ \quad - [q_n \beta_n + \sigma_n D(t) + \mu_n + \kappa_n] u_n(t), \quad n = 1, 2, \dots, \\ D' = N \sum_{n=1}^{\infty} (1 - q_n) \beta_n u_n(t) - \left( \delta + N \sum_{n=0}^{\infty} \sigma_n u_n(t) \right) D. \end{cases}$$

The system is equipped with initial conditions,

$$u_j(0) = \check{u}_j \quad \forall j \in \mathbb{N}, \quad \text{and} \quad D(0) = \check{D} \geq 0.$$

In addition, since  $\check{u}_j$  are proportions, they satisfy

$$0 \leq \check{u}_j \leq 1 \quad \forall j \in \mathbb{N}$$

and they all add to one,

$$(2.2) \quad \sum_{j=0}^{\infty} \check{u}_j = 1.$$

Adding all equations for the proportions in system (2.1), we obtain

$$\sum_{j=0}^{\infty} u'_j = 0,$$

which implies that the sum of all  $u_j$  is a constant, namely,

$$(2.3) \quad \sum_{j=0}^{\infty} u_j(t) = 1 \quad \forall t \geq 0.$$

This property reflects the biological meaning of  $u_j(t)$ , namely the proportion of patches occupied by  $j$  individuals.

We introduce some reasonable assumptions concerning the parameters of the system.

**ASSUMPTION 2.1.** *Throughout this paper we assume the following*

- (a)  $\beta_n, \kappa_n \geq 0$ ,  $\mu_n > 0$  for all  $n \in \mathbb{N}$ ,  $\sup_{n=1}^{\infty} \frac{\beta_n}{n} < \infty$ .
- (b)  $0 \leq q_n \leq 1$  for all  $n \in \mathbb{N}$ .
- (c)  $\sigma_n \geq 0$  for all  $n \geq 0$ ,  $\sup_{n=0}^{\infty} \sigma_n < \infty$ .

Since our system consists of infinitely many differential equations, it cannot be solved as such. If we integrate both sides of each equation in system (2.1), we obtain an infinite system of integral equations the solutions of which are called integral solutions of (2.1). The theorem below demonstrates that system (2.1) together with the appropriate initial conditions always has a unique integral solution. The biological interpretation suggests the state space  $\mathbb{R} \times \ell^{11}$  where  $\ell^{11}$  is the Banach space of sequences  $u = (u_n)_{n=0}^{\infty}$  whose norm  $\|u\| = |u_0| + \sum_{n=1}^{\infty} n|u_n|$  is finite.

**Theorem 2.2** ([40]). *Let the Assumptions 2.1 be satisfied. Then, for every nonnegative initial condition satisfying  $\sum_{j=1}^{\infty} j\check{u}_j < \infty$ , there exists a unique non-negative continuous integral solution  $(D, u) : [0, \infty) \rightarrow \mathbb{R} \times \ell^{11}$  of (2.1),  $u(t) = (u_n(t))$ .*

### 3. EXTINCTION AND PERSISTENCE EQUILIBRIA

There is one obvious equilibrium, the extinction (trivial) equilibrium which is given by  $u_0 = 1$ ,  $u_n = 0$  for  $n \geq 1$ ,  $D = 0$ . In the remainder of this section, we discuss the persistence (nontrivial) equilibria. In order to get explicit expressions which can be interpreted biologically, we consider the case without catastrophes,  $\kappa_n = 0$  for all  $n \in \mathbb{N}$ . Let  $u_n(t) = u_n^*$ ,  $D(t) = D^*$  be an equilibrium solution. First we notice that an equilibrium solution must satisfy

$$(3.1) \quad \sum_{n=0}^{\infty} u_n^* = 1.$$



By setting the time derivatives equal to zero in (2.1), we obtain

$$(3.2) \quad \begin{aligned} 0 &= \mu_1 u_1^* - \sigma_0 D^* u_0^*, \\ 0 &= [q_{n-1} \beta_{n-1} + \sigma_{n-1} D^*] u_{n-1}^* + \mu_{n+1} u_{n+1}^* \\ &\quad - [q_n \beta_n + \sigma_n D^* + \mu_n] u_n^*, \quad n \geq 1. \end{aligned}$$

For the number of dispersers,  $D^*$ , setting

$$\delta = N\rho,$$

we obtain

$$(3.3) \quad 0 = \sum_{n=1}^{\infty} (1 - q_n) \beta_n u_n^* - \left[ \rho + \sum_{n=0}^{\infty} \sigma_n u_n^* \right] D^*.$$

Recalling  $\beta_0 = 0$  we can rewrite (3.2) as

$$\begin{aligned} \mu_1 u_1^* - \sigma_0 D^* u_0^* &= 0, \\ \mu_{n+1} u_{n+1}^* - [q_n \beta_n + \sigma_n D^*] u_n^* \\ &= \mu_n u_n^* - [q_{n-1} \beta_{n-1} + \sigma_{n-1} D^*] u_{n-1}^*, \quad n \geq 1. \end{aligned}$$

By complete induction,

$$0 = \mu_n u_n^* - [q_{n-1} \beta_{n-1} + \sigma_{n-1} D^*] u_{n-1}^*, \quad n \geq 1,$$

that is,

$$\frac{u_n^*}{u_{n-1}^*} = \frac{1}{\mu_n} [q_{n-1} \beta_{n-1} + \sigma_{n-1} D^*], \quad n \geq 1.$$

We notice that we obtain a non-trivial equilibrium if and only if  $D^* > 0$ ,  $u_n^* > 0$ . Actually,

$$(3.4) \quad \frac{u_n^*}{u_0^*} = \gamma(n, D^*) \frac{\sigma_0}{\mu_n} D^*,$$

with

$$(3.5) \quad \begin{aligned} \gamma(1, D^*) &= 1, \\ \gamma(n, D^*) &= \prod_{j=1}^{n-1} \frac{q_j \beta_j + \sigma_j D^*}{\mu_j}, \quad n \geq 2. \end{aligned}$$

We notice that

$$(3.6) \quad \gamma(n+1, D) = \gamma(n, D) \frac{q_n \beta_n + \sigma_n D}{\mu_n}.$$

We make the following assumption.

