DYNAMICS OF AN AGE-STRUCTURED
METAPOPULATION MODEL

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ABSTRACT. We introduce a metapopulation model that includes both landscape changes (patch destruction and recreation) and age-dependent metapopulation dynamics. A threshold quantity is derived and related to the existence of an ecologically nontrivial equilibrium, to the stability of the species-free equilibrium, and to weak and strong persistence of the species. We provide examples to illustrate how age-related changes in patch colonization and extinction rates can alter metapopulation persistence. Future field studies may need to address the temporal dynamics that characterize local populations in fragmented landscapes.

KEY WORDS: Differential equations, colonization, extinction, patch destruction, persistence thresholds, mathematical models.

1. Introduction. Natural disturbances occur with varying levels of frequency and severity across a landscape. Destruction and fragmentation of native habitats are widespread and viewed as the most important threats to biodiversity worldwide (Wilcox and Murphy [1985]). In landscapes where habitat fragmentation is prevalent, the metapopulation paradigm provides a useful model for assessing viability of many species. Within these landscapes, critical thresholds derived from metapopulation models become useful for conservation by highlighting key factors that dictate a species' ability to survive.

The classic metapopulation model (Levins [1969]) emphasizes changes in patch occupancy as a function of rates of patch colonization. Within this metapopulation framework, two structures have emerged as being critical in the study of species' persistence within patchy landscapes. The important role of spatial structure, i.e., heterogeneity, has been supported by many studies (Durrett and Levin [1994], With and Crist [1995], Bascompte and Sole [1996], Bevers and Flather [1999], Hanski [1998]). These papers have concluded that several spatial features such as connectivity of the patches, patch size and the assumption of local dispersal are essential to understanding the dynamics of a population. In addition to the spatial structure of the landscape, recent research has also focused on the effects of the temporal features of the landscape (Merriam et al. [1991], Fahrig [1992], Brachet et al. [1999], Keymer et al. [2000]). The general consensus is that temporal components interact with the spatial components to determine metapopulation persistence (Keymer et al. [2000]). Since most landscapes are indeed dynamic in nature, especially in areas dominated by humans, the role of patch dynamics should be considered carefully. Keymer et al. [2000] studied an ordinary differential equation model that incorporates changes in the configuration of habitable patches in the landscape. Metapopulation persistence was estimated as a function of rate of habitat destruction.

Existing models of dynamic landscapes emphasize destruction followed by instantaneous restoration of patches. In many systems, though, vital rates may be linked to the elapsed time since a patch was restored, i.e., age of a patch. In this context, age structure of patches may influence metapopulation dynamics. Assume that emigration is related to resource availability and that resources are more plentiful on a per capita basis following initial occupancy of a patch. Further, assume that, as the population grows, emigration increases, i.e., emigration is density dependent, rather than density independent as in current formulations. Then newly occupied patches will be characterized by lower emigration rates and higher extinction rates. Extinction rates should initially be high because demographic stochasticity will have greater effects on the small number of initial colonists. As population size approaches the carrying capacity of the patch, extinction rates should approach a constant. Thus, age structure of patches should be considered when studying the impact of age-dependent rates of extinction and emigration on metapopulation dynamics. In this

article we generalize the model in Keymer et al. [2000] by incorporating age-dependent colonization and extinction rates. The introduction of these types of age distributions into the model may provide more realistic predictions for conservation purposes, see Feng and Thieme [2000a, b], Feng et al. [2002b]. We identify a threshold quantity $\mathcal{R}_d$ (d for destruction) and show that the existence of the nontrivial equilibrium is linked to $\mathcal{R}_d$ being larger than 1. We derive a characteristic equation, the roots of which determine the local stability of the metapopulation-extinction and -persistence equilibria. We show that the metapopulation-extinction equilibrium is locally asymptotically stable if $\mathcal{R}_d < 1$ and unstable if $\mathcal{R}_d > 1$, and that metapopulation-persistence is expected if and only if $\mathcal{R}_d > 1$. Computation of $\mathcal{R}_d$, in this article, helps understand the role that age-related parameters play in the maintenance of metapopulations.

2. The model formulation. Keymer et al. [2000] developed the following model (the notations have been changed for comparison purposes):

(1)
$$\frac{d}{dt} X(t) = \delta(Y(t) + Z(t)) - \gamma X(t),$$
$$\frac{d}{dt} Y(t) = \gamma X(t) - cY(t)Z(t) + \varepsilon Z(t) - \delta Y(t),$$
$$\frac{d}{dt} Z(t) = cZ(t)Y(t) - (\varepsilon + \delta)Z(t).$$

Here $X(t)$, $Y(t)$ and $Z(t)$ denote the fractions of patches that are nonhabitable, habitable but unoccupied and occupied, respectively, at time t; δ is the patch destruction rate for the habitable patches; γ is the patch recreation rate for the destroyed patches; c and ε are the rates of colonization and extinction, respectively. We generalize the model (1) by incorporating age-dependent colonization and extinction rates as follows. Introduce the following notation: $z(a, t)$ is occupancy-age density of fraction of occupied patches at time t, $c(a)$ is per capita colonization rate by patches of age a and $\varepsilon(a)$ is per capita extinction rate of patches of age a. Here the variable a denotes the *age of occupancy of a patch*, i.e., the time that has lapsed since the patch became colonized. In this context, then, $\int_{a_1}^{a_2} z(a, t) \, da$ is simply the fraction of patches between ages a_1 and a_2. Throughout this paper

we assume that both $c(a)$ and $\varepsilon(a)$ are bounded functions. Then the dynamical changes of the metapopulation are governed by the following system of differential and integral equations:

$$\frac{d}{dt}X(t) = \delta\left(Y(t) + \int_0^\infty z(a,t)\,da\right) - \gamma X(t),$$

$$\frac{d}{dt}Y(t) = \gamma X(t) - \delta Y(t) - Y(t)\int_0^\infty c(a)z(a,t)\,da$$

$$+ \int_0^\infty \varepsilon(a)z(a,t)\,da,$$

(2)

$$\frac{\partial}{\partial t}z(a,t) + \frac{\partial}{\partial a}z(a,t) = -(\delta + \varepsilon(a))z(a,t),$$

$$z(0,t) = Y(t)\int_0^\infty c(a)z(a,t)\,da, \qquad X(0) = X_0 > 0,$$

$$Y(0) = Y_0 > 0, \qquad z(a,0) = z_0(a) \geq 0,$$

where the density z_0 is assumed to be in $L^1(0,\infty)$ with $\int_0^\infty z_0(a)\,da \leq 1$. Let

