THE IMPACT OF THE ALLEE EFFECT IN DISPERSAL AND PATCH-OCCUPANCY AGE ON THE DYNAMICS OF METAPOPULATIONS

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ABSTRACT. In this paper we introduce a Levins-type metapopulation model with empty and occupied patches, and dispersing population. We structure the proportion of occupied patches according to the patch-occupancy age. We observe that patch-occupancy age may destabilize the metapopulation, leading to persistent oscillations. We also allow for the dispersal rate to vary with the proportion of empty patches in a monotone or unimodal way. The unimodal dependence leads to multiple non-trivial equilibria and bistability when the reproduction number of the metapopulation $\mathcal{R} < 1$ but greater than a lower critical value $\mathcal{R}^*$. We show that the metapopulation will persist independently of its initial status if $\mathcal{R} > 1$.

KEYWORDS: Metapopulations, patch-occupancy age, Allee effect in dispersal, oscillatory dynamics, persistence

1. INTRODUCTION

Metapopulations, classically defined as assemblages of patches that become empty through population extinction and occupied through colonization, have become one of the standard paradigms of theoretical and applied ecology [11]. While the first metapopulation models assumed that the per-patch extinction rate was constant and the per-patch colonization rate was proportional to the density of occupied patches [18], a great many variations on the theme have since been explored by ecologists. Simple but important variants allow for different dependences of colonization and extinction rates with occupied patch density, such as a density-independent patch colonization rate (e.g., mainland-archipelago models or "propagule rain") or a density-dependent patch extinction rate (e.g., rescue effects) [5, 12]. Other more complex variants include models for community dynamics (patch occupancy by more than one species) [25]; models allowing variation in colonization and extinction rates according to patch characteristics such as area [11]; models allowing distance-dependent colonization [11]; models with dynamic patches [16]; and, much more generally, models that track distributions of population densities within patches rather than simple patch occupancy [15].

Hastings [14] recently drew attention to the importance of patch age in metapopulation models. He was concerned with age as it affected the probability of disturbance (i.e., extinction of the population within the patch), and commented on the consequences of different patch age distributions (or equivalently the distribution of times between disturbances) on the persistence of the metapopulation. Non-constant disturbance rates, or non-exponential distributions of times between disturbance, imply that some environmental process leads to (e.g.) periodic or temporally aggregated disturbance. A related question is the importance of patch-occupancy, as distinct from patch age. Patch-occupancy or population age is measured from the time of colonization, rather than from the time of the last disturbance, and variation in extinction rates with patch-occupancy age suggests ecological (biotic) rather than environmental (abiotic) factors (e.g. resource depletion, attraction or growth of pathogen or predator populations, or other forms of habitat degradation by the population). Dynamical models that include patch age or patch-occupancy age have been considered in [13, 4].

In this paper we present formal results on the persistence of metapopulations with patch-occupancy age-dependent emigration (contribution to colonizing pool) and extinction rates. We also allow for the possibility that the emigration rate depends on the fraction of empty patches, as either an increasing function or a unimodal function of the proportion of available (empty) patches. In terms of patch occupancy, the first possibility corresponds to a decelerating increase in per-patch colonization rate with increasing patch occupancy. The second corresponds to a unimodal function analogous to Harding and McNamara's [12] "Allee effect"; they attribute this phenomenon, where patch colonization rates drop at low levels of patch occupancy, to the difficulty of colonizing patches with small numbers of colonists because of low genetic diversity or demographic effects such as failure to mate. (The metapopulation framework has also been applied in epidemiological contexts, where each individual of the host species is considered a "patch" to be colonized by disease [23]. In this case, Allee effects correspond to a dose-dependent mechanism where colonization is more likely to be successful when more infectious particles are available.) Our model structure attributes this decrease in colonization effectiveness to a decreased probability of emigration at low metapopulation occupancy, but the actual effects are likely to be similar whether the decrease is caused by processes occurring (1) during emigration, as we suggest here; (2) during movement between patches (e.g. because of increased predator efficiency with small absolute numbers of colonists) or (3) during colonization, because of density-dependent colonization success [1]. While Allee effects in metapopulations have been suggested by Hanski [10], Amarasekare [1], and Harding and McNamara [12], and dependence of emigration on the presence of a (single) empty patch has been tested in an experimental setting by Le Galliard et al. [17], we are not aware of any efforts to detect such an effect empirically from records of observed colonizations and extinctions in natural metapopulations.

2. A patch-occupancy age structured model with dispersal

In this section we introduce a patch-occupancy age-structured model with dispersal. We denote the number of empty patches available for colonization by $E(t)$. We call the property of a patch being occupied patch occupancy and we denote the density of the proportion of occupied patches by $u(\theta, t)$ where θ is the time since the last colonization of the patch (i.e., occupancy of the patch after it has been empty). We will refer to θ as *patch-occupancy age*. The occupied patches can become empty due to local population extinction. The per patch rate of local population extinction $\kappa(\theta)$ depends on the patch-occupancy age. We assume that $\kappa(\theta)$ is a continuous bounded function of θ with $\sup \kappa(\theta) = \bar{\kappa}$. Furthermore, there is a threshold patch-occupancy age θ^* and a positive number κ^* such that $\kappa(\theta) \geq \kappa^*$ for all $\theta \geq \theta^*$. This assumption guarantees that the probability that the patch is still occupied for θ time units declines exponentially to zero when $\theta \geq \theta^*$. Although some models discriminate between habitable and non-habitable patches [16] we will not make this distinction here.

We determine the per-patch colonization rate by combining all emigrants from all occupied patches into a dispersal pool: emigration increases colonization rates but does not affect extinction rates since we assume that the loss of a few individuals from an established population is negligible. The total number of dispersers is denoted by $D(t)$. The rate at which dispersers leave the dispersers' pool to settle is denoted by γ. We call γ dispersers' emigration rate. Empty patches are colonized by dispersers at a colonization rate c. The model takes the form

$$(2.1) \quad \begin{aligned} E' &= \int_0^\infty \kappa(\theta)u(\theta, t)d\theta - cE(t)D(t) \\ u_\theta + u_t &= -\kappa(\theta)u(\theta, t) \\ u(0, t) &= cE(t)D(t) \\ D' &= \int_0^\infty \beta(E, \theta)u(\theta, t)d\theta - \gamma E(t)D(t) - \rho D(t) \end{aligned}$$

In the above model $\beta(E, \theta)$ is the patch-emigration rate. We will assume that the patch-emigration rate depends both on the availability of empty patches and the duration of occupancy of the patch which is the source of emigration (for example, patch-occupancy age could be considered a surrogate for population size). Furthermore, the emigration rate is a separable function, that is $\beta(E, \theta) = \alpha(E)\beta_0(\theta)$ where the occupancy age dependent component $\beta_0(\theta)$ is a continuous and bounded function $\sup \beta_0(\theta) = \bar{\beta}$. We will consider three cases for dependence of the emigration rate on availability of empty patches:

(1) The function $\alpha(E)$ is a constant, that is the emigration rate does not depend on the availability of empty patches: $\alpha(E) = \alpha = $ constant (analogous to the original Levins patch-occupancy model [18]).

(2) The function $\alpha(E)$ is non-constant and increasing. This possibility covers the case when the patch-emigration rate increases with the availability of empty patches.
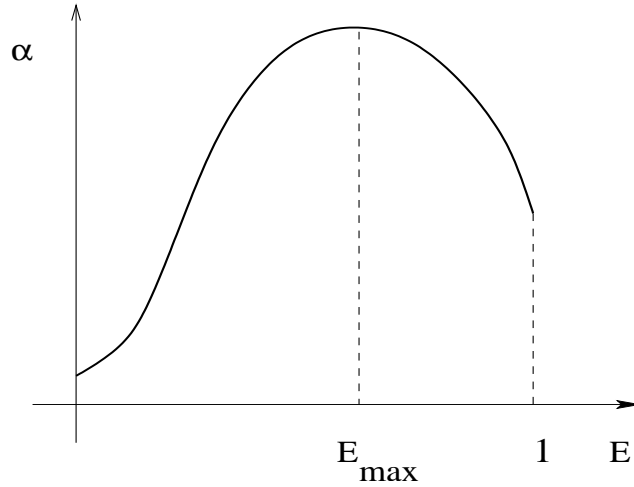
FIGURE 1.   Possible graph of the function $\alpha(E)$ in Case 3.