**ASSUMPTION 3.1.** *The sequence  $(\sigma_n)$  is bounded and  $\kappa_n = 0$  for all  $n \in \mathbb{N}$ ; further*

$$\mu_n \rightarrow \infty, \quad n \rightarrow \infty; \quad \limsup_{n \rightarrow \infty} \frac{\beta_n}{\mu_n} < 1.$$

The quotient criterion then guarantees that the forthcoming series converge. From (3.1),

$$(3.7) \quad \frac{1}{u_0^*} = \sum_{n=0}^{\infty} \frac{u_n^*}{u_0^*} = 1 + \sum_{n=1}^{\infty} \gamma(n, D^*) \frac{\sigma_0}{\mu_n} D^*.$$

We rewrite (3.3) as

$$(3.8) \quad 0 = \sum_{n=1}^{\infty} (1 - q_n) \beta_n \frac{u_n^*}{u_0^* D^*} - \frac{\rho}{u_0^*} - \left( \sigma_0 + \sum_{n=1}^{\infty} \sigma_n \frac{u_n^*}{u_0^*} \right).$$

Fitting (3.4) and (3.7) into (3.8) we obtain

$$\begin{aligned} 0 &= \sum_{n=1}^{\infty} (1 - q_n) \beta_n \gamma(n, D^*) \frac{\sigma_0}{\mu_n} - \rho \left( 1 + \sum_{n=1}^{\infty} \gamma(n, D^*) \frac{\sigma_0}{\mu_n} D^* \right) \\ &\quad - \sigma_0 - \sum_{n=1}^{\infty} \sigma_n \gamma(n, D^*) \frac{\sigma_0}{\mu_n} D^*. \end{aligned}$$

We rewrite this equation as

$$(3.9) \quad \left( \frac{\rho}{\sigma_0} + 1 \right) = \sum_{n=1}^{\infty} \frac{\gamma(n, D^*)}{\mu_n} [(1 - q_n) \beta_n - D^* (\rho + \sigma_n)] =: f(D^*).$$

It is instructive to also consider

$$f(D^*) - 1 = \sum_{n=1}^{\infty} \gamma(n, D^*) \left[ \frac{\beta_n}{\mu_n} - \frac{\rho D^*}{\mu_n} - \frac{q_n \beta_n + \sigma_n D^*}{\mu_n} \right] - 1.$$

By (3.6),

$$f(D^*) - 1 = \sum_{n=1}^{\infty} \left( \gamma(n, D^*) \left[ \frac{\beta_n}{\mu_n} - \frac{\rho D^*}{\mu_n} \right] - \gamma(n+1, D^*) \right) - 1.$$

After separating the sums and changing the summation index in the second sum,

$$f(D^*) - 1 = \sum_{n=1}^{\infty} \left( \gamma(n, D^*) \left[ \frac{\beta_n}{\mu_n} - \frac{\rho D^*}{\mu_n} \right] \right) - \sum_{n=2}^{\infty} \gamma(n, D^*) - 1.$$

Since  $\gamma(1, D^*) = 1$ ,

$$f(D^*) - 1 = \sum_{n=1}^{\infty} \left( \gamma(n, D^*) \left[ \frac{\beta_n}{\mu_n} - \frac{\rho D^*}{\mu_n} \right] \right) - \sum_{n=1}^{\infty} \gamma(n, D^*).$$

So we can rewrite (3.9) as

$$(3.10) \quad \frac{\rho}{\sigma_0} = f(D^*) - 1 = \sum_{n=1}^{\infty} \frac{\gamma(n, D^*)}{\mu_n} [\beta_n - \mu_n - \rho D^*].$$

Before we continue, it is convenient to introduce the notion of the *carrying patch-capacity*. Recall that  $\beta_n/\mu_n$  is the average amount of offspring an individual begets during its life-time on a patch with  $n$  individuals. If

$\beta_n/\mu_n \leq 1$  for all  $n \geq 0$  we define the carrying patch-capacity to be zero. In other words: If the carrying patch-capacity is zero, then on patches of all sizes, the birth rates do not exceed the death rates. If there exists some  $n \in \mathbb{N}$  such that  $\beta_n/\mu_n > 1$ , then the carrying patch-capacity is the uniquely determined number  $k$  such that

$$(3.11) \quad \frac{\beta_k}{\mu_k} > 1, \quad \text{but} \quad \frac{\beta_n}{\mu_n} \leq 1 \quad \forall n > k.$$

Such  $k$  exists because of Assumptions 3.1.

If the carrying patch-capacity  $k$  is not zero, we introduce

$$(3.12) \quad \bar{D} = \frac{1}{\rho} \max\{\beta_n - \mu_n; n = 1, \dots, k\}.$$

Apparently  $f(D) - 1 \leq 0$  for all  $D \geq \bar{D}$ . Hence we know that necessarily  $D^* < \bar{D}$  for any non-trivial equilibrium solution.

**Theorem 3.2.** *Let the Assumptions 3.1 be satisfied.*

- a) *If  $\beta_n \leq \mu_n$  for all  $n \in \mathbb{N}$ , then there exists only the trivial equilibrium (the extinction equilibrium).*
- b) *If*

$$\frac{\rho}{\sigma_0} \geq \sum_{n=1}^{\infty} \frac{\gamma(n, \bar{D})}{\mu_n} [\beta_n - \mu_n],$$

*then there exists only the extinction equilibrium.*

- c) *If*

$$\frac{\rho}{\sigma_0} < f(0) - 1,$$

*then there exists a non-trivial equilibrium solution (persistence equilibrium). This solution necessarily is strictly smaller than  $\bar{D}$  in (3.12).*

Part (c) follows from the intermediate value theorem and the fact that  $f(D) - 1 \leq 0$  for  $D \geq \bar{D}$ . The condition in part (c) can be rewritten as

$$1 < \frac{\sigma_0}{\sigma_0 + \rho} f(0) =: \mathcal{R}_0.$$

By (3.9),

$$(3.13) \quad \mathcal{R}_0 = \frac{\sigma_0}{\sigma_0 + \rho} (1 - q_1) \frac{\beta_1}{\mu_1} + \frac{\sigma_0}{\sigma_0 + \rho} \sum_{n=2}^{\infty} \left( \prod_{j=1}^{n-1} q_j \frac{\beta_j}{\mu_j} \right) (1 - q_n) \frac{\beta_n}{\mu_n}.$$

In order to interpret  $\mathcal{R}_0$  let us assume that all patches are empty and that we introduce a few dispersing individuals at a very small constant rate  $\epsilon$ . The probability for any of these individuals to survive and settle on a patch is

$$\frac{\sigma_0}{\sigma_0 + \rho}.$$

The rate at which these individuals settle is  $\sigma_0 D^*$  with  $D^* = \epsilon/(\sigma_0 + \rho)$ . By (3.4) and (3.7), the resulting patch distribution is approximately given by

$$\frac{\gamma(n, 0)}{\mu_n} \frac{\sigma_0}{\sigma_0 + \rho} \epsilon$$

with  $\gamma(n, 0)$  given by (3.5). A patch with  $n$  adult individuals produces dispersers at the rate  $(1 - q_n)\beta_n$ . So the first generation of dispersers that has been introduced at the rate  $\epsilon$  produces the second generation of dispersers at the rate  $\mathcal{R}_0\epsilon$ . For this reason, we call  $\mathcal{R}_0$  the *basic reproduction number* of the metapopulation and obtain the following corollary.