(3)
$$Z(t) = \int_0^\infty z(a,t)\,da.$$

Then $Z(t)$ is the fraction of patches occupied at time t. We integrate the z equation in (2) over all ages a to obtain

(4)　$$\frac{d}{dt}Z(t) = Y(t)\int_0^\infty c(a)z(a,t)\,da - \delta Z(t) - \int_0^\infty \varepsilon(a)z(a,t)\,da.$$

Addition of the X, Y equations in (2) and the Z equation (4) yields $d/dt(X(t) + Y(t) + Z(t)) = 0$, and hence,

(5)　　　　　　$$X(t) + Y(t) + Z(t) = 1, \quad t > 0,$$

with initial data satisfying $X_0 + Y_0 + Z_0 = 1$ where $Z_0 = \int_0^\infty z_0(a)\,da$. Then the X equation in (2) can be simplified and solved

(6)　　　　$$X(t) = X_0 e^{-(\delta+\gamma)t} + \frac{\delta}{\delta + \gamma}(1 - e^{-(\delta+\gamma)t}).$$

Obviously, $X(t) > 0$ for all $t > 0$ with $X_0 > 0$. Equations (5) and (6) allow us to simplify the original system by eliminating the X equation.

The system (2) can be reformulated as a system of Volterra integral equations. The following notation will be used later in the paper:

$$K_0(a) = e^{-\delta a - \int_0^a \varepsilon(s)\,ds},$$

$$K_1(a) = \varepsilon(a)K_0(a) = -\left(\frac{d}{da}K_0(a) + \delta K_0(a)\right),$$

(7)

$$K_2(a) = c(a)K_0(a),$$

$$K_i = \int_0^\infty K_i(a)\,da, \quad i = 0, 1, 2.$$

$K_0(a)$ is the probability of a patch remaining occupied at age a, hereafter termed the age-specific survival probability of an occupied patch. $K_2(a)$ is a product of the survival probability of a patch of age a and the rate at which a habitable empty patch is colonized by an occupied patch of age a. It is clear that $K_2(a)$ represents the production of newly occupied patches, which were habitable but empty, produced by a patch of occupancy age a. Hence, $\mathcal{K}_2$ gives the total production of newly occupied patches by a (typical) patch during its entire life of occupancy in a patch network consisting of only habitable patches. This quantity is called the basic reproduction number and denoted by $\mathcal{R}_0$.

For mathematical convenience we introduce the new variable, $B(t)$, to describe the rate at which an empty habitable patch becomes occupied at time t by patches of all occupancy ages,

$$(8) \qquad B(t) = \int_0^\infty c(a)z(a,t)\,da.$$

Integrating the z equation in the system (2) along the characteristic lines, $t - a = $ constant, we get the following formula

$$(9) \qquad z(a,t) = \begin{cases} Y(t-a)B(t-a)K_0(a) & \text{for } a < t, \\ z_0(a-t)K_0(a)/K_0(a-t) & \text{for } a \geq t \end{cases}$$

Substituting (6), (8) and (9) into the Y equation in (2), we get

$$\frac{d}{dt}Y(t) = \frac{\delta\gamma}{\delta+\gamma} - \delta Y(t) - Y(t)B(t)$$

(10)

$$+ \int_0^t Y(t-a)B(t-a)K_1(a)\,da + \tilde{F}_1(t),$$

where

$$\widetilde{F}_1(t) = \int_t^\infty z_0(a - t) \frac{K_1(a)}{K_0(a - t)} \, da + \gamma e^{-(\delta+\gamma)t} \left(X_0 - \frac{\delta}{\delta + \gamma} \right).$$

Clearly $\widetilde{F}_1(t) \to 0$ as $t \to \infty$. Integrating equation (10) and changing the order of integration, we obtain

(11)
$$Y(t) = Y_0 e^{-\delta t} + \int_0^t e^{-\delta(t-s)} \left[\frac{\delta\gamma}{\delta + \gamma} - Y(s)B(s) \right.$$
$$\left. + \int_0^s Y(s-a)B(s-a)K_1(a) \, da + \widetilde{F}_1(s) \right] ds$$
$$= \int_0^t \left[e^{-\delta(t-s)} \left(\frac{\delta\gamma}{\delta+\gamma} - Y(s)B(s) \right) + H(t-s)Y(s)B(s) \right] ds + F_1(t)$$

where

$$H(t) = e^{-\delta t} \int_0^t e^{\delta\tau} K_1(\tau) \, d\tau,$$
$$F_1(t) = Y_0 e^{-\delta t} + \int_0^t e^{-\delta(t-s)} \widetilde{F}_1(s) \, ds.$$

For the derivation of (11) we have used the following fact:

$$\int_0^t e^{-\delta(t-s)} \int_0^s Y(s-a)B(s-a)K_1(a) \, da \, ds$$
$$= \int_0^t \int_0^s e^{-\delta(t-s)} Y(u)B(u)K_1(s-u) \, du \, ds$$
$$= \int_0^t \int_u^t e^{-\delta(t-s)} Y(u)B(u)K_1(s-u) \, ds \, du$$
$$= \int_0^t Y(u)B(u)e^{-\delta(t-u)} \int_0^{(t-u)} e^{\delta r} K_1(r) \, dr \, du.$$