(3) The function $\alpha(E)$ is non-constant unimodal and concave down after the maximum (see Fig. 1). The maximum is attained for $E_{\max}$ and $\alpha(E_{\max}) = \alpha_{\max}$. This form of the function reflects the possibility that at the beginning when all patches are empty, and the opportunities for colonization are ample, the emigration rate at first increases as more and more patches get occupied and the proportion of empty patches declines. After reaching some maximum at certain occupancy pattern, the emigration rate declines as the proportion of empty patches goes to zero. We call the temporary increase in the patch-emigration rate while the proportion of empty patches decreases "Allee effect in dispersal".

With the assumption of separability the equation for the dispersers becomes:

$$D' = \alpha(E) \int_0^\infty \beta_0(\theta)u(\theta,t)d\theta - \gamma E(t)D(t) - \rho D(t)$$

Finally, $\rho > 0$ is the natural death rate of dispersing individuals. We specify non-negative initial conditions $E(0) = E_0$, $u(\theta,0) = u_0(\theta)$ and $D(0) = D_0$ for the system, and assume that the initial distribution of the proportion of occupied patches $u_0(\theta)$ is an integrable function. We denote the total proportion of occupied patches at time t by $U(t)$; it is given by the integral of the age distribution across all ages,

$$U(t) = \int_0^\infty u(\theta,t)d\theta \qquad \Longrightarrow \qquad U_0 := U(0) = \int_0^\infty u_0(\theta)d\theta.$$

Here U_0 denotes the initial proportion of occupied patches. Furthermore, we have that the initial conditions satisfy $E_0 + U_0 = 1$. Integrating the equation for the proportion of occupied patches we have

$$U'(t) = cE(t)D(t) - \int_0^\infty \kappa(\theta)u(\theta,t)d\theta.$$

Adding the above equation to the equation for $E'(t)$ we obtain $E'(t) + U'(t) = 0$ which leads to the conclusion that $E(t) + U(t) = $ constant for all time. Thus, from the assumption for the initial conditions, we have $E(t) + U(t) = 1$ for all time. The last equation says that the sum of the proportion of empty and occupied patches equals all patches. This corresponds to the Levins model [18]. Some authors have extended the Levins model by assuming that a proportion of all patches $1 - h$ is permanently uninhabitable [22, 25, 24, 11], reducing the proportion of all habitable patches to $h < 1$: $E(t) + U(t) = h$. Although we will only consider the case of all-habitable patches, our results extend to the case when a fixed proportion of all patches is permanently uninhabitable.

We introduce the probability of a patch still being occupied θ time units after it is first occupied: $\pi(\theta) = e^{-\int_0^\theta \kappa(\sigma)d\sigma}$. We note that the probability function clearly does not exceed one for all values of θ and that $\pi(\theta)$ approaches zero as θ goes to infinity as a result of the assumption $\kappa(\theta) \geq \kappa^*$ for $\theta \geq \theta^*$. Furthermore, integration by parts shows that

$$(2.2) \qquad \int_0^\infty \kappa(\theta)\pi(\theta)d\theta = 1$$

Intuitively this equality says that every occupied patch will eventually become empty. Next, we define the quantity

$$(2.3) \qquad \mathcal{B} = \int_0^\infty \beta_0(\theta)\pi(\theta)d\theta.$$

We note that if all patches are empty, and one disperser is introduced in the system and settles on a patch, $\alpha(1)\mathcal{B}$ gives the number of secondary dispersers that will be produced. We call $\mathcal{B}$ total patch emigration. A proportion $\frac{c}{\gamma+\rho}$ of them will survive the dispersers' state and settle on a patch, given that all patches are empty. Thus the reproduction number of the metapopulation is given by:

$$(2.4) \qquad \mathcal{R} = \frac{c\alpha(1)\mathcal{B}}{\gamma + \rho}$$

The characteristic lines of the partial differential equation are lines with slope one. As the partial differential equation reduces to an ordinary differential equation along these lines, it can be integrated. This procedure is described in more detail in [6]. It leads to the following solution in terms of E and D:

$$(2.5) \qquad u(\theta, t) = \begin{cases} u_0(\theta - t)\dfrac{\pi(\theta)}{\pi(\theta - t)} & \theta \geq t \\ cE(t - \theta)D(t - \theta)\pi(\theta) & \theta < t \end{cases}$$

Substituting this expression for $u(\theta, t)$ we obtain a closed system of integro-differential equations for E and D:

(2.6)
$$E' = c \int_0^t \kappa(\theta) E(t - \theta) D(t - \theta) \pi(\theta) d\theta + F_1(t) - cE(t)D(t)$$
$$D' = c\alpha(E) \int_0^t \beta_0(\theta) E(t - \theta) D(t - \theta) \pi(\theta) d\theta + F_2(t) - \gamma E(t)D(t) - \rho D(t)$$

We note that the first integrals on the right hand side of each equation above are convolution integrals. The functions F_1 and F_2 are given functions determined by the initial condition u_0 and the parameters of the system (2.1):

$$F_1(t) = \int_t^\infty \kappa(\theta) u_0(\theta - t) \frac{\pi(\theta)}{\pi(\theta - t)} d\theta, \qquad F_2(t) = \int_t^\infty \beta_0(\theta) u_0(\theta - t) \frac{\pi(\theta)}{\pi(\theta - t)} d\theta.$$

The function $F_1(t)$ and $F_2(t)$ go to zero as time goes to infinity. This follows from the assumptions on the parameters which lead to the following estimate on F_i, $i = 1, 2$ for $t \geq \theta^*$: $F_i(t) \leq K e^{-\kappa^*(t - \theta^*)} \|u_0\|_1$ where $i = 1, 2$, $\|u_0\|_1$ is the integral of the initial condition u_0, and $K = \max\{\bar{\beta}, \bar{\kappa}\}$.

In conclusion, consider the case when all parameters in the system (2.1) are independent of θ: $\kappa(\theta) = \kappa$ and $\beta_0(\theta) = \beta$. The system (2.1) turns into a system of ordinary differential equations which we state here for future reference:

(2.7)
$$\begin{aligned} E' &= \kappa U(t) - cE(t)D(t) \\ U' &= cE(t)D(t) - \kappa U(t) \\ D' &= \beta\alpha(E)U(t) - \gamma E(t)D(t) - \rho D(t) \end{aligned}$$

Using the equality $E(t) + U(t) = 1$ we can eliminate one of the equations for E or U and obtain a two-dimensional system.