**Corollary 3.3.** *Assume that Assumptions 3.1 are satisfied and that the basic reproduction number,  $\mathcal{R}_0$ , exceeds one. Then there exists a non-trivial equilibrium.*

#### 4. SUBCRITICAL BIFURCATION AND MULTIPLE PERSISTENCE EQUILIBRIA

Subcritical bifurcation is a frequent source of multiple equilibria. We choose  $\rho$  as a bifurcation parameter. Another natural choice would be the colonization rate  $\sigma_0$ . This is the quantity used as a bifurcation parameter in some of the simplest metapopulation models leading to subcritical bifurcation (see [29] and also [22], p.62). Our choice is motivated by our interest in including examples in which the colonization rate  $\sigma_0$  and the immigration rates  $\sigma_n$  are all the same.

In equation (3.10), we consider  $\rho$  as a function of  $D^*$ . Instead of expressing explicitly  $\rho$  in terms of  $D^*$ , we rewrite (3.10) in the following form:

$$(4.1) \quad \rho \left( \frac{1}{\sigma_0} + D^* \sum_{n=1}^{\infty} \frac{\gamma(n, D^*)}{\mu_n} \right) = \sum_{n=1}^{\infty} \frac{\gamma(n, D^*)}{\mu_n} [\beta_n - \mu_n].$$

To be able to determine a nonnegative value of the parameter  $\rho$  we must make the following

**ASSUMPTION 4.1.** *Assume that  $\kappa_n = 0$  for all  $n \in \mathbb{N}$  and that the sequences  $(q_n)$ ,  $(\beta_n)$  and  $(\mu_n)$  satisfy*

$$\sum_{n=1}^{\infty} \frac{\gamma(n, 0)}{\mu_n} [\beta_n - \mu_n] > 0.$$

If Assumption 4.1 is satisfied, the system has subcritical bifurcation if and only if  $\rho'(0) > 0$ . The subcritical bifurcation in  $\rho$  is actually forward, but it is a backward bifurcation in the reproduction number because, by (3.13),  $\mathcal{R}_0$  depends on  $\rho$  in a strictly decreasing way. Before computing the derivative, we evaluate  $\rho$  when  $D^* = 0$ :

$$(4.2) \quad \rho(0) = \sigma_0 \sum_{n=1}^{\infty} \frac{\gamma(n, 0)}{\mu_n} [\beta_n - \mu_n].$$

We compute the derivative  $\rho'(D^*)$  ( $\rho = \rho(D^*)$ ):

$$(4.3) \quad \frac{\rho'}{\sigma_0} + (\rho'D^* + \rho) \sum_{n=1}^{\infty} \frac{\gamma(n, D^*)}{\mu_n} = \sum_{n=1}^{\infty} \frac{\partial \gamma(n, D^*)}{\partial D^*} \left[ \frac{\beta_n - \mu_n - \rho D^*}{\mu_n} \right].$$

Since  $\frac{\partial \gamma(1, D^*)}{\partial D^*} = 0$ , the sum in the right hand side actually starts at  $n = 2$ . The explicit form of the derivatives is given by

$$(4.4) \quad \frac{\partial \gamma(n, D^*)}{\partial D^*} = \sum_{k=1}^{n-1} \frac{\sigma_k}{\mu_k} \prod_{j=1, j \neq k}^{n-1} \frac{q_j \beta_j + \sigma_j D^*}{\mu_j} \quad n \geq 2.$$

We note that this derivative is nonnegative which implies that  $\gamma(n, D^*)$  is a nondecreasing function of  $D^*$ . If  $q_n \beta_n \neq 0$  for all  $n \geq 1$ , the above expression can be rewritten in the following form which is also defined for  $D^* = 0$ .

$$(4.5) \quad \frac{\partial \gamma(n, D^*)}{\partial D^*} = \gamma(n, D^*) \sum_{k=1}^{n-1} \frac{\sigma_k}{q_k \beta_k + \sigma_k D^*}.$$

For  $D^* = 0$ , the expression above becomes

$$(4.6) \quad \frac{\rho'(0)}{\sigma_0} = \sum_{n=1}^{\infty} \frac{\partial \gamma(n, 0)}{\partial D^*} \left[ \frac{\beta_n - \mu_n}{\mu_n} \right] - \rho(0) \sum_{n=1}^{\infty} \frac{\gamma(n, 0)}{\mu_n},$$

where  $\rho(0)$  is given by (4.2). The condition  $\rho'(0) > 0$  reduces to the inequality in the following proposition which gives a necessary and sufficient condition for subcritical bifurcation.

**Proposition 4.2.** *Let Assumption 4.1 be satisfied. The system (2.1) exhibits subcritical bifurcation and has nontrivial equilibria in the case  $\mathcal{R}_0 < 1$  if and only if  $\sigma_0 > 0$  and*

$$\sum_{n=1}^{\infty} \frac{\partial \gamma(n, 0)}{\partial D^*} \left[ \frac{\beta_n - \mu_n}{\mu_n} \right] > \sigma_0 \left( \sum_{n=1}^{\infty} \frac{\gamma(n, 0)}{\mu_n} [\beta_n - \mu_n] \right) \left( \sum_{n=1}^{\infty} \frac{\gamma(n, 0)}{\mu_n} \right).$$

We notice that the right hand side of this inequality is nonnegative by Assumption 4.1. The example in the next section shows that the assumptions of this proposition are feasible.

Theorem 3.1 shows that system (2.1) has at least one nontrivial equilibrium if  $\mathcal{R}_0 > 1$ . Condition (4.2) implies that the system has at least one nontrivial equilibrium even if  $\mathcal{R}_0 < 1$  for sufficiently large values of  $\mathcal{R}_0 < 1$ . Each nontrivial equilibrium is given by (3.4) where  $D^*$  is a solution of the equation (3.9) (or, equivalently (3.10)). We call a nontrivial equilibrium *simple* if  $D^*$  is a simple root of (3.9). If  $D^*$  is a root of (3.9), a necessary and sufficient condition  $D^*$  to be simple is  $f'(D^*) \neq 0$ .

If  $\mathcal{R}_0 < 1$ , then

$$f(0) < \frac{\rho + \sigma_0}{\sigma_0}.$$

We also have  $f(D) < 1$  for all  $D \geq \bar{D}$ , hence the equation (3.9) has no solutions for  $D \geq \bar{D}$  and

$$f(\bar{D}) < \frac{\rho + \sigma_0}{\sigma_0}.$$

Thus, in the case  $\mathcal{R}_0 < 1$ , if all solutions of the equation are simple, their number is even, possibly zero. We number the equilibria in increasing order of  $D^*$ . At each odd-numbered equilibrium  $D^*$ , the function  $f(D)$  crosses the horizontal line  $f = \frac{\rho + \sigma_0}{\sigma_0}$  in a locally increasing fashion such that  $f'(D^*) > 0$ . It is shown in [40] that this implies that the instability of the equilibrium. At each even-numbered equilibrium  $D^*$ , the function  $f(D)$  crosses this line in a locally decreasing fashion and  $f'(D^*) < 0$ . In this case, a stability statement is only possible under extra assumptions which will be explored elsewhere.