Substitution of (9) into (3) and (8) yields

(12) $$Z(t) = \int_0^t Y(s)B(s)K_0(t - s) \, ds + F_0(t)$$

and

$$(13) \qquad B(t) = \int_0^t Y(s)B(s)K_2(t-s)\, ds + F_2(t),$$

where

$$F_i(t) = \int_t^\infty z_0(a-t)\frac{K_i(a)}{K_0(a-t)}\, da, \quad i = 0, 2.$$

Equations (11), (12) and (13) form a system of Volterra integral equations which, together with the equation (6), is equivalent to the original system (2). Notice from (12) that Z can be completely determined by Y and B. Hence, for the discussion of existence and uniqueness of the solutions, we only need to consider the following system

$$(14)$$
$$Y(t) = \int_0^t \left[e^{-\delta(t-s)}\left(\frac{\delta\gamma}{\delta+\gamma} - Y(s)B(s)\right) + H(t-s)Y(s)B(s)\right] ds + F_1(t),$$
$$B(t) = \int_0^t Y(s)B(s)K_2(t-s)\, ds + F_2(t).$$

3. Analysis. In this section we provide analytic results on the existence of positive solutions, equilibria and their stabilities, and persistence of the metapopulation.

3.1 Existence of positive solutions. Set $v(t) = (Y(t), B(t))$. Then system (14) can be written in the form

$$v(t) = \int_0^t \kappa(t-s)g(v(s))\, ds + f(t),$$

$f(t) = (F_1(t), F_2(t))$ being a continuous function from $[0, \infty)$ to $[0, \infty)^2$, κ being a locally integrable function from $[0, \infty)$ to the 2×2 matrix,

$$\kappa(t) = \begin{pmatrix} \gamma\delta e^{-\delta t}/(\delta+\gamma) & H(t) - e^{-\delta t} \\ 0 & K_2(t) \end{pmatrix},$$

and $g : \mathbf{R}_2 \to \mathbf{R}_2$,

$$g(v) = (1, YB).$$

Obviously, $f \in C([0, \infty); \mathbf{R}^2)$, $g \in C(\mathbf{R}^2, \mathbf{R}^2)$ and $\kappa \in L^1_{\text{loc}}([0, \infty); \mathbf{R}^{2 \times 2})$. Theorem 1.1 in Gripenberg et al. [1990, Section 12.1], now provides us with a continuous solution defined on a maximal interval such that the solution goes to infinity if this maximal interval is finite.

We proceed to show that $Y(t) \geq 0$, $B(t) \geq 0$ for all $t > 0$ for nonnegative initial data. If there exists a $\bar{t} > 0$ such that $Y(\bar{t}) = 0$ and $Y(t) > 0$, $B(t) > 0$ for all $0 < t < \bar{t}$, then, since $X(t) > 0$ for all $t > 0$, and $K_0(a) > 0$, $K_1(a) \geq 0$ for all $a > 0$ and $i = 0, 1$,

$$
\begin{aligned}
\frac{d}{dt} Y(\bar{t}) &= \gamma X(\bar{t}) - \delta Y(\bar{t}) - Y(\bar{t})B(\bar{t}) + \int_0^{\bar{t}} Y(s)B(s)K_1(\bar{t} - s)\, ds \\
&\quad + \int_{\bar{t}}^{\infty} z_0(a - \bar{t}) \frac{K_1(a)}{K_0(a - \bar{t})}\, da \\
&\geq \gamma X(\bar{t}) + \int_{\bar{t}}^{\infty} z_0(a - \bar{t}) \frac{K_1(a)}{K_0(a - \bar{t})}\, da \\
&> 0
\end{aligned}
$$

This shows that $Y(t)$ will never become negative as long as $B(t)$ remains positive. On the other hand, suppose that there exists a $\bar{t} > 0$ such that $B(\bar{t}) = 0$ and $Y(t) > 0$, $B(t) > 0$ for all $0 < t < \bar{t}$. Then, since $K_2(a) > 0$, $F_2(t) > 0$,

$$
B(\bar{t}) = \int_0^{\bar{t}} Y(s)B(s)K_2(\bar{t} - s)\, ds + F_2(\bar{t}) > 0,
$$

which contradicts our original supposition that $B(\bar{t}) = 0$. It follows that all variables remain nonnegative. This, together with the fact that $X + Y + Z = 1$, implies that all solutions are bounded. Therefore, we have found a solution of our original problem, which is defined for all positive t because it does not go to infinity in finite time. Once we have a continuous solution for system (14), we also have solutions to the original system (2). It is possible to prove uniqueness of solutions and continuous dependence of solutions on initial conditions by standard methods, see Iannelli [1995] and Webb [1985]. Hence, the following result holds.

Result 1. The system (2) has a continuous nonnegative solution for all $t > 0$ and, for all data $X_0 > 0$, $Y_0 > 0$, $z_0(a) \in L^1_+[0, \infty)$. The solution is uniquely determined and continuously depends on the initial data.

3.2 Equilibria and stability. Instead of using an argument of the limiting system of the Volterra integral equations (11)–(13), our stability analysis will be based on the following system which is also equivalent to the system (2):

$$
\begin{aligned}
\frac{d}{dt} Y(t) &= \gamma(1 - Y(t) - Z(t)) - \delta Y(t) - Y(t)B(t) \\
&\quad + \int_0^\infty \varepsilon(a)z(a, t)\, da,
\end{aligned}
$$

(15)
$$
z(a, t) =
\begin{cases}
Y(t - a)B(t - a)K_0(a) & \text{for } a < t, \\
z_0(a - t)K_0(a)/K_0(a - t) & \text{for } a \geq t,
\end{cases}
$$

$$
Z(t) = \int_0^\infty z(a, t)\, da
$$

$$
B(t) = \int_0^\infty c(a)z(a, t)\, da
$$

We stress that the relevant dependent variables in this formulation are Y and z; Z and B are convenient shorthand.