3. Subthreshold and supertheshold equilibria of the system and their linear stability

In this section we consider the time independent solutions of the system (2.1). These solutions satisfy a system in which the time derivatives are equal to zero. Let E and D be time-independent, that is constant. Then $u(\theta)$ satisfies a simple ordinary differential equation which can be solved to give $u(\theta) = cED\pi(\theta)$ where E and D are still to be determined. Next, substituting this expression in the first equation in the time independent system it can be seen that thanks to identity (2.2) it is automatically satisfied for all values of E and D. Finally, substituting the expression for $u(\theta)$ in the third equation of the time independent version of system (2.1) we obtain the following equation

$$\alpha(E)cED \int_0^\infty \beta_0(\theta)\pi(\theta)d\theta - \gamma ED - \rho D = 0$$

This equation is satisfied when $D = 0$. This gives the first equilibrium of the system — the extinction equilibrium. From the fact that the number of dispersers is zero we get $u(\theta) = 0$ and, consequently, the proportion of occupied patches is

zero: $U = 0$. Thus from the equality $E + U = 1$ we have $E = 1$ and all patches are empty — the metapopulation is extinct. The extinction equilibrium is the ordered triple $\mathcal{E}_0 = (1, 0, 0)$. We conclude that dispersal is necessary for population to persist. Next, if $D \neq 0$ then it can be canceled from the equation above and we obtain an equation in E which with the notation for the integral introduced in (2.3) takes the form:

$$(3.1) \qquad\qquad c\alpha(E)E\mathcal{B} = \gamma E + \rho$$

The number of solutions of this equation in the interval $(0, 1)$ depends on the function $\alpha(E)$. The three cases for $\alpha(E)$ that we consider give the following equilibria:

Case 1: If $\alpha(E) = \alpha = $ constant then equation (3.1) is linear. Since the left hand side is zero when $E = 0$ while the right hand side is ρ, this equation has exactly one solution if and only if when $E = 1$ the left hand side is larger than the right hand side, that is if and only if $\mathcal{R} > 1$. The unique solution can be explicitly computed. From (3.1) the value of E^* is

$$(3.2) \qquad\qquad E^* = \frac{\rho}{c\alpha\mathcal{B} - \gamma} = \frac{\rho}{(\gamma + \rho)\mathcal{R} - \gamma}.$$

We note that $\mathcal{R} > 1$ implies both that $E^* > 0$ and $E^* < 1$. We determine the corresponding value of D^* from the equation $E^* + U^* = 1$. Substituting the respective value of $u^*(\theta)$ we get the equation for D^*: $E^* + cE^*D^*\mathcal{P} = 1$ where $\mathcal{P}$ is the integral from zero to infinity of $\pi(\theta)$, $\int_0^\infty \pi(\theta)d\theta$. Therefore,

$$(3.3) \qquad\qquad D^* = \frac{1 - E^*}{cE^*\mathcal{P}} = \frac{(\gamma + \rho)(\mathcal{R} - 1)}{c\rho\mathcal{P}}.$$

Finally the corresponding value of U^* is

$$(3.4) \qquad\qquad U^* = \frac{(\gamma + \rho)(\mathcal{R} - 1)}{(\gamma + \rho)\mathcal{R} - \gamma}.$$

As expected the proportion of occupied patches at equilibrium U^* increases with increasing of the reproduction number $\mathcal{R}$, emigration rate α, and total patch emigration $\mathcal{B}$, and decreases when the natural death rate of dispersers ρ increases — a conclusion that can be reached by taking the corresponding derivatives in the expression above. We summarize this discussion in the proposition at the end of Case 2.

Case 2: When $\alpha(E)$ is an increasing function of E, an argument as in Case 1 shows that if $\mathcal{R} > 1$ then the equation (3.1) has at least one solution. We claim that if $\mathcal{R} > 1$ then the equation (3.1) has exactly one solution and if $\mathcal{R} < 1$ then it has no solutions. To see this, rewrite equation (3.1) in the form

$$(3.5) \qquad\qquad c\alpha(E)\mathcal{B} = \gamma + \frac{\rho}{E}.$$

The right hand side is an increasing function of E while the left hand side is a decreasing function of E. Consequently, there is at most one intersection. Hence, if $\mathcal{R} > 1$ there is a unique solution.
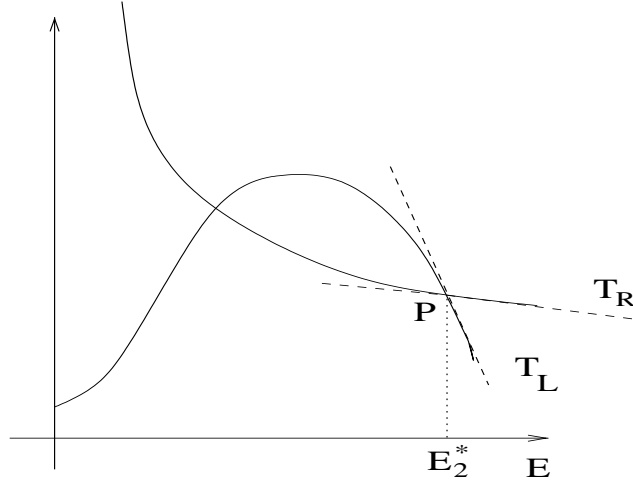
FIGURE 2.   The decreasing curve is $\gamma + \frac{\rho}{E}$. Its tangent at the second point of intersection is T_R. The non-monotone function is a scalar multiple of the function $\alpha(E)$, that is $c\alpha(E)\mathcal{B}$. Its tangent is T_L.

When $\mathcal{R} < 1$ the same argument as above shows that there is at most one solution. If we assume that $c\alpha(E^*)E^*\mathcal{B} = \gamma E^* + \rho$ for some $E^* < 1$ then the left-hand side is above the right-hand side for $E > E^*$ and, in particular for $E = 1$ we have $c\alpha(1)\mathcal{B} > \gamma + \rho$ which implies $\mathcal{R} > 1$ — a contradiction. Thus, E^* does not exist and there are no solutions.

Let $E^* < 1$ be the unique solution when $\mathcal{R} > 1$. Its value cannot be explicitly computed without further knowledge of the function $\alpha(E)$. Then the corresponding value of D^* can be computed from the first expression in (3.3). We summarize these results in the following proposition.

Proposition 3.1. *Let $\alpha(E)$ be a constant ($\alpha(E^*) = \alpha$) or an increasing function of E. Then the system (2.1) has a unique nontrivial equilibrium $\mathcal{E} = (E^*, cE^*D^*\pi(\theta), D^*)$ if and only if $\mathcal{R} > 1$. In the case when $\alpha(E^*) = \alpha$ the values of E^* and D^* are given respectively in (3.2) and (3.3).*

Case 3: When $\alpha(E)$ is unimodal and $\alpha(E)$ is concave down for $E > E_{\max}$ we claim that if $\mathcal{R} > 1$ there is always a unique solution of equation (3.1). For $\mathcal{R}^* < \mathcal{R} < 1$ there are exactly two solutions if $\frac{\rho}{\gamma+\rho}\alpha(1) < -\alpha'(1)$ and no solutions otherwise. We note that $\alpha'(1) < 0$ here as α is a decreasing function near one. To see this consider first the case when $\mathcal{R} > 1$. From the argument in Case 1 we know that there is at least one solution. Assume there is another intersection of the curves in equation (3.5), namely E_2^*. It necessarily occurs for $E_2^* > E_{\max}$ because for $E < E_{\max}$ there could be at most one intersection. Let $P = (E_2^*, Y)$, where $Y = c\alpha(E_2^*)\mathcal{B}$, be the point of intersection. Let T_L be the tangent of $c\alpha(E)\mathcal{B}$ and T_R be the tangent of $\gamma + \rho/E$ at the point P. Whenever $\alpha(E)$ is concave down it lies below its tangent, that is, $c\alpha(E)\mathcal{B}$ is smaller than T_L for $E > E_2^* > E_{\max}$. The curve $\gamma + \rho/E$ is everywhere concave up and thus lies above its tangent T_R.
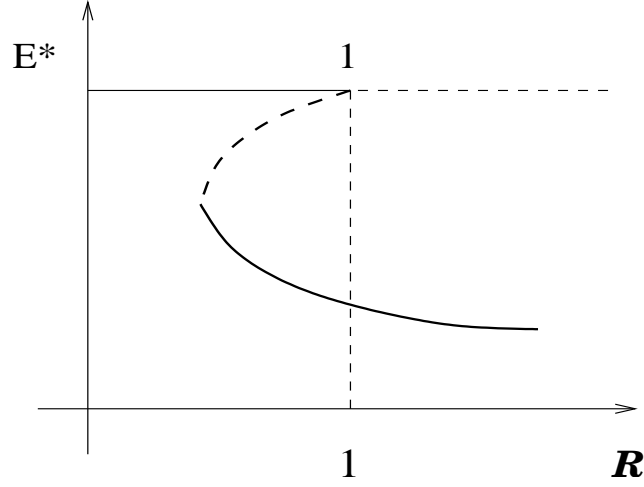
FIGURE 3. Backward bifurcation diagram with respect to the re-production number $\mathcal{R}$. In the case $\mathcal{R}^* < \mathcal{R} < 1$ there are two non-trivial equilibria - the lower one is stable, at least in the constant coefficient case, while the upper one is unstable.