**Proposition 4.3.** *Let  $\mathcal{R}_0 < 1$  and Assumption 4.1 be valid. If condition (4.2) is satisfied, then the system has multiple persistence equilibria for sufficiently large values of  $\mathcal{R}_0 < 1$ . If all equilibria are simple, then their number is even. Moreover, every odd-numbered equilibrium satisfies  $f'(D^*) > 0$  and is unstable, while every even-numbered equilibrium satisfies  $f'(D^*) < 0$ .*

A similar result is satisfied for the values of the reproductive number  $\mathcal{R}_0 > 1$ . We note that Assumption 4.1 is automatically satisfied in this case.

**Proposition 4.4.** *Let  $\mathcal{R}_0 > 1$  and the Assumptions 3.1 be valid. Then the system has at least one nontrivial equilibrium. If there are more equilibria and they are all simple, then their number is odd. Moreover, every odd-numbered equilibrium satisfies  $f'(D^*) < 0$ , and every even-numbered equilibrium satisfies  $f'(D^*) > 0$  and is unstable.*

## 5. OBLIGATORY JUVENILE EMIGRATION

As an example, we consider the extreme but reasonable special case that all juveniles have to leave their birth patch,  $q_n = 0$  for all  $n \in \mathbb{N}$ . We continue to assume that there are no catastrophes,  $\kappa_n = 0$  for all  $n \in \mathbb{N}$ . By (3.5),

$$\gamma(n, D) = \frac{\prod_{j=1}^{n-1} \sigma_j}{\prod_{j=1}^{n-1} \mu_j} D^{n-1}, \quad n \geq 2.$$

We start from equation (3.10),

$$\frac{\rho}{\sigma_0} = \sum_{n=1}^{\infty} \frac{\gamma(n, D^*)}{\mu_n} (\beta_n - \mu_n - \rho D^*).$$

We multiply by  $\sigma_0$  and write  $w$  for  $D^*$ ,

$$\rho = \sum_{n=1}^{\infty} \frac{\prod_{j=1}^{n-1} \sigma_j}{\prod_{j=1}^n \mu_j} w^{n-1} (\beta_n - \mu_n - \rho w).$$

We solve for  $\rho$ ,

$$(5.1) \quad \rho = g(D^*), \quad g(w) = \frac{\sum_{n=1}^{\infty} \frac{\prod_{j=1}^{n-1} \sigma_j}{\prod_{j=1}^n \mu_j} w^{n-1} (\beta_n - \mu_n)}{1 + \sum_{n=1}^{\infty} \frac{\prod_{j=1}^{n-1} \sigma_j}{\prod_{j=1}^n \mu_j} w^n}.$$

$g(0) \geq 0$  if and only if  $\sigma_0 \left( \frac{\beta_1}{\mu_1} - 1 \right) > 0$ .  $g'(w)$  has the same sign as

$$\begin{aligned} & \left( \sum_{n=2}^{\infty} \frac{\prod_{j=1}^{n-1} \sigma_j}{\prod_{j=1}^n \mu_j} (n-1) w^{n-2} (\beta_n - \mu_n) \right) \left( 1 + \sum_{n=1}^{\infty} \frac{\prod_{j=1}^{n-1} \sigma_j}{\prod_{j=1}^n \mu_j} w^n \right) \\ & - \left( \sum_{n=1}^{\infty} \frac{\prod_{j=1}^{n-1} \sigma_j}{\prod_{j=1}^n \mu_j} w^{n-1} (\beta_n - \mu_n) \right) \left( \sum_{n=1}^{\infty} \frac{\prod_{j=1}^{n-1} \sigma_j}{\prod_{j=1}^n \mu_j} n w^{n-1} \right). \end{aligned}$$

For  $w = 0$ , we obtain that  $g'(0)$  has the same sign as

$$\frac{\sigma_0 \sigma_1}{\mu_1 \mu_2} (\beta_2 - \mu_2) - \frac{\sigma_0}{\mu_1} (\beta_1 - \mu_1) \frac{\sigma_0}{\mu_1}.$$

So the direction of the bifurcation is determined by

$$\sigma_1 \left( \frac{\beta_2}{\mu_2} - 1 \right) - \sigma_0 \left( \frac{\beta_1}{\mu_1} - 1 \right).$$

We summarize

**Proposition 5.1.** *The metapopulation model with obligatory juvenile emigration has a subcritical bifurcation of persistence equilibria from the extinction equilibrium in the parameter  $\rho = \frac{\delta}{N}$  if and only if*

$$\sigma_1 \left( \frac{\beta_2}{\mu_2} - 1 \right) > \sigma_0 \left( \frac{\beta_1}{\mu_1} - 1 \right) > 0.$$

While subcritical bifurcation implies the existence of multiple persistence equilibria for this model, supercritical bifurcation does not necessarily imply

the existence of at most one persistence equilibrium. To see this, we choose  $\sigma_n = 0$  for  $n \geq 3$ . Then  $g$  takes the form

$$g(w) = \frac{\frac{\sigma_0}{\mu_1}(\beta_1 - \mu_1) + \frac{\sigma_0\sigma_1}{\mu_1\mu_2}(\beta_2 - \mu_2)w + \frac{\sigma_0\sigma_1\sigma_2}{\mu_1\mu_2\mu_3}(\beta_3 - \mu_3)w^2}{1 + \frac{\sigma_0}{\mu_1}w + \frac{\sigma_0\sigma_1}{\mu_1\mu_2}w^2 + \frac{\sigma_0\sigma_1\sigma_2}{\mu_1\mu_2\mu_3}w^3}.$$

We can choose  $\beta_3 > 0$  so large that  $g(1) > \max\{0, g(0)\}$ . Since  $g(w) \rightarrow 0$  as  $w \rightarrow \infty$ , we have multiple solutions, if  $\rho$  is between  $\max\{0, g(0)\}$  and  $g(1)$ .