3.2.1 *The induced semi-flow.* From Result 1 we know that the system (15) has a continuous solution for nonnegative data, which allows us to consider the mapping

$$
\Theta : [0, \infty) \times U \to U, \quad U = (0, \infty) \times L^1_+(0, \infty),
$$

defined by
$$
\Theta(t, (Y_0, z_0)) = (Y(t), z(\cdot, t)),
$$

where Y and z are the solutions to system (15) with initial data Y_0 and z_0. It is easy to verify that Θ is a semi-flow, i.e., Θ satisfies

$$
\Theta(t + r, x) = \Theta(t, \Theta(r, x)) \quad \forall\, t, r \geq 0, \quad x \in U.
$$

U will be endowed with the metric induced by the norm

$$\|(y, f)\| = |y| + \int_0^\infty |f(a)| \, da.$$

Similarly to Feng and Thieme [2000a] we can show that Θ is a continuous semi-flow with a compact attracting set.

An equilibrium of (15) satisfies the equations

$$\delta(1 - X^*) - \gamma X^* = 0,$$

(16)
$$\gamma X^* - \delta Y^* - Y^* B^* + \int_0^\infty \varepsilon(a) z^*(a) \, da = 0,$$

$$z^*(a) = Y^* B^* K_0(a),$$

$$B^* = Y^* B^* \mathcal{K}_2,$$

$\mathcal{K}_2$ is given in (7). From the first equation we have $X^* = \delta/(\delta + \gamma)$. An equilibrium is nontrivial if $Z^* = \int_0^\infty z^*(a) \, da \neq 0$. The system (15) always has the trivial equilibrium

(17)
$$Y_0^* = \frac{\gamma}{\delta + \gamma}, \quad Z_0^* = 0, \quad B_0^* = 0.$$

If $Z^* > 0$, then $B^* \neq 0$ (otherwise $z^* = 0$) and the last equation in (16) yields $Y^* = 1/\mathcal{K}_2$. Hence,

(18)
$$Z^* = 1 - X^* - Y^* = \frac{1}{\mathcal{K}_2} \left(\frac{\gamma \mathcal{K}_2}{\delta + \gamma} - 1 \right).$$

It is easy to see that the unique nontrivial equilibrium

(19)
$$Y^* = \frac{1}{\mathcal{K}_2}, \quad Z^* = \frac{1}{\mathcal{K}_2} \left(\frac{\gamma \mathcal{K}_2}{\delta + \gamma} - 1 \right), \quad B^* = \frac{\mathcal{K}_2}{\mathcal{K}_0} Z^*$$

exists if and only if $Z^* > 0$, or

(20)
$$\left(\frac{\gamma}{\delta + \gamma} \right) \mathcal{K}_2 > 1.$$

Denote the quantity on the lefthand side by $\mathcal{R}_d$, i.e.,

(21)
$$\mathcal{R}_d = \left(\frac{\gamma}{\delta + \gamma} \right) \mathcal{K}_2 = \left(\frac{\gamma}{\delta + \gamma} \right) \int_0^\infty c(a) e^{-\delta a - \int_0^a \varepsilon(s) \, ds} \, da.$$

Recall that $\mathcal{K}_2 = \mathcal{R}_0$ is the basic reproduction number and notice that $\gamma/(\delta + \gamma) = 1 - X^*$ is the fraction of habitable patches. Hence, $\mathcal{R}_d$ is the reproduction number of the metapopulation in a patch network where a fraction, i.e., $\delta/(\delta + \gamma)$ of patches is destroyed. The threshold condition $\mathcal{R}_d > 1$ given by (20) indicates that, for persistence to be possible, an occupied patch has to be able to replace itself during its entire period of occupancy in a landscape where only a fraction, i.e., $\gamma/(\delta + \gamma)$ of patches is habitable.

3.2.2 *Stability of equilibria.* Our stability analysis follows the same approach as in Feng and Thieme [2000a]. An equilibrium solution $x^* = (Y^*, z^*)$, i.e., $x^* = \Theta(t, x^*)$, of the system (15) is called *locally stable* if for every $\varepsilon > 0$ there exists some $\eta > 0$ such that

$$\|\Theta(t, x) - x^*\| < \varepsilon \quad \forall\, t \geq 0, \quad \text{whenever} \quad \|x - x^*\| < \eta.$$

x^* is *locally asymptotically stable* if x^* is locally stable and if there exists some $\eta > 0$ such that

$$\Theta(t, x) \longrightarrow x^*, \quad t \longrightarrow \infty; \quad \text{whenever} \quad \|x - x^*\| < \eta.$$

Moreover, if we let $\tilde{x}(t) = x(t) - x^*$ and denote by $\Theta'(t)$ the derivative of $\Theta(t, x)$ in x evaluated at $x = x^*$, then the local stability of x^* is given by the stability of 0 for the linear expression

$$(22) \qquad\qquad \tilde{x}(t) = \Theta'(t)\tilde{x}(0),$$

which is approached by studying solutions of the form

$$(23) \qquad\qquad \tilde{x}(t) = e^{\lambda t}\bar{x}, \quad \bar{x} \neq 0.$$

Similarly to the proof in Feng and Thieme [2000a] we can show that Θ' satisfies the compactness condition of Corollary 4.3 in Thieme [1990] and, hence, x^* is locally asymptotically stable if all eigenvalues λ have strictly negative real parts, while x^* is unstable if at least one eigenvalue has a strictly positive real part.