At the point P the tangent T_L crosses T_R, going from above T_R to below T_R. Consequently, $c\alpha(E)\mathcal{B} < T_L < T_R < \gamma + \frac{\rho}{E}$ for $E > E_2^*$. Consequently there are no more intersections of the two curves in the interval $(E_2^*, 1)$. Hence for $E = 1$ we have $c\alpha(1)\mathcal{B} < \gamma + \rho$ which implies $\mathcal{R} < 1$ — a contradiction. We conclude that E_2^* does not exist and the solution is unique (see Fig. 2).

In the case $\mathcal{R} < 1$ there are equilibria if and only if a backward bifurcation occurs, that is, the nontrivial equilibrium bifurcates from the extinction equilibrium and even for E^* very close to one it exists for values of the reproduction number below one (see Fig. 3). Since there is always a unique equilibrium for $\mathcal{R} > 1$ it is not possible to have nontrivial equilibria for $\mathcal{R} < 1$ if the bifurcation at the critical value $\mathcal{R} = 1$ is forward. If we consider $\mathcal{R}$ as a function of E we can find that function explicitly if in (3.1) we solve for $\mathcal{R}$ to obtain

$$\mathcal{R} = \frac{\alpha(1)}{\gamma + \rho}\frac{\gamma E + \rho}{\alpha(E)E}.$$

Then (see Fig. 3) the bifurcation is backward if the derivative of $\mathcal{R}$ with respect to E when $E = 1$ is positive - respectively, the slope of the tangent line at $(1, 1)$ is positive:

$$\frac{d\mathcal{R}}{dE}\big|_{E=1} > 0.$$

This leads to the necessary and sufficient condition for existence of backward bifurcation $\frac{\rho}{\gamma+\rho}\alpha(1) < -\alpha'(1)$. From this inequality we see that increased rate of colonization of new patches or decreased mortality of dispersers increase the chance of subthreshold and multiple equilibria. Furthermore, the larger the decline of α

near one, that is, the more pronounced the Allee effect in dispersal, the more likely it is the backward bifurcation to occur.

If subthreshold equilibria occur, there are at least two of them — E_1^* and E_2^* — since at E_1^* the left-hand side of (3.1) becomes from smaller to larger than the right-hand side and at E_2^* the left-hand side of (3.1) becomes from larger to smaller than the right-hand side and stays smaller until $E = 1$ in accordance with $\mathcal{R} < 1$. An argument as above shows that for $E > E_2^*$ there can be no more intersections. Thus, there are exactly two equilibria for $\mathcal{R}^* < \mathcal{R} < 1$. Looking at Fig. 3 we see that if $0 < \mathcal{R} < \mathcal{R}^*$ there are no equilibria. Since $\mathcal{R}' < 0$ when E is near zero and $\mathcal{R}' > 0$ when $E = 1$ then there is an $\hat{E}$ such that $\mathcal{R}' = 0$ when $E = \hat{E}$ and the function $\mathcal{R}$ attains a minimum at that point. Let

$$\mathcal{R}^* = \frac{\alpha(1)}{\gamma + \rho} \frac{\gamma \hat{E} + \rho}{\alpha(\hat{E}) \hat{E}}.$$

The value $\mathcal{R}^*$ is called *minimal transition value* [29]. After the solutions of (3.1) have been determined, the corresponding values of D^* are determined from the first expression in (3.3). We summarize this result in the following proposition:

Proposition 3.2. *Let $\alpha(E)$ be unimodal and concave down after its maximum function of E. The the system (2.1) has a unique nontrivial equilibrium $\mathcal{E} = (E^*, cE^*D^*\pi(\theta), D^*)$ if $\mathcal{R} > 1$. If $\mathcal{R}^* < \mathcal{R} < 1$ there are two nontrivial equilibria $\mathcal{E}_1 = (E_1^*, cE_1^*D_1^*\pi(\theta), D_1^*)$ and $\mathcal{E}_2 = (E_2^*, cE_2^*D_2^*\pi(\theta), D_2^*)$ if and only if $\frac{\rho}{\gamma + \rho}\alpha(1) < -\alpha'(1)$. If $0 < \mathcal{R} < \mathcal{R}^*$ there are no non-trivial equilibria.*

If $\alpha(E)$ is not concave down after its maximum, then there can be more equilibria. We call an equilibrium *simple* if it satisfies (3.1) but does not satisfy the equation obtained by differentiating (3.1) — that is, the curve in the left-hand side of (3.1) crosses the curve at the right-hand side and the tangents at the intersection point have different slopes. If that condition is not satisfied we call the equilibrium *not simple*. In the case when $\mathcal{R} > 1$ if all equilibria are simple there must be an odd number of them. In the case when $\mathcal{R} < 1$ if all equilibria are simple there must be an even number of them.

Concerning the stabilities of the equilibria, some partial results are given the propositions below. Their justification can be found in Appendix A. We have full understanding of the local stability of the extinction equilibrium.

Proposition 3.3. *If $\mathcal{R} < 1$ then the extinction equilibrium $\mathcal{E}_0$ is locally asymptotically stable. If $\mathcal{R} > 1$ the extinction equilibrium is unstable.*

When there are multiple non-extinction equilibria and they are all simple we can show that every other one is unstable. Suppose they are ordered in increasing order of the equilibrium value of empty patches E^*, namely, $\mathcal{E}_1 < \mathcal{E}_2 < \cdots < \mathcal{E}_n$. Proposition 3.2 gives the specific conditions for two equilibria to exist. We have the following result on the instability of every other one of them:

Proposition 3.4. *If there are multiple non-extinction equilibria which are all simple and ordered in an increasing order of E^*, then every other one is unstable with the even-numbered ones being unstable.*
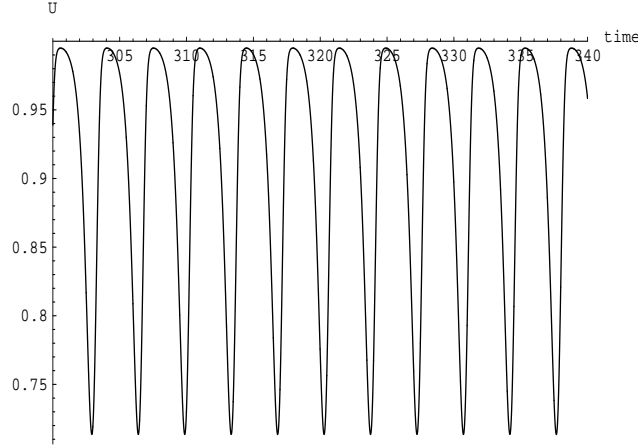
FIGURE 4.   Total proportion of occupied patches $U(t)$ exhibits sustained oscillation as a result of the presence of patch-occupancy age structure. Parameters as given in text.