To find a sufficient condition for the existence of at most one persistence equilibrium, we assume that  $\sigma_n = \sigma_1$  for all  $n \in \mathbb{N}$ . Then  $g'(w)$  has the same sign as

$$\begin{aligned} & \left( \sum_{n=2}^{\infty} \frac{\sigma_0\sigma_1^{n-1}}{\prod_1^n \mu_j} (n-1)w^{n-2}(\beta_n - \mu_n) \right) \left( 1 + \sum_{n=1}^{\infty} \frac{\sigma_0\sigma_1^{n-1}}{\prod_1^n \mu_j} w^n \right) \\ & - \left( \sum_{n=1}^{\infty} \frac{\sigma_0\sigma_1^{n-1}}{\prod_1^n \mu_j} w^{n-1}(\beta_n - \mu_n) \right) \left( \sum_{n=1}^{\infty} \frac{\sigma_0\sigma_1^{n-1}}{\prod_1^n \mu_j} n w^{n-1} \right). \end{aligned}$$

We assume that  $\mu_n = n\mu_1$ . Then, after dividing by  $\mu_1$  and  $\sigma_0$ ,  $g'(w)$  has the same sign as

$$\begin{aligned} & \left( \sum_{n=2}^{\infty} \frac{\sigma_1^{n-1}}{n-2} w^{n-2} \left( \frac{\beta_n}{\mu_n} - 1 \right) \right) \left( 1 + \sum_{n=1}^{\infty} \frac{\sigma_0\sigma_1^{n-1}}{\prod_1^n \mu_j} w^n \right) \\ & - \left( \sum_{n=1}^{\infty} \frac{\sigma_1^{n-1}}{n-1} w^{n-1} \left( \frac{\beta_n}{\mu_n} - 1 \right) \right) \left( \sum_{n=1}^{\infty} \frac{\sigma_0\sigma_1^{n-1}}{\prod_1^{n-1} \mu_j} w^{n-1} \right). \end{aligned}$$

We change indices of summation,

$$\begin{aligned} & \left( \sum_{n=1}^{\infty} \frac{\sigma_1^n}{n-1} w^{n-1} \left( \frac{\beta_{n+1}}{\mu_{n+1}} - 1 \right) \right) \left( 1 + \sum_{n=1}^{\infty} \frac{\sigma_0\sigma_1^{n-1}}{\prod_1^n \mu_j} w^n \right) \\ & - \left( \sum_{n=1}^{\infty} \frac{\sigma_1^{n-1}}{n-1} w^{n-1} \left( \frac{\beta_n}{\mu_n} - 1 \right) \right) \left( \sigma_0 + \sum_{n=1}^{\infty} \frac{\sigma_0\sigma_1^n}{\prod_1^n \mu_j} w^n \right). \end{aligned}$$



We assume  $\sigma_1 \leq \sigma_0$  and that  $\frac{\beta_n}{\mu_n}$  is decreasing with the decrease being strict at least once. For  $w > 0$ , this expression satisfies

$$\begin{aligned} &< \left( \sum_{n=1}^{\infty} \frac{\sigma_1^n}{\prod_{j=1}^{n-1} \mu_j} w^{n-1} \left( \frac{\beta_n}{\mu_n} - 1 \right) \right) \left( 1 + \sum_{n=1}^{\infty} \frac{\sigma_0 \sigma_1^{n-1}}{\prod_{j=1}^n \mu_j} w^n \right) \\ &- \left( \sum_{n=1}^{\infty} \frac{\sigma_1^{n-1}}{\prod_{j=1}^{n-1} \mu_j} w^{n-1} \left( \frac{\beta_n}{\mu_n} - 1 \right) \right) \left( \sigma_1 + \sum_{n=1}^{\infty} \frac{\sigma_0 \sigma_1^n}{\prod_{j=1}^n \mu_j} w^n \right) = 0 \end{aligned}$$

and  $g'(w) < 0$  for all  $w > 0$ . So we have shown the following uniqueness result for obligatory juvenile emigration.

**Proposition 5.2.** *There exists at most one persistence equilibrium, if  $\sigma_0 \geq \sigma_1 = \sigma_n$ ,  $\mu_n = n\mu_1$  for all  $n \in \mathbb{N}$ ,  $q_n = 0$  for all  $n \in \mathbb{N}$ , and  $\frac{\beta_n}{\mu_n}$  is decreasing with the decrease being strict at least once.*

A result by Barbour and Pugliese for a different model [2] suggests that a more general result should hold. Analogy suggests the following

**CONJECTURE 5.3.** Let  $q_n$  and  $\sigma_n$  be independent of  $n \in \mathbb{Z}_+$  and  $\beta_n$  be an increasing concave function of  $n \in \mathbb{Z}_+$  and  $\mu_n$  an increasing convex function in  $n \in \mathbb{Z}_+$ ,  $\beta_0 = \mu_0 = 0$ . Then there exists at most one persistence equilibrium.

Our example shows that such a result (if it holds) may be the best possible, except that it may also hold if  $\sigma_0 \geq \sigma_1 = \sigma_n$  for all  $n \in \mathbb{N}$ .

## 6. CONDITIONS FOR PERSISTENCE AND EXTINCTION OF THE METAPOPOPULATION

The extinction equilibrium is given by

$$D = 0; \quad u_0 = 1; \quad u_n = 0, \quad n \geq 1.$$

The following result gives the local stability of the extinction equilibrium when  $\mathcal{R}_0 < 1$ . It is established rigorously in [40].

**Theorem 6.1.** *Let the Assumptions 2.1 be satisfied and  $\mathcal{R}_0 < 1$ . Further assume that  $\kappa_n = 0$  for all  $n \in \mathbb{N}$  and that there exist constants  $c_4, \epsilon_4 > 0$  such that  $\beta_k - \mu_k \leq c_4 - \epsilon_4 k$  for all  $k \in \mathbb{N}$ . Then the extinction equilibrium is locally asymptotically stable.*

The assumption concerning  $(\beta_k)$  and  $(\mu_k)$  specifies one way in which the death rate dominates the birth rate on crowded patches. As we showed in Section 4,  $\mathcal{R}_0 < 1$  is not sufficient for the global stability of the extinction equilibrium, as there may be persistence equilibria. The local stability of the extinction equilibrium implies extinction of the metapopulation only for appropriate, sufficiently close to the extinction equilibrium, initial conditions. Scenarios which lead to extinction, independently of the initial status of the

metapopulation (even if there are no local catastrophes,  $\kappa_n = 0$ ) are these: there is no emigration from the patches into the dispersers' pool,  $q_n = 1$  for all  $n$ , or the empty patches are not colonized,  $\sigma_0 = 0$  (whether or not dispersers settle on already occupied patches,  $\sigma_n \geq 0$  for  $n \geq 1$ ).

**Theorem 6.2** ([40]). *Let the Assumptions 2.1 be satisfied. Further assume that there exist constants  $c_4, \epsilon_4 > 0$  such that  $\beta_k - \mu_k - k\kappa_k \leq c_4 - \epsilon_4 k$  for all  $k \in \mathbb{N}$ . If  $q_k = 1$  for all  $k \in \mathbb{N}$  or if  $\sigma_0 = 0$ , the total population size,  $P(t) = D(t) + R(t)$ , converges to 0 as time tends to infinity.*

The metapopulation will also become extinct if the birth rate is smaller than the death rate on every patch.