Let

$$Y(t) = Y^* + \widetilde{Y}(t), \quad z(a, t) = z^*(a) + \tilde{z}(a, t), \quad B(t) = B^* + \widetilde{B}(t).$$

We will study the local stability of the equilibria of the following linearized system, corresponding to (22),

(24)
$$
\begin{aligned}
\widetilde{Y}'(t) = & -\gamma\left(\widetilde{Y}(t) + \widetilde{Z}(t)\right) - \delta\widetilde{Y}(t) - Y^*\widetilde{B}(t) - \widetilde{Y}(t)B^* \\
& + \int_0^\infty \varepsilon(a)\tilde{z}(a,t)\,da, \\
\tilde{z}(a,t) = & (Y^*\widetilde{B}(t-a) + \widetilde{Y}(t-a)B^*)K_0(a), \\
\widetilde{B}(t) = & \int_0^\infty c(a)\tilde{z}(a,t)\,da,
\end{aligned}
$$

where Y^* and B^* are given in (16). Substituting nontrivial solutions of the form (23) into (24) we get

(25)
$$
\begin{aligned}
\lambda\overline{Y} &= -\gamma\left(\overline{Y} + \overline{Z}\right) - \delta\overline{Y} - Y^*\overline{B} - \overline{Y}B^* + (Y^*\overline{B} + \overline{Y}B^*)\widehat{K}_1(\lambda), \\
\overline{Z} &= (Y^*\overline{B} + \overline{Y}B^*)\widehat{K}_0(\lambda), \\
\overline{B} &= (Y^*\overline{B} + \overline{Y}B^*)\widehat{K}_2(\lambda),
\end{aligned}
$$

where $\hat{\phi}(\lambda)$ is the Laplace transform of $\phi(a)$ defined by

$$
\hat{\phi}(\lambda) = \int_0^\infty e^{-\lambda a}\phi(a)\,da.
$$

From the second equation in (25) we have $Y^*\overline{B} + \overline{Y}B^* = \overline{Z}/\widehat{K}_0(\lambda)$. Substituting this into the first equation in (25) yields

(26)
$$
\overline{Y} = \frac{\widehat{K}_1(\lambda) - 1 - \gamma\widehat{K}_0(\lambda)}{(\lambda + \gamma + \delta)\widehat{K}_0(\lambda)}\overline{Z} = -\overline{Z}.
$$

For the last equality we have used the second equation in (7) to obtain the following relation

$$
\widehat{K}_1(\lambda) = 1 - (\delta + \lambda)\widehat{K}_0(\lambda).
$$

Noticing that, from the $\overline{Z}$ and $\overline{B}$ equations in (25),

$$
\overline{B} = \overline{Z}\frac{\widehat{K}_2(\lambda)}{\widehat{K}_0(\lambda)},
$$

and substituting this and (26) into the $\overline{Z}$ equation in (25), we get

$$\overline{Z} = \overline{Z}(Y^*\widehat{K}_2(\lambda) - B^*\widehat{K}_0(\lambda)).$$

Since the exponential solution is nontrivial, $\overline{Z} \neq 0$. By dividing the equation above by $\overline{Z}$, we obtain the characteristic equation

$$(27) \qquad\qquad 1 = Y^*\widehat{K}_2(\lambda) - B^*\widehat{K}_0(\lambda).$$

An equilibrium with X^*, Y^* and Z^* giving the fractions of patches in the three stages is locally asymptotically stable if all roots of the characteristic equation (27) have strictly negative real parts. The equilibrium is unstable if there exists at least one root with a strictly positive real part.

Result 2. The trivial equilibrium (17) is locally asymptotically stable if $\mathcal{R}_d < 1$ and unstable if $\mathcal{R}_d > 1$.

Proof. At the trivial equilibrium the characteristic equation (27) becomes

$$(28) \qquad\qquad 1 = \frac{\gamma}{\delta + \gamma}\,\widehat{K}_2(\lambda) \overset{\text{def}}{=} G(\lambda).$$

Notice that $G(0) = \mathcal{R}_d$ and that $G'(\lambda) < 0$ for all $-\infty < \lambda < \infty$, i.e., $G(\lambda)$ is a decreasing function. If $\mathcal{R}_d < 1$, then, whenever the real part of λ is positive, i.e., $\lambda = \alpha + i\beta$ with $\alpha > 0$, we have

$$|G(\lambda)| \leq |G(\alpha)| \leq G(0) = \mathcal{R}_d < 1.$$

Hence, all roots of (28) have negative real parts and the stability follows. If $\mathcal{R}_d > 1$, then, since $G(0) = \mathcal{R}_d > 1$ and $G(\lambda) \to 0$ as $\lambda \to \infty$, there exists a $\bar{\lambda} > 0$ such that $G(\bar{\lambda}) = 1$. In this situation, instability follows.

Recall that a nontrivial equilibrium exists if and only if the reproduction number $\mathcal{R}_d = \mathcal{K}_2\gamma/(\delta + \gamma)$ exceeds one. At the nontrivial equilibrium, the characteristic equation takes the form

$$(29) \qquad\qquad 1 = \frac{\widehat{K}_2(\lambda)}{\mathcal{K}_2} - (\mathcal{R}_d - 1)\frac{\widehat{K}_0(\lambda)}{\mathcal{K}_0}.$$

Since $\mathcal{R}_d > 1$ and $\widehat{K}_0(\lambda) > 0$ for $-\infty < \lambda < \infty$, it is easy to show that the equation (29) cannot have a positive real eigenvalue. However, we cannot rule out the possibility of complex eigenvalues with positive real parts when $\mathcal{R}_d > 1$. In fact, Castillo-Chavez and Thieme [1993] considered an HIV/AIDS model with a similar structure as the one we considered here, and they proved that under certain conditions the nontrivial equilibrium may lose its stability leading to the existence of periodic solutions, see also Milner and Pugliese [1999]. While we have not identified conditions for instability, we provide a stability result for the case in which the patch extinction rate $\varepsilon(a)$ is a nonincreasing function, based on the logic that young (and small) populations are more prone to demographic stochasticity. This assumption is satisfied by the example used in the discussion section in which the extinction rate of patches was assumed to be m_1 for all patch ages less than some threshold age and m_2 thereafter with $m_1 > m_2$.