In particular for the subthreshold equilibria in Proposition 3.2 $\mathcal{E}_2$ is unstable. We note that the present bifurcation diagram (see Fig 3) is a mirror image of the usual one (see e.g. [20], or Fig. 4.2 in [11]) and the extinction equilibrium is at the largest value of the bifurcation variable, rather than the smallest value. The remaining equilibria are locally asymptotically stable at least in the case when all parameters of the system are constant, that is for the system (2.7).

Proposition 3.5. *Let $\kappa(\theta) = \kappa$ and $\beta_0(\theta) = \beta$ be constant. If the non-extinction equilibria are all simple and ordered in increasing order of E^*, then every other one is stable with odd-numbered equilibria being locally asymptotically stable. Furthermore, if $\mathcal{R} > 1$ and there is a unique non-trivial equilibrium, then it is locally and globally stable.*

The situation with the patch-occupancy age structured model (2.1) is rather different. Even when there is only one non-extinction equilibrium in the case $\mathcal{R} > 1$ this equilibrium may lose stability and sustain oscillations through Hopf bifurcation occur if the parameters $\kappa(\theta)$ and $\beta_0(\theta)$ vary in particular ways with age. This situation is illustrated here in Fig. 4 where the parameters are taken as follows: $\rho = 2.1248$, $c = 19.713435$, $\gamma = 19.713435$, $\alpha(E) = 2$,

$$\kappa(\theta) = \begin{cases} 0 & 0 \leq \theta \leq 3 \\ 10 & \theta > 3 \end{cases} \qquad \beta_0(\theta) = \begin{cases} 10\theta(1 - \theta) & 0 \leq \theta \leq 1 \\ 0 & \theta > 1 \end{cases}$$

with $\mathcal{R} \approx 3$. Thus, the dependence of local extinction and emigration of a patch duration of occupancy can lead to a different and more complex dynamical behavior of the system. This situation has been known to occur in epidemiological models with host age. Dependence of transition rates on both chronological age and

infection age (equivalent to our patch-occupancy age) has been found to destabilize the equilibrium and cause sustained oscillations [26, 28, 19].

4. Scenarios for persistence and extinction of the metapopulation

A metapopulation is defined as a set of populations occupying separate areas and connected by dispersal. From this description it is clear that dispersal is a vital element of the survival of the metapopulation. We saw that if there is no dispersal only the extinction equilibrium exists. Thus, processes related and essential to population dispersal are vital for the persistence of the metapopulation. In particular, if there is no emigration, that is if $\beta(E, \theta) = 0$, there is no source of dispersers. The disperser population will die out and with it the entire metapopulation. In the model (2.1) this is easy to see since $D' \leq -\rho D$, or equivalently $D(t) \leq D_0 e^{-\rho t}$ which implies that $D(t) \to 0$ as $t \to \infty$. From the expression for u in (2.5) one can see that the extinction of the dispersers population automatically leads to decline to zero of the proportion of occupied patches and the vanishing of the metapopulation.

Another process critical for the metapopulation survival is new patch colonization. If there is no colonization of empty patches $c = 0$, then the process of turning empty patches into occupied is interrupted and the initial supply of occupied patches gradually declines to zero. We summarize these results in the following proposition.

Proposition 4.1. *If there is no emigration into the disperser pool $\beta(E, \theta) = 0$ or there is no colonization of empty patches $c = 0$ then the metapopulation is bound to go extinct, that is, $U(t) \to 0$ and $D(t) \to 0$ while $E(t) \to 1$, independently of the initial conditions.*

When all parameters are non-trivial then the fate of the metapopulation is to some extent described by its basic reproduction number. We already saw in Section 3 that the extinction equilibrium is locally asymptotically stable if $\mathcal{R} < 1$. In particular this means that for initial conditions sufficiently close to the extinction equilibrium the metapopulation will go extinct. In the case when there can be subthreshold equilibria while $\mathcal{R}^* < \mathcal{R} < 1$ this is perhaps the sharpest possible result on extinction as one of the subthreshold equilibria might be locally stable. Therefore solutions that start sufficiently close to it will converge to a non-extinction equilibrium and for these initial statuses the metapopulation will in fact persist despite that $\mathcal{R} < 1$. This outcome is a result of the Allee effect in dispersal, that is of the fact that the emigration rate is increasing with decreasing availability of empty patches (E). We expect, although we have not shown rigorously, that if $\mathcal{R} < \mathcal{R}^*$ the metapopulation will go extinct independently of the starting conditions. In this case the colonization ability of the population is simply too small to sustain the metapopulation. In the case when α is constant or increasing, there are no subthreshold equilibria. We conjecture that in this case if $\mathcal{R} < 1$ the extinction equilibrium is also globally stable and the metapopulation will vanish independently of its initial status.

If $\mathcal{R} > 1$ the metapopulation persists. We distinguish two forms of persistence – *uniform weak persistence* and *uniform strong persistence*. Formally, we call the metapopulation *uniformly weakly persistent* if there exists an $\eta > 0$, independent of the initial conditions, such that if $D_0 > 0$ we also have

$$\limsup_t D(t) > \eta.$$

Roughly speaking, the population is uniformly weakly persistent if the number of dispersers is above a certain constant value at least occasionally, independent of the initial condition.

In Appendix B we establish that the metapopulation described by the model (2.1) is uniformly weakly persistent when $\mathcal{R} > 1$.

Formally, we call the metapopulation *uniformly strongly persistent* if there exists an $\eta > 0$, independent of the initial conditions, such that if $D_0 > 0$ we also have

$$\liminf_t D(t) > \eta.$$

Intuitively, the uniform strong persistence of the metapopulation means that the number of dispersers stays above certain constant value η for all time after some initial time $t_0 > 0$. If the metapopulation is uniformly strongly persistent, it is also uniformly weakly persistent. The converse is not always true but our results below show that it is for the metapopulation described by the model (2.1).

If the solutions of (2.1) are uniformly weakly persistent, they are uniformly strongly persistent if they are attracted in time by a maximal compact set. In Appendix B we explain the concept of maximal compact set and we show that to be the case for the system (2.1). In Appendix B we also establish that the metapopulation described by the model (2.1) is uniformly strongly persistent when $\mathcal{R} > 1$:

Proposition 4.2. *If $\mathcal{R} > 1$ then the metapopulation is uniformly strongly persistent.*

Both uniformly weak and uniformly strong persistence require the metapopulation to stay away from extinction independently of its initial status. In particular uniform weak persistence implies that the extinction equilibrium is unstable. For these reasons, when $\mathcal{R} < 1$ although the metapopulation may persist for some initial conditions, it is neither uniformly weakly, nor uniformly strongly persistent.

5. Conclusions

We have explored the effects of two interacting kinds of complexity in patch-occupancy models, dependence of emigration (colonization) rate on occupancy and of emigration and extinction on patch-occupancy age. As is typical, we find that the ability of the metapopulation to persist (instability of the extinction equilibrium) depends only on the reproductive number $\mathcal{R}$, which in turn depends only on the colonization probability c, mortality rate ρ, the expected lifetime emigration $\mathcal{B}$, and the emigration rate at low densities $\alpha(1)$; the potential dynamical

complexities disappear in the low-density limit. However, the number and stability of non-trivial equilibria does depend critically on the details of the model. For unimodal $\alpha(E)$ (dependence of emigration *or* effective colonization rate on total occupancy), two or more stable equilibria are possible (more than two only if $\alpha(E)$ is not concave down above its maximum). While multiple stable equilibria in metapopulation dynamics have been observed before [10, 12] and also in the context of size-structured metapopulations [7, 8, 2, 3, 21], our paper gives formal and rigorous characterization of when and how many of them can exist. Dependence on patch-occupancy age, although at least as ecologically plausible as Allee effects [31], has only been explored through its analogues in disease dynamics [26, 28, 19], where it has been shown to have the potential to destabilize metapopulation dynamics. However, we are also able to show that despite any possible oscillatory dynamics, the metapopulation will still persist as long as $\mathcal{R} > 1$. Harding and McNamara [12] recommended that ecologists "systematically investigate how the form of the colonization and extinction functions affects metapopulation dynamics"; we suggest that in order to understand the long-term dynamics of metapopulations, ecologists should try to characterize the dependence of colonization and extinction rate both on metapopulation occupancy and on patch-occupancy age.