**Corollary 6.3** ([40]). *Let the Assumptions 2.1 be satisfied. Assume that there exists some  $\epsilon > 0$  such that  $\beta_k - \mu_k \leq -\epsilon k$  for all  $k \in \mathbb{N}$ . Then the total population size,  $P(t)$ , converges to 0 as time tends to infinity.*

In the remaining part of this section we examine the problem of the persistence of the metapopulation. Intuitively, the metapopulation persists if it does not die out. We will consider two types of persistence. The stronger type of persistence, called uniformly strong persistence, means that the population size remains bounded away from zero, at a minimum level that does not depend on the initial state if enough time has passed. Formally, we call the metapopulation *uniformly strongly persistent* if there exists an  $\epsilon > 0$  independent of the initial conditions such that

$$\liminf_{t \rightarrow \infty} P(t) > \epsilon \quad \text{whenever} \quad P(0) > 0,$$

for all solutions of the system (2.1). The weaker type, called uniform weak persistence, means that, while the population size may become very close to 0 every now and then, it always bounces back to a positive level that does not depend on the initial status provided one waits long enough. Formally, we call the metapopulation *uniformly weakly persistent* if there exists some  $\epsilon > 0$  independent of the initial conditions such that

$$\limsup_{t \rightarrow \infty} P(t) > \epsilon \quad \text{whenever} \quad P(0) > 0,$$

for all solutions of the system (2.1). Here  $P(t) = R(t) + D(t)$ .

As uniform weak persistence implies that the extinction equilibrium is unstable, the metapopulation cannot be uniformly weakly persistent when  $\mathcal{R}_0 < 1$ , in spite of the fact that there may be persistence equilibria some of which could be even locally stable. This fact demonstrates that the presence of locally stable persistence equilibria in itself does not guarantee the uniform weak persistence of the population. We need the following assumptions.

**ASSUMPTION 6.4.** (a)  $\sigma_0 > 0$ ,  $\kappa_n = 0$  for all  $n \in \mathbb{N}$ .

(b)  $\limsup_{n \rightarrow \infty} \frac{q_n \beta_n}{\mu_n} < 1$ .

(c) Further let one of the following be satisfied:

- (c<sub>1</sub>)  $q_j\beta_j > 0$  for all  $j \in \mathbb{N}$  and  $(1 - q_k)\beta_k > 0$  for some  $k \in \mathbb{N}$ .  
or  
(c<sub>2</sub>) There exists some  $k_0 \in \mathbb{N}$  such that  $q_j\beta_j > 0$  for  $j = 1, \dots, k_0 - 1$ ,  
 $q_j\beta_j = 0$  for all  $j \geq k_0$ , and that  $(1 - q_j)\beta_j > 0$  for some  
 $j \in \{1, \dots, k_0\}$ .

**Proposition 6.5** ([40]). *Let Assumptions 2.1 and 6.4 be satisfied. If  $\mathcal{R}_0 > 1$ , the metapopulation is uniformly weakly persistent.*

Clearly, if the population is uniformly strongly persistent, it is also uniformly weakly persistent. The other way around is not always true; but if the metapopulation is uniformly weakly persistent and the solutions of the system (2.1) have a global compact attractor (see [40] for definition), then the metapopulation is also uniformly strongly persistent [40].

## 7. A BANG-BANG PRINCIPLE OF PERSISTENCE-OPTIMAL EMIGRATION

As we have seen in Sections 4 and 5, the following number plays a significant role. If  $\mathbf{q} = (q_1, q_2, \dots)$

$$(7.1) \quad \mathcal{D} = \mathcal{D}(\mathbf{q}) = (1 - q_1) \frac{\beta_1}{\mu_1} + \sum_{n=2}^{\infty} \left( \prod_{j=1}^{n-1} q_j \frac{\beta_j}{\mu_j} \right) (1 - q_n) \frac{\beta_n}{\mu_n}.$$

$\mathcal{D}$  can be interpreted as the average number of dispersers a typical individual which has settled on an empty patch produces during its life-time.

$$(7.2) \quad \mathcal{R}_0 = \frac{\sigma_0}{\sigma_0 + \rho} \mathcal{D}$$

is the basic reproduction number of the metapopulation, that is, the average number of secondary dispersing individuals that one dispersing individual will produce if all patches are empty initially. The factor  $\frac{\sigma_0}{\sigma_0 + \rho}$  is the probability to survive the dispersal state if all patches are practically empty.

If  $\mathcal{R}_0 > 1$ , then the extinction state of the metapopulation is unstable, there exists a persistence equilibrium, and, under the reasonable extra Assumptions 6.4, the metapopulation is uniformly weakly persistent. For this reason,  $\mathcal{D}$  can be considered a measure for the ability of the metapopulation to persist. We try to find an emigration strategy - expressed in terms of the probabilities  $q_n$  of staying on a patch - which maximizes  $\mathcal{D}(\mathbf{q})$ . We call such a strategy *persistence-optimal* (though it does not necessarily lead to persistence of the metapopulation). We assume that

$$(7.3) \quad \beta_1 > 0,$$

otherwise  $\mathcal{D} = 0$  no matter how we choose the other parameters. We further assume that

$$(7.4) \quad \frac{\beta_n}{\mu_n} \rightarrow 0, \quad n \rightarrow \infty.$$

Recall the definition of the carrying patch-capacity. If  $\frac{\beta_n}{\mu_n} > 1$  for some  $n \in \mathbb{N}$ , there exists a unique number  $k \in \mathbb{N}$  such that  $\frac{\beta_k}{\mu_k} > 1$ , but  $\frac{\beta_n}{\mu_n} \leq 1$  for all  $n > k$ . We call  $k$  the *carrying patch-capacity*. If  $\frac{\beta_n}{\mu_n} \leq 1$  for all  $n \in \mathbb{N}$ , then we say that the carrying patch-capacity is zero.

**Theorem 7.1.** *Let  $k = 0$  or  $k = 1$ . Then a persistence-optimal strategy is given by*

$$q_n = 0 \quad \forall n \geq 1.$$

*If  $k \geq 2$ , then there exists a persistence-optimal strategy satisfying*

$$q_n = 0 \quad \forall n \geq k, \quad q_{k-1} = 1.$$

One cannot expect persistence-optimal strategies to be unique. Once  $q_m = 0$  for some  $m$ ,  $q_n$  can be arbitrary chosen for  $n > m$ . Under specific circumstances, certain uniqueness statements can be made, however. In order to obtain more precise information in case that  $k \geq 2$  we assume that the metapopulation is of Verhulst or Allee type. We call the metapopulation to be of *Verhulst* or logistic type if the sequence  $\frac{\beta_n}{\mu_n}$  is monotone decreasing (not necessarily strictly). We call it of *Allee* type if the sequence  $\frac{\beta_n}{\mu_n}$  is unimodal, i.e., the sequence is first increasing and then decreasing.