Result 3. Let $\mathcal{R}_d > 1$. If the extinction rate $\varepsilon(a)$ is a nonincreasing function, then the unique nontrivial equilibrium (19) is locally asymptotically stable.

Proof. We need to show that all eigenvalues of (29) have negative real parts. To simplify the characteristic equation we introduce the following functions:

$$p(a) = \frac{K_2(a)}{\mathcal{K}_2}, \quad q(a) = \frac{K_0(a)}{\mathcal{K}_0}.$$

Clearly, $p(a) > 0$, $q(a) > 0$ and $\int_0^\infty p(a)\,da = \int_0^\infty q(a)\,da = 1$. Then (29) can be written as

$$(30) \qquad\qquad 1 = \hat{p}(\lambda) - (\mathcal{R}_d - 1)\,\hat{q}(\lambda).$$

Notice that $\hat{p}(0) = 1$, $\hat{p}'(\lambda) \leq 0$ and $\hat{q}(\lambda) > 0$ for $0 \leq \lambda < \infty$. It is easy to see that (30) cannot have positive real roots when $\mathcal{R}_d > 1$. Let $\lambda = x + iy$ denote a complex root of (30) with $y \neq 0$ (x and y are real numbers). We remark that, whenever $x + iy$ is an eigenvalue, $x - iy$ is also an eigenvalue. Separate (30) into real and imaginary parts as follows:

$$(31) \ \ 1 = \int_0^\infty p(a)e^{-xa}\cos(ya)\,da - (\mathcal{R}_d - 1)\int_0^\infty q(a)e^{-xa}\cos(ya)\,da$$

and

$$(32) \quad \int_0^\infty p(a) e^{-xa} \sin(ya)\, da = (\mathcal{R}_d - 1) \int_0^\infty q(a) e^{-xa} \sin(ya)\, da.$$

We first show that (31) and (32) cannot have imaginary roots. Suppose that $i\tilde{y}$, $\tilde{y} > 0$, is a root. Then

$$(33) \quad 1 = \int_0^\infty p(a) \cos(\tilde{y}a)\, da - (\mathcal{R}_d - 1) \int_0^\infty q(a) \cos(\tilde{y}a)\, da$$

$$\int_0^\infty p(a) \sin(\tilde{y}a)\, da = (\mathcal{R}_d - 1) \int_0^\infty q(a) \sin(\tilde{y}a)\, da.$$

Since the first term on the righthand side of (33) is strictly less than 1, the equation (33) yields

$$(34) \quad \int_0^\infty q(a) \cos(\tilde{y}a)\, da < 0.$$

Noticing that $q(a) \to 0$ as $a \to \infty$ we have

$$\int_0^\infty q(a) \cos(\tilde{y}a)\, da = -\frac{1}{y} \int_0^\infty q'(a) \sin(\tilde{y}a)\, da.$$

Hence, from (34),

$$(35) \quad \int_0^\infty q'(a) \sin(\tilde{y}a)\, da > 0.$$

On the other hand, since $\varepsilon(a)$ is nonincreasing on $[0, \infty]$,

$$q''(a) > 0.$$

Using $q'(a) = -\int_a^\infty q''(t)\, dt$ we obtain

$$\int_0^\infty q'(a) \sin(\tilde{y}a)\, da = -\int_0^\infty \int_a^\infty q''(t) \sin(\tilde{y}a)\, dt\, da$$

$$= -\int_0^\infty \int_0^t q''(t) \sin(\tilde{y}a)\, da\, dt$$

$$= \frac{1}{\tilde{y}} \int_0^\infty q''(t)(\cos(\tilde{y}t) - 1)\, dt$$

$$\leq 0.$$

This contradicts (35). Therefore, (31) and (32) cannot have roots with $x = 0$.

Next we show that (31) and (32) cannot have roots with $x > 0$ and $y > 0$.

Claim. *There exists an $\overline{\mathcal{R}}_d > 1$ such that, for all $\mathcal{R}_d \in (1, \overline{\mathcal{R}}_d)$, (31) and (32) have no roots with $x > 0$ and $y > 0$.*

Suppose that the claim is not true. Then there is a sequence $\{\mathcal{R}_{dj}\}_{j=1}^{\infty}$ with $\mathcal{R}_{dj} > 1$ and $\mathcal{R}_{dj} \to 1$ as $j \to \infty$, and corresponding sequences $\{x_j\}_{j=1}^{\infty}$, $\{y_j\}_{j=1}^{\infty}$ with $x_j > 0$ and $y_j > 0$ satisfying (31) and (32). From (31) and $\mathcal{R}_{dj} \to 1$,

$$\int_0^{\infty} p(a)e^{-x_j a} \cos(y_j a)\, da \longrightarrow 1, \quad j \to \infty.$$

It follows that $x_j \to 0$, $y_j \to 0$. If we divide both sides of (32) (with x and y being replaced by x_j and y_j) by y_j and let j go to infinity, then the lefthand side yields a positive constant, $\int_0^{\infty} ap(a)\, da$, whereas the righthand side goes to 0. This leads to a contradiction and therefore the claim is proved.   □

We now show that for any $\mathcal{R}_d > 1$ (31) and (32) cannot have roots with $x > 0$. Suppose that this is not true. Then, for some $\mathcal{R}_d > \overline{\mathcal{R}}_d$, (31) and (32) have a root with $x > 0$, $y > 0$. Since all roots for $\mathcal{R}_d \in (1, \overline{\mathcal{R}}_d)$ satisfy $x < 0$, from the continuous dependence of roots of the characteristic equation on the parameter $\mathcal{R}_d$ we know that the curve of roots must cross the imaginary axis as $\mathcal{R}_d$ decreases to $\overline{\mathcal{R}}_d$. The crossing cannot occur at $y = \infty$ because all integrals in (31) and (32) tend to zero as $y \to \infty$. This implies that (31) and (32) have an imaginary root which is impossible as shown above. Therefore, (31) and (32) cannot have roots with $x > 0$. The proof of Result 3 is completed. □

All the stability results given above are local. We end this section by providing a global stability result for the trivial equilibrium.