Acknowledgements

Appendix A. Local stability of equilibria

We consider the linearization of the system (2.1). If $\mathcal{E} = (E^*, u^*(\theta), D^*)$ is an equilibrium we denote its perturbations by $\epsilon(t)$, $\chi(\theta, t)$ and $d(t)$ respectively, that is $E(t) = E^* + \epsilon(t)$, $u(\theta, t) = u^*(\theta) + \chi(\theta, t)$ and $D(t) = D^* + d(t)$. Substituting in the system (2.1) and taking into account the equations for the equilibria we obtain the following system for the perturbations:

$$
\begin{aligned}
&\epsilon'(t) = \int_0^\infty \kappa(\theta)\chi(\theta, t)d\theta - cE^*d(t) - cD^*\epsilon(t) \\
&\chi_\theta + \chi_t = -\kappa(\theta)\chi(\theta, t) \\
\text{(A.1)} \quad &\chi(0, t) = cE^*d(t) + cD^*\epsilon(t) \\
&d'(t) = \alpha(E^*)\int_0^\infty \beta_0(\theta)\chi(\theta, t)d\theta + c\alpha'(E^*)E^*D^*\mathcal{B}\epsilon(t) \\
&\qquad\qquad\qquad\qquad -\gamma E^*d(t) - \gamma D^*\epsilon(t) - \rho d(t)
\end{aligned}
$$

We look for exponential solutions $\epsilon(t) = e^{\lambda t}\bar{\epsilon}$, $\chi(\theta, t) = e^{\lambda t}\bar{\chi}(\theta)$, $d(t) = e^{\lambda t}\bar{d}$ where $\bar{\epsilon}$, $\bar{d}$ are constants. In the remaining considerations we drop the bars. Substituting these forms in the system above we obtain a linear eigenvalue problem which consists of one ordinary differential equation that corresponds to the equation for χ and two integral equations. Solving the differential equation we obtain $\chi(\theta) = (cE^*d + cD^*\epsilon)e^{-\lambda\theta}\pi(\theta)$. Substituting into the integrals in the equations for ϵ and d

we obtain a linear system for ϵ and d whose coefficients depend on λ. This system has a non-zero solution if and only if the determinant is zero. This condition leads to the characteristic equation of the system (2.1):

$$(A.2) \quad \begin{aligned} [\lambda + \rho + \gamma E^* - cE^*\alpha(E^*)B(\lambda)][\lambda + cD^* - cD^*K(\lambda)] \\ = cE^*D^* \left[c\alpha(E^*)B(\lambda) + c\alpha'(E^*)E^*\mathcal{B} - \gamma \right](K(\lambda) - 1) \end{aligned}$$

where $B(\lambda)$ and $K(\lambda)$ are the following Laplace transforms:

$$(A.3) \quad B(\lambda) = \int_0^\infty \beta_0(\theta)e^{-\lambda\theta}\pi(\theta)d\theta, \qquad K(\lambda) = \int_0^\infty \kappa(\theta)e^{-\lambda\theta}\pi(\theta)d\theta.$$

Denoting by $L(\lambda)$ the Laplace transform of $\pi(\theta)$ we note that integration by parts leads to $K(\lambda) + \lambda L(\lambda) = 1$. We note here that this identity implies that $\lambda = 0$ is a solution of the equation (A.2). However, if $\mathcal{E}$ is a simple equilibrium, $\lambda = 0$ is not an eigenvalue. To see this let $\lambda = 0$ and let $\mathcal{E}$ be a non-trivial simple equilibrium. In the eigenvalue problem corresponding to (A.1) the first equation is automatically satisfied. Taking into account (3.1) from the last equation we obtain $D^*(c\alpha(E^*)\mathcal{B} + c\alpha'(E^*)E^*\mathcal{B} - \gamma)\epsilon = 0$ which implies that $\epsilon = 0$. The coefficient is non-zero since $\mathcal{E}$ is simple. Linearizing the identity $E(t) + U(t) = 1$ leads to $\epsilon + (cE^*d + cD^*\epsilon)L(\lambda) = 0$ from which it follows that $d = 0$ if $\epsilon = 0$.

Using the identity $K(\lambda) + \lambda L(\lambda) = 1$ and some algebra one can rewrite the characteristic equation in the form:

$$(A.4) \quad \begin{aligned} (\lambda + \rho)[1 + cD^*L(\lambda)] + cE^*cD^* \left[\alpha(E^*)B(\lambda) + \alpha'(E^*)E^*\mathcal{B}\right]L(\lambda) + \gamma E^* = \\ = cE^*\alpha(E^*)B(\lambda)[1 + cD^*L(\lambda)] \end{aligned}$$

Concerning the extinction equilibrium, one can see directly from the system (A.1) that $\lambda = 0$ is not an eigenvalue. The eigenvalues corresponding to the extinction equilibrium are solutions of the following characteristic equation of the extinction equilibrium, obtained from the expression above with $E^* = 1$ and $D^* = 0$:

$$(A.5) \quad \lambda + \rho + \gamma = c\alpha(1)B(\lambda)$$

If $\mathcal{R} > 1$ this equation has a positive real solution. To see that notice that for $\lambda = 0$ we have $\rho + \gamma < c\alpha(1)\mathcal{B}$ where $B(0) = \mathcal{B}$. For $\lambda > 0$ and real the left-hand side increases from $\rho + \gamma$ to infinity while the right-hand side decreases from $c\alpha(1)\mathcal{B}$ to zero. Thus, the two must intersect for $\lambda^* > 0$. Consequently, the extinction equilibrium $\mathcal{E}_0$ is unstable.

If $\mathcal{R} < 1$ consider λ's with nonnegative real part: $\lambda = x + iy$. In this case $|\lambda + \rho + \gamma| > x + \rho + \gamma \geq \rho + \gamma$. At the same time $|c\alpha(1)B(\lambda)| \leq c\alpha(1)B(x) \leq c\alpha(1)B(0) = c\alpha(1)\mathcal{B} = (\rho + \gamma)\mathcal{R} < \rho + \gamma$. Thus, the equation (A.5) has no solution λ with nonnegative real part. Consequently, the extinction equilibrium is locally asymptotically stable which justifies Proposition 3.3.

To see the claim in Proposition 3.4 let $\mathcal{F}(\lambda)$ denote the left-hand side in (A.4) and $\mathcal{G}(\lambda)$ denote the right hand side of (A.4). An equilibrium value of empty

patches E^* is a solution of (3.1). If we consider the left-hand side and the right-hand side of (3.1) as functions of the variable E the key observation that gives us this result is how the slopes of these two curves relate at an even-numbered equilibrium. In particular, for every even-numbered equilibrium the left-hand side crosses the right-hand side from above to below. Consequently, the left-hand side has a smaller slope than the right-hand side. Equivalently,

$$c\alpha'(E^*)E^*\mathcal{B} + c\alpha(E^*)\mathcal{B} < \gamma$$

Using this inequality we have that $\mathcal{F}(0) < (\rho + \gamma E^*)(1 + cD^*\mathcal{P})$ while by (3.1) $\mathcal{G}(0) = cE^*\alpha(E^*)\mathcal{B}(1+cD^*\mathcal{P}) = (\rho+\gamma E^*)(1+cD^*\mathcal{P})$. Consequently, $\mathcal{F}(0) < \mathcal{G}(0)$. Furthermore, for λ real, $\mathcal{F}(\lambda) \to \infty$ while $\mathcal{G}(\lambda) \to 0$ as $\lambda \to \infty$. Hence, there is a real and positive λ that solves the equation $\mathcal{F}(\lambda) = \mathcal{G}(\lambda)$.