If the population is of either Verhulst or Allee type, there always is a persistence-optimal strategy which has one of the following forms:

$$q_n = 0 \quad \forall n \geq 1,$$

or

$$q_n = \begin{cases} 1; & n = 1, \dots, k-1, \\ 0; & n \geq k. \end{cases}$$

In the first case  $k = 0$  or  $k = 1$ , in the second we necessarily have  $k \geq 2$ . In any case these strategies are of bang-bang type: If the number of adults is below the carrying capacity, all the juveniles should stay; if the number of adults is at or above the carrying capacity, all the juveniles should leave.

**Theorem 7.2.** *Assume that the metapopulation is of Verhulst type and that the carrying capacity  $k$  satisfies  $k \geq 2$ . Then a persistence optimal strategy is given by*

$$q_n = \begin{cases} 1; & n = 1, \dots, k-1, \\ 0; & n \geq k, \end{cases}$$

*and, with this strategy,*

$$\mathcal{D} = \prod_{n=1}^k \frac{\beta_n}{\mu_n} > 1.$$

**REMARK 7.3.** Under the assumptions of Theorem 7.2, the persistence-optimal strategy is unique in so far as necessarily  $q_n = 1$  for  $n = 1, \dots, k-1$ . If  $\beta_{k+1}/\mu_{k+1} < 1$ , then necessarily  $q_k = 0$ .

**Theorem 7.4.** *Assume that the carrying capacity  $k$  satisfies  $k \geq 2$  and that the metapopulation is of Allee type.*

a) *Let*

$$\prod_{n=2}^k \frac{\beta_n}{\mu_n} \geq 1.$$

*Then a persistence-optimal dispersal strategy is given by*

$$q_n = \begin{cases} 1; & 1 \leq n \leq k-1, \\ 0; & n \geq k. \end{cases}$$

*For this optimizing sequence  $(q_n)$ , we have*

$$\mathcal{D} = \prod_{n=1}^k \frac{\beta_n}{\mu_n} \geq 1.$$

b) *Let*

$$\prod_{n=2}^k \frac{\beta_n}{\mu_n} \leq 1.$$

*Then a persistence-optimizing dispersal strategy is given by*

$$q_n = 0 \quad \forall n \geq 1.$$

REMARK 7.5. Under the assumptions of Theorem 7.4 (a), the persistence-optimal dispersal strategy is unique in so far as necessarily  $q_n = 1$  for  $n = 1, \dots, k-1$ .

Our statement concerning persistent-optimal dispersal strategies can be generalized to metapopulations which are not necessarily of Verhulst or Allee type at the expense of some terminology. Again the persistence-optimal emigration strategies will be of bang-bang type.

A natural number  $k$  is called *weak (carrying patch) capacity* if  $\beta_k/\mu_k > 1$  and  $\beta_{k+1}/\mu_{k+1} \leq 1$ .

A weak capacity  $k$  is called *pervasive* if  $k = 1$  or if

$$k > 1 \quad \text{and} \quad \prod_{j=m}^k \frac{\beta_j}{\mu_j} \geq 1 \quad \forall m = 2, \dots, k.$$

Notice that, for two pervasive weak capacities  $k_1 < k_2$ , we have

$$\prod_{j=1}^{k_1} \frac{\beta_j}{\mu_j} \leq \prod_{j=1}^{k_2} \frac{\beta_j}{\mu_j}.$$

If there exist a pervasive weak capacity we define  $\ell$  to be the largest pervasive weak capacity.

**Theorem 7.6.** *Let  $\frac{\beta_n}{\mu_n} \rightarrow 0$  as  $n \rightarrow \infty$ .*

- a) *If no pervasive weak capacity exists or the largest pervasive weak capacity is 1, then a persistence-optimal emigration strategy is given by  $q_n = 0$  for all  $n \geq 1$ .*
- b) *If  $\ell$  is the largest pervasive weak capacity and it satisfies  $\ell > 1$ , then a persistence-optimal emigration strategy is given by*

$$q_n = \begin{cases} 1; & n = 1, \dots, \ell - 1, \\ 0; & n \geq \ell. \end{cases}$$

#### APPENDIX A. PROOFS OF THE RESULTS IN SECTION 7

We notice from (3.10) that

$$\mathcal{D} - 1 = f(0) - 1 = \sum_{n=1}^{\infty} \gamma(n, 0) \left( \frac{\beta_n}{\mu_n} - 1 \right),$$

$$\gamma(n, 0) = 1, \quad \gamma(n, 0) = \prod_{j=1}^{n-1} \frac{q_j \beta_j}{\mu_j}.$$

Hence a dispersal strategy  $(q_n)$  is persistence-optimal if and only if it maximizes  $\mathcal{D} - 1$ .

We first differentiate  $\gamma(n, 0)$  with respect to  $q_m$ :

$$\begin{aligned} \frac{\partial \gamma(n, 0)}{\partial q_m} &= 0, \quad n \leq m, \\ \frac{\partial \gamma(n, 0)}{\partial q_m} &= \frac{\beta_m}{\mu_m} \prod_{\substack{j=1 \\ j \neq m}}^{n-1} \frac{q_j \beta_j}{\mu_j}, \quad n > m. \end{aligned}$$

Hence,

$$\frac{\partial (\mathcal{D} - 1)}{\partial q_m} = \sum_{n=m+1}^{\infty} \frac{\beta_m}{\mu_m} \left( \prod_{\substack{j=1 \\ j \neq m}}^{n-1} \frac{q_j \beta_j}{\mu_j} \right) \left( \frac{\beta_n}{\mu_n} - 1 \right).$$

Reorganizing terms,

(A.1)

$$\frac{\partial \mathcal{D}}{\partial q_m} = \frac{\beta_m}{\mu_m} \left( \prod_{j=1}^{m-1} \frac{q_j \beta_j}{\mu_j} \right) \left( \frac{\beta_{m+1}}{\mu_{m+1}} - 1 + \sum_{n=m+2}^{\infty} \left( \prod_{j=m+1}^{n-1} \frac{q_j \beta_j}{\mu_j} \right) \left( \frac{\beta_n}{\mu_n} - 1 \right) \right).$$

Thus

$$\frac{\partial \mathcal{D}}{\partial q_m} \leq 0 \quad \forall m \geq k.$$

Hence we do not decrease  $\mathcal{D}$  by setting

$$q_n = 0 \quad \forall n \geq k$$

if  $k > 0$ , and

$$q_n = 0 \quad n \geq 1,$$

if  $k = 0$ . This completely settles the question for  $k = 0, 1$ . Let us assume that  $k \geq 2$ . The previous considerations show that it is sufficient to find a persistence-optimal dispersal strategy with  $q_n = 0$  for all  $n \geq k$ . Such a strategy exists, because  $D$  takes a maximum on the compact set of sequences  $(q_n)$  with  $q_n = 0$  for  $n \geq k$  and  $0 \leq q_n \leq 1$  for  $n = 1, \dots, k-1$ .