Result 4. The trivial equilibrium of the system (14) is globally asymptotically stable when $\mathcal{R}_d < 1$.

Proof. Noticing that in the Y equation in (14)

$$H(t-s) - e^{-\delta(t-s)} = e^{-\delta(t-s)} \left(\int_0^{t-s} e^{\delta\tau} K_1(\tau) \, d\tau - 1 \right)$$
$$= -e^{-\delta(t-s) - \int_0^{t-s} \varepsilon(s) \, ds} < 0,$$

we obtain

$$Y(t) \le \frac{\gamma\delta}{\delta + \gamma} \int_0^t e^{-\delta(t-s)} \, ds + F_1(t).$$

Therefore, from $\lim_{t\to\infty} F_1(t) = 0$, $\limsup_{t\to\infty} Y(t) \le \gamma/(\delta+\gamma)$. From the B equation in (14),

$$\limsup_{t\to\infty} B(t) = \limsup_{t\to\infty} \int_0^t Y(t-u)B(t-u)K_2(u) \, du$$
$$\le \frac{\gamma\mathcal{K}_2}{\delta+\gamma} \limsup_{t\to\infty} B(t)$$
$$= \mathcal{R}_d \limsup_{t\to\infty} B(t).$$

This implies that $\limsup_{t\to\infty} B(t) = 0$ as $\mathcal{R}_d < 1$. Hence, $B(t) \to 0$ as $t \to \infty$, and consequently from (12), $Z(t) \to 0$ as $t \to \infty$. This completes the proof. □

3.3 Species persistence. Denote the rate of patch colonization by $C(t)$, i.e., $C(t) = z(0,t) = Y(t)B(t)$. Let $f^\infty = \limsup_{t\to\infty} f(t)$ denote the limit of supremum (maximum) of a function $f(t)$, and let $f_\infty = \liminf_{t\to\infty} f(t)$ denote the limit of minimum of $f(t)$. The metapopulation is called *uniformly weakly persistent*, if there exists some small constant $\mu > 0$ such that $C^\infty > \mu$ for every ecologically non-trivial solution of the model. The metapopulation is called *uniformly strongly persistent*, if there exists some small constant $\mu > 0$ such that $C_\infty > \mu$ for every ecologically nontrivial solution of the model. We discuss the persistence properties using the similar approach as in Feng and Thieme [2000a]. We need the following lemmas.

Lemma 1. *The semi-flow Θ has a compact attracting set.*

We call a set $\mathcal{D}$ in U an attracting set for the semi-flow if

$$\Theta(t, x) \longrightarrow \mathcal{D}, \quad t \to \infty, \quad \text{for all} \quad x \in U,$$

with the interpretation that for every set E, $\mathcal{D} \subseteq E \subseteq U$, E relatively open in U, we have some $t_E > 0$ such that $\Theta(t, x) \in E$ for all $t \geq t_E$.

Proof of Lemma 1. First we notice from (5) and (6) that all solutions of the system satisfy

$$(36) \qquad\qquad |Y(t)| < 1 \quad \text{for all} \quad t > 0.$$

Let $\bar{c}$ denote the upper bound of $c(a)$. Noticing also that $Z_0 \leq 1$ and $\mathcal{K}_0 \leq 1/\delta$, from (8) and (9) we have

$$(37) \qquad\qquad \int_0^t Y(t-a)B(t-a)K_0(a)\, da \; \leq \; \frac{\bar{c}}{\delta},$$

and

$$(38) \qquad\qquad \int_t^\infty z_0(a-t)\, \frac{K_0(a)}{K_0(a-t)}\, da \; \leq \; e^{-\delta t}.$$

This implies that we can write the solution z, see (9), as

$$(39) \quad z(a,t) = u(a,t) + v(a,t) \quad \text{with} \quad \int_0^\infty v(a,t)\, da \longrightarrow 0, \quad t \to \infty$$

and

$$(40) \qquad u(a,t) = \begin{cases} Y(t-a)B(t-a)K_0(a) & \text{for } a < t, \\ 0 & \text{for } a \geq t. \end{cases}$$

Let D be the subset of U defined by $D = \{(Y(t), u(\cdot, t))\}$, where u is given in (39) and $(Y(t), z(\cdot, t)) = \Theta(t, (\widetilde{Y}, \tilde{z}))$ for $(\widetilde{Y}, \tilde{z}) \in U$, $t > 0$. Let $\mathcal{D} = \overline{D}$, the closure of D. Then from (36)–(39) we know that $\mathcal{D} \subseteq U$ is a bounded attracting set for the semi-flow Θ.

Now we show that $\mathcal{D}$ is a compact set of U, or equivalently, D is a conditionally compact set of U. According to a theorem in Dunford

and Schwartz [1971, IV.8.19], D is conditionally compact if and only if D is bounded and

(a) $\lim_{h \to 0} \int_0^\infty |u(a + h, t) - u(a, t)|\, da = 0$ uniformly in $t \geq 0$ and uniformly for all u in D, and

(b) $\lim_{A \to \infty} \int_A^\infty u(a, t)\, da = 0$ uniformly in $t \geq 0$ and uniformly for all u in D.