To see the claim in Proposition 3.5 we notice that if we eliminate $U = 1 - E$ from the system (2.7) we obtain

(A.6)
$$\begin{aligned} E' &= \kappa(1 - E) - cED \\ D' &= \beta\alpha(E)(1 - E) - \gamma ED - \rho D \end{aligned}$$

Setting the derivatives equal to zero we obtain the following equations for the equilibria

(A.7) $\kappa(1 - E) = cED\beta\alpha(E)(1 - E) = (\gamma E + \rho)D$

We multiply the second equation by κ and use the first equation to replace $\kappa(1-E)$ by cED. We can then eliminate D since we are only interested in nontrivial equilibria and $D \neq 0$ for those. We reach the following equation for the equilibrium value of E:

(A.8) $c\beta\alpha(E)E = (\gamma E + \rho)\kappa$

which is exactly the equation we will obtain from (3.1) by setting all parameters constant. We also have for the odd numbered equilibria

(A.9) $c\beta\alpha'(E^*)E^* + c\beta\alpha(E^*) > \gamma\kappa$

The Jacobian of the system (A.6) at equilibrium (E^*, D^*) is given by

(A.10) $J = \begin{pmatrix} -\kappa - cD^* & -cE^* \\ \beta\alpha'(E^*)(1 - E^*) - \beta\alpha(E^*) - \gamma D^* & -\gamma E^* - \rho \end{pmatrix}$

Since the trace is clearly always negative, the eigenvalues have negative real parts if and only if the discriminant is positive. The discriminant is given by

(A.11) $(\kappa + cD^*)(\gamma E^* + \rho) + cE^*[\beta\alpha'(E^*)(1 - E^*) - \beta\alpha(E^*) - \gamma D^*]$

We notice that if we distribute the sum in the first parenthesis the term $\kappa(\gamma E^* + \rho)$ can be replaced by the left-hand side of equation (A.8) while the term $cD^*(\gamma E^* + \rho) = \beta c\alpha(E^*)(1 - E^*)$ from the second equation for the equilibria in the system (A.7). Combining these two terms back again we see that $(\gamma E^* + \rho)(\kappa + cD^*) =$

$\beta c \alpha(E^*)$. ¿From the first equation for the equilibria the term $\gamma c E^* D^* = \gamma \kappa (1-E^*)$. After replacing these expressions in the discriminant, it becomes

(A.12)
$$\beta c \alpha(E^*) + \beta c \alpha'(E^*) E^*(1 - E^*) - \beta c \alpha(E^*) E^* - \gamma \kappa (1 - E^*)$$
$$= [\beta c \alpha'(E^*) E^* + \beta c \alpha(E^*) - \gamma \kappa](1 - E^*)$$

The expression in the brackets $[\cdot]$ is positive exactly when E^* is the equilibrium value of empty patches in an odd numbered equilibrium (see inequality (A.9)) and negative in even-numbered equilibria. This implies local stability of the odd-numbered equilibria and instability of the even-numbered equilibria which we know from the age-dependent case.

If there is a unique non-extinction equilibrium, then it is locally stable. This is, in particular, the case when α is constant or $\alpha(E)$ is strictly increasing. When the system (2.7) is reduced by eliminating through the identity $U(t) = 1 - E(t)$ it becomes a 2×2 system. Then Dulac's criterion applies (see [19]) and leads to global stability of the non-trivial equilibrium.

APPENDIX B. UNIFORMLY WEAK AND UNIFORMLY STRONG PERSISTENCE OF THE METAPOPULATION

First we show that if $\mathcal{R} > 1$ the metapopulation is uniformly weakly persistent.

Proposition B.1. *If $\mathcal{R} > 1$ then the metapopulation is uniformly weakly persistent.*

To see this, we show that there exists an $\eta_1 > 0$ such that $\limsup_t D(t) > \eta_1$ if $D(0) > 0$. We proceed by contradiction. We assume the contrary, that is, we assume that for every $\eta_0 > 0$ no matter how small we have $\limsup_t D(t) < \eta_0$ for any initial condition. This in particular means that there exists $t_0 > 0$ such that $D(t) < \eta_0$ for all $t \geq t_0$. Now, let $\tau = t - t_0$. We can evaluate the system (2.1) at $\tau + t_0$ and set $\hat{D}(\tau) = D(\tau + t_0)$, $\hat{E}(\tau) = E(\tau + t_0)$ and $\hat{u}(\theta, \tau) = u(\theta, \tau + t_0)$. We obtain the same system as (2.1) for the variables with hats and in τ. However $\hat{D}(0) = D(t_0) < \eta_0$. Dropping the hats and renaming τ as t we see that for the original system we may assume without loss of generality that $D(t) < \eta_0$ for all $t \geq 0$. This property is referred to as the *semiflow property* of the system. Using formula (2.5) in the identity $E + U = 1$ we obtain $E(t) = 1 - \phi(t)$ where $\phi \geq 0$

$$\phi(t) = c \int_0^\infty E(t - \theta) D(t - \theta) \pi(\theta) d\theta + F_3(t)$$

The function $\phi(t)$ is a "small" function and can be bounded. In particular, $E(t) \leq 1$, $D(t) \leq \eta_0$ for all $t \geq 0$. The function $F_3(t)$ is given by

(B.1)
$$F_3(t) = \int_t^\infty u_0(\theta - t) \frac{\pi(\theta)}{\pi(\theta - t)} d\theta$$

and satisfies $F_3(t) \leq e^{-\kappa^*(t - \theta^*)} \|u_0\|_1$ similarly to the functions $F_i(t)$ for $i = 1, 2$. Consequently, there exists t_1 such that $F_3(t) \leq \eta_0$ for all $t \geq t_1$. Thus for $t \geq t_1$ we have $\phi(t) \leq c \eta_0 \mathcal{P} + \eta_0 = \eta$ where we have denoted by $\eta = c \eta_0 \mathcal{P} + \eta_0$. We recall that $\mathcal{P}$ is the integral of π and is a constant just as c. Since η is proportional to

η_0 it is also small. Consequently, $E(t) \geq 1 - \eta$ for all $t \geq t_1$. Using again the semiflow property of the system we get $E(t) \geq 1 - \eta$ for all $t \geq 0$. Furthermore, expanding α in Taylor's series (assuming this can be done near one) $\alpha(E) = \alpha(1 - \phi(t)) = \alpha(1) - \alpha'(1)\phi(t) + H(\phi(t))$ where $H(\phi(t))$ denotes the higher order terms in ϕ. The first case for $\alpha(E)$ is simple. In the second case $\alpha'(1) > 0$ so $\alpha'(1)\phi(t) - H(\phi(t)) > 0$ and at the same time $\alpha'(1)\phi(t) - H(\phi(t)) \leq C\eta$ where $C > 0$ is a positive constant. Consequently, $\alpha(E) \geq \alpha(1) - C\eta$. In the third case $\alpha'(1) < 0$ and therefore $-\alpha'(1)\phi(t) + H(\phi(t)) > 0$ which leads to the conclusion that $\alpha(E) \geq \alpha(1)$. Summarizing, in all three cases we have $\alpha(E) \geq \alpha(1) - C\eta$. ¿From the integro-differential equation for D in (2.6) we have after neglecting F_2 and using the inequalities above the following inequality:

$$D'(t) \geq c[\alpha(1) - C\eta](1 - \eta) \int_0^t \beta_0(\theta) D(t - \theta)\pi(\theta)d\theta - \gamma D - \rho D$$

Taking the Laplace transform from both sides of this inequality and denoting the Laplace transform of D by $\hat{D}(\lambda)$ we have

$$\lambda\hat{D}(\lambda) - D(0) \geq \{c[\alpha(1) - C\eta](1 - \eta)B(\lambda) - (\gamma + \rho)\} \hat{D}(\lambda)$$

Moving $\lambda\hat{D}(\lambda)$ to the right-hand side and factoring out $(\gamma + \rho + \lambda)$ we have

$$-D(0) \geq (\gamma + \rho + \lambda)\left\{\frac{c[\alpha(1) - C\eta](1 - \eta)B(\lambda)}{\gamma + \rho + \lambda} - 1\right\}\hat{D}(\lambda)$$

For $\lambda = 0$ and $\eta = 0$ the expression in the big brackets on the right-hand side is equal to $(\mathcal{R} - 1)$ and therefore the right-hand side is positive for λ and η small enough, while the left-hand side is negative and cannot be larger. This is a contradiction with our assumption that for every η_0 we have $\limsup_t D(t) < \eta_0$. Consequently there is an η_1 such that $\limsup_t D(t) \geq \eta_1$. This justifies that the metapopulation is uniformly weakly persistent if $\mathcal{R} > 1$.