Let us take a dispersal-optimal strategy with  $q_n = 0$  for  $n \geq k$ . Then, for  $m \leq k-1$ ,

$$\frac{\partial \mathcal{D}}{\partial q_m} = \frac{\beta_m}{\mu_m} \left( \prod_{j=1}^{m-1} \frac{q_j \beta_j}{\mu_j} \right) \left( \frac{\beta_{m+1}}{\mu_{m+1}} - 1 + \sum_{n=m+2}^k \left( \prod_{j=m+1}^{n-1} \frac{q_j \beta_j}{\mu_j} \right) \left( \frac{\beta_n}{\mu_n} - 1 \right) \right).$$

Hence, for  $m = k-1$ ,

$$\frac{\partial \mathcal{D}}{\partial q_m} = \frac{\beta_m}{\mu_m} \left( \prod_{j=1}^{m-1} \frac{q_j \beta_j}{\mu_j} \right) \left( \frac{\beta_{m+1}}{\mu_{m+1}} - 1 \right) \geq 0.$$

Thus we do not decrease  $\mathcal{D}$  by setting  $q_{k-1} = 1$ . This proves Theorem 7.1.

Now assume that we have  $m \leq k-2$ ,

$$(A.2) \quad \prod_{j=m+2}^k \frac{\beta_j}{\mu_j} \geq 1$$

and that we have set  $q_n = 1$  for  $n = m+1, \dots, k-1$ . Then

$$\frac{\partial \mathcal{D}}{\partial q_m} = \frac{\beta_m}{\mu_m} \left( \prod_{j=1}^{m-1} \frac{q_j \beta_j}{\mu_j} \right) \left( \frac{\beta_{m+1}}{\mu_{m+1}} - 1 + \sum_{n=m+2}^k \left( \prod_{j=m+1}^{n-1} \frac{\beta_j}{\mu_j} \right) \left( \frac{\beta_n}{\mu_n} - 1 \right) \right).$$

We reorganize the terms,

$$\frac{\partial \mathcal{D}}{\partial q_m} = \frac{\beta_m}{\mu_m} \left( \prod_{j=1}^{m-1} \frac{q_j \beta_j}{\mu_j} \right) \left( \frac{\beta_{m+1}}{\mu_{m+1}} - 1 + \sum_{n=m+2}^k \left( \prod_{j=m+1}^n \frac{\beta_j}{\mu_j} - \prod_{j=m+1}^{n-1} \frac{\beta_j}{\mu_j} \right) \right).$$

We change the summation index,

$$\begin{aligned} \frac{\partial \mathcal{D}}{\partial q_m} &= \frac{\beta_m}{\mu_m} \left( \prod_{j=1}^{m-1} \frac{q_j \beta_j}{\mu_j} \right) \\ &\quad \left( \frac{\beta_{m+1}}{\mu_{m+1}} - 1 + \sum_{n=m+2}^k \left( \prod_{j=m+1}^n \frac{\beta_j}{\mu_j} \right) - \sum_{n=m+2}^k \left( \prod_{j=m+1}^{n-1} \frac{\beta_j}{\mu_j} \right) \right), \end{aligned}$$

and simplify

$$\frac{\partial \mathcal{D}}{\partial q_m} = \frac{\beta_m}{\mu_m} \prod_{j=1}^{m-1} \frac{q_j \beta_j}{\mu_j} \left( \prod_{j=m+1}^k \frac{\beta_j}{\mu_j} - 1 \right).$$

Then we do not decrease  $\mathcal{D}$  by setting

$$(A.3) \quad \begin{aligned} q_m &= 1 & \text{if} & \quad \prod_{j=m+1}^k \frac{\beta_j}{\mu_j} \geq 1, \\ q_m &= 0 & \text{if} & \quad \prod_{j=m+1}^k \frac{\beta_j}{\mu_j} \leq 1. \end{aligned}$$

If the population is of Verhulst type, the second case cannot occur because, by (A.2), this requires  $\frac{\beta_{m+1}}{\mu_{m+1}} \leq 1$  which contradicts

$$\frac{\beta_{m+1}}{\mu_{m+1}} \geq \frac{\beta_k}{\mu_k} > 1.$$

Hence we do not decrease  $\mathcal{D}$  by successively setting  $q_n = 1$ ,  $n = k-2, \dots, 1$ . This proves Theorem 7.2.

Let the metapopulation be of Allee type. Assume that

$$\prod_{j=2}^k \frac{\beta_j}{\mu_j} \geq 1.$$

Since  $\frac{\beta_n}{\mu_n}$  is uni-modal, this implies that

$$\prod_{j=m+1}^k \frac{\beta_j}{\mu_j} \geq 1, \quad m = 1, \dots, k-1.$$

Hence, by (A.3), we do not decrease  $\mathcal{D}$  by setting  $q_n = 1$  for  $n = 1, \dots, k-1$ . Let now assume that

$$\prod_{j=2}^k \frac{\beta_j}{\mu_j} < 1.$$

Then there exists exactly one  $l \leq k-2$ ,  $l \geq 1$ , such that

$$\prod_{j=l+1}^k \frac{\beta_j}{\mu_j} < 1, \quad \prod_{j=l+2}^k \frac{\beta_j}{\mu_j} \geq 1.$$

By (A.3), we do not decrease  $\mathcal{D} - 1$  by setting  $q_l = 0$ . But now we can set  $q_n = 0$  for  $n > l$  without affecting  $\mathcal{D} - 1$  because  $\gamma(n, 0) = 0$  for  $n > l$  anyway. Moreover  $\frac{\beta_n}{\mu_n} < 1$  for  $n = 1, \dots, l+1$ . Now, from (A.1),

$$\frac{\partial \mathcal{D}}{\partial q_m} \leq 0, \quad m = 1, \dots, l-1.$$

Hence we do not decrease  $\mathcal{D}$  by setting  $q_m = 0$  for  $m = 1, \dots, l-1$ . Finally let

$$\prod_{j=2}^k \frac{\beta_j}{\mu_j} = 1.$$



We have seen that setting  $q_n = 1$  for  $n = 1, \dots, k-1$  provides a persistence-optimal strategy with

$$\mathcal{D} = \prod_{j=1}^k \frac{\beta_j}{\mu_j} = \frac{\beta_1}{\mu_1}.$$

Thus the strategy with  $q_n = 0$  for all  $n \geq 1$  is equally good.

As for the Remarks following Theorem 7.2 and 7.4, let us assume that the respective assumptions are satisfied. Then a persistence-optimal dispersal strategy is given by  $q_n = 1$  for  $n = 1, \dots, k-1$  and  $q_n = 0$  for  $n \geq k$ . Then (A.3) holds with  $q_n = 1$  for  $m = 1, \dots, k-1$ , and we find that

$$\frac{\partial \mathcal{D}}{\partial q_m} > 0, \quad m = 1, \dots, k-1.$$

Hence making one of the  $q_n$ ,  $n = 1, \dots, k-1$ , strictly smaller than one, would make  $\mathcal{D}$  strictly smaller.

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