Next, we continue with establishing the uniform strong persistence. The main component necessary to establish this result is to verify that the solutions of the system (2.1) have a global compact attractor. A *global compact attractor* $\mathcal{K}$ is a maximal compact invariant set such that for any open set that contains $\mathcal{K}$, all solutions of the system (2.1) that start at zero from a bounded set, are contained in that open set, at least for sufficiently large time. For more precise definition see [9], Section 3.4.

Solutions of the system (2.1) are bounded. This is obvious for $E(t) \leq 1$ and $U(t) \leq 1$ but it is also true for the dispersing population. From the last equation in (2.1) we have $D' \leq \alpha_{\max}\bar{\beta} - \rho D$. Consequently,

$$D(t) \leq e^{-\rho t}\left(D_0 - \frac{\alpha_{\max}\bar{\beta}}{\rho}\right) + \frac{\alpha_{\max}\bar{\beta}}{\rho}$$

This implies that $D(t) \leq \frac{\alpha_{\max}\bar{\beta}}{\rho}$, at least for t large enough. Thus, all solutions that start from a bounded set remain bounded. Furthermore, any set $\mathcal{S}_r = \{(E, U, D) : E + U = 1, D \leq r\}$ with $r \geq \frac{\alpha_{\max}\bar{\beta}}{\rho}$ is invariant, that is solutions (E, U, D) that

start in it remain in it. In addition, the solutions that start in any bounded set, end in $\mathcal{S}_r$ for time large enough. See [9], Section 3.4.

We split the expression for $u(\theta, t)$ in two components: one component corresponds to taking the partial differential equation in (2.1) with the boundary condition and zero initial condition:

$$\hat{u}(\theta, t) = \begin{cases} 0 & \theta \geq t \\ cE(t-\theta)D(t-\theta)\pi(\theta) & \theta < t \end{cases}$$

the other - corresponds to taking the partial differential equation in (2.1) with zero boundary condition and the initial condition:

$$\tilde{u}(\theta, t) = \begin{cases} u_0(\theta-t)\dfrac{\pi(\theta)}{\pi(\theta-t)} & \theta \geq t \\ 0 & \theta < t \end{cases}$$

Clearly, $u(\theta, t) = \hat{u}(\theta, t) + \tilde{u}(\theta, t)$. Consequently, we consider the system (2.1) with $\hat{u}$ in place of u and solutions $(E(t), \hat{u}(\theta, t), D(t))$ and the "solutions" that $\tilde{u}$ generates: $(0, \tilde{u}(\theta, t), 0)$. Both solutions are non-negative.

We show that $\tilde{u} \to 0$ at $t \to \infty$ or more precisely we show that the integral of $\tilde{u}$ goes to zero as time goes to infinity. That integral is given by $F_3(t)$ in (B.1) and we already saw that $F_3(t) \leq e^{-\kappa^*(t-\theta^*)}\|u_0\|_1$. Clearly $F_3(t)$ goes to zero as time goes to infinity. In addition, the same is true for $\tilde{u}$ for every θ fixed.

Considering the solutions $(E(t), \hat{u}(\theta, t), D(t))$ we see that they are also bounded since $\hat{u} \leq u$. Consider all initial data that are in the set of (E_0, U_0, D_0) satisfying $E_0 + U_0 = 1$ and $D_0 \leq K$ where K is some constant. We show that for a fixed t large enough, the family of functions $(E(t), \hat{u}(\cdot, t), D(t))$ obtained from taking various initial conditions for D_0 is a compact family of functions. Then by Lemma 3.2.3 and Theorem 3.4.6 in [9] the solutions of (2.1) have a global compact attractor. To see the compactness of the family of functions $(E(t), \hat{u}(\cdot, t), D(t))$ we use the Fréchet-Kolmogorov theorem for compactness (see e.g. [30]). From the three conditions in the theorem the first and the third have already been established since the third follows trivially from the fact that $\hat{u}(\theta, t) = 0$ for $\theta > t$. The second condition follows from the uniform (with respect to all functions in the family) boundedness of the derivatives with respect to θ of $\hat{u}$. Differentiating $\hat{u}$ we get

$$\hat{u}_\theta = \begin{cases} 0 & \theta > t \\ -c[E'(t-\theta)D(t-\theta) + E(t-\theta)D'(t-\theta)]\pi(\theta) & \\ \qquad\qquad -c\kappa(\theta)cE(t-\theta)D(t-\theta)\pi(\theta) & \theta < t \end{cases}$$

¿From the differential equation for E taking into account that $\kappa(\theta) \leq \bar{\kappa}$ we have $E' \leq \bar{\kappa}$. For $D_0 \leq K$ we have that $D \leq K + \dfrac{\bar{\beta}\alpha_{\max}}{\rho} = K_1$. Consequently, $E' \geq -cED \geq -cK_1$. To bound D' we notice that $D' \leq \bar{\beta}\alpha_{\max}$ while $D' \geq -\gamma ED - \rho D \geq -(\gamma+\rho)K_1$. Let M be the maximum of the constants $\bar{\kappa}, (\gamma+\rho)K_1,$

and $\bar{\beta}\alpha_{\max}$. Then $|E'| \leq M$ and $|D'| \leq M$. Hence,

$$|\hat{u}_\theta(\theta, t)| \leq \begin{cases} 0 & \theta > t \\ cM(K_1 + 1)\pi(\theta) + cK_1\kappa(\theta)\pi(\theta) & \theta < t \end{cases}$$

Consequently,

$$\int_0^\infty |\hat{u}_\theta(\theta, t)| d\theta \leq cM(K_1 + 1)\mathcal{P} + cK_1 = C$$

where the constant C depends on the parameters of the system and the bound on the initial conditions K. The second condition in the Fréchet-Kolmogorov theorem follows directly.

Thus, we have established that there is a global compact attractor. To complete the proof of uniformly strong persistence we use Theorem 2.6 in [27]. If $\Psi(t, E_0, u_0, D_0) = (E(t), u(\cdot, t), D(t))$ denotes the solution of the system (2.1) that starts from the initial condition (E_0, u_0, D_0) we define

$$\psi(\Psi(t, E_0, u_0, D_0)) = D(t)$$

We established that if $\mathcal{R} > 1$ then the solutions are uniformly weakly ψ-persistent. Furthermore, the solution has a global compact attractor. Since the solutions are nonnegative we have that $D(t) \geq D(s)e^{-(\gamma+\rho)(t-s)}$ for time $t > s$. Therefore $D(t)$ is strictly positive, provided $D(s) > 0$. Thus, the conditions of Theorem 2.6 in [27] are satisfied and the solutions are uniformly ψ-persistent. We conclude that there exists $\eta > 0$ so that $\liminf_t D(t) \geq \eta$.

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