Obviously D is bounded. First we show that (a) holds. From (9) it suffices to show that

$$(41) \qquad \lim_{h \to 0} \int_0^t |Y(a + h)B(a + h) - Y(a)B(a)|K_0(t - a)\, da = 0$$

uniformly in $t \geq 0$ and uniformly for all u in D. Since $Y(t)$ and $Z(t)$ are uniformly bounded in $t \geq 0$ and uniformly for all solutions, using (8) and the fact that $c(a)$ is bounded we know that $B(t)$ is also uniformly bounded in $t \geq 0$ and uniformly for all solutions. Then using (14) it can be shown that $Y(t)$ and $B(t)$, and hence $Y(t)B(t)$, are uniformly continuous on $[0, \infty)$ and uniformly for all solutions. Notice that $\varepsilon(a) \leq \bar{\varepsilon}$ for some constant $\bar{\varepsilon} > 0$ and that

$$\int_0^t K_0(t - a)\, da \leq \frac{1}{\delta + \bar{\varepsilon}}.$$

For any given $\mu > 0$, we can choose $\eta > 0$ such that $|Y(a + h)B(a + h) - Y(a)B(a)| \leq \mu(\delta + \bar{\varepsilon})$ for all $Y(a)$ and $B(a)$ whenever $h < \eta$. Then

$$\int_0^t |Y(a + h)B(a + h) - Y(a)B(a)|K_0(t - a)\, da \leq \mu,$$

whenever $h < \eta$ uniformly for all u in D. Therefore, (41) holds and (a) is proved.

Next we show that (b) holds. For any given $\mu > 0$, we can choose A_μ large enough so that

$$\frac{\bar{c}}{\delta} e^{-\delta A_\mu / 2} < \mu.$$

Let $A > A_\mu$. If $t \leq A_\mu$, then $t < A$ and from (40) we get $\int_A^\infty u(a, t)\, da = 0$ for all u. If $t > A_\mu$, then

$$\int_A^\infty u(a, t)\, da \leq \int_{A_\mu}^\infty u(a, t)\, da = \int_{A_\mu}^t Y(t - a)B(t - a)K_0(a)\, da$$

$$\leq \bar{c} \int_{A_\mu}^\infty K_0(a)\, da \leq \frac{\bar{c}}{\delta} e^{-\delta A_\mu} < \mu$$

uniformly for all u. Thus, we have proved that $\int_A^\infty u(a,t)\,da < \mu$ for all $A > A_\mu$ uniformly in t and uniformly for all u, and therefore (b) holds.

This completes the proof of Lemma 1.   □

Lemma 2 (Feng and Thieme [2000a]). *Consider a Volterra integral inequality*

$$C(t) \geq (C * L)(t) + F(t), \quad t > 0,$$

where F, L, C are nonnegative, F is continuous and not identically 0 and L is not 0 almost everywhere. Then there exists some $\lambda \in \mathbf{R}$ such that

$$\liminf_{t \to \infty} e^{\lambda t} C(t) > 0.$$

In particular, there exists some $t_0 > 0$ such that B_0 is strictly positive on $[t_0, \infty)$. If

$$\hat{L}(0) = \int_0^\infty L(s)\,ds > 1,$$

λ can be chosen to be strictly negative.

Using Lemmas 1 and 2 we can prove the following result.

Result 5. Let $\mathcal{R}_d > 1$. Then the species is uniformly strongly persistent, i.e., there exists a small $\mu > 0$ (independent of initial data) such that

$$\liminf_{t \to \infty} C(t) \geq \mu$$

for all solutions of the model with nonnegative initial data and $Z_0 > 0$.

Proof. We first show that the species is uniformly weakly persistent. Suppose it is not uniformly weakly persistent. Then we can find an arbitrarily small $\mu > 0$ such that

$$\limsup_{t \to \infty} C(t) < \mu$$

for an ecologically nontrivial solution of the model. Choose $\mu_1 > 0$ such that $\mu_1 \leq \min\{\mu, \mu\mathcal{K}_0\}$. Then from equation (12) we have

$$\limsup_{t \to \infty} Z(t) < \limsup_{t \to \infty} C(t)\mathcal{K}_0 \leq \mu_1.$$

Noticing that $Y(t) + Z(t) = 1 - X(t) \to \gamma/(\delta + \gamma)$, as $t \to \infty$, we have

$$\liminf_{t\to\infty} Y(t) \geq \left(\frac{\gamma}{\delta + \gamma} - \limsup_{t\to\infty} Z(t)\right) \geq \left(\frac{\gamma}{\delta + \gamma} - \mu_1\right).$$

Also notice that

$$\limsup_{t\to\infty} Y(t) \leq \limsup_{t\to\infty}(Y(t) + Z(t)) = \frac{\gamma}{\delta + \gamma}.$$

By the semi-flow property (Lemma 1), we can assume that

$$\left|Y(t) - \frac{\gamma}{\delta + \gamma}\right| < \mu_1, \quad t \geq 0.$$

Then

$$C(t) = Y(t)B(t) = Y(t)((C * K_2)(t) + F_2(t))$$
$$\geq \left(\frac{\gamma}{\delta + \gamma} - \mu_1\right)(C * K_2)(t) + \overline{F}_2(t),$$

where $\overline{F}_2(t) = Y(t)F_2(t)$ is nonnegative, continuous, and not identically 0. Clearly,

$$\left(\frac{\gamma}{\delta + \gamma} - \mu_1\right)\int_0^\infty K_2(s)\,ds = \mathcal{R}_d - \mu_1\mathcal{K}_2 > 1$$

if $\mu_1 > 0$ is chosen small enough. By Lemma 2, with $\lambda < 0$, $C(t) \to \infty$ as $t \to \infty$, a contradiction.   ∎

We next use persistence theory to show that the species is uniformly strongly persistent. Consider the solution semi-flow Θ on U. We define a functional $\rho : U \to [0, \infty)$ by

$$\rho(Y_0, z_0) = Y_0 \int_0^\infty c(a)z_0(a)\,da,$$

i.e.,

$$\rho(\Theta(t, (Y_0, z_0))) = z(0, t) = C(t).$$

From the proof above we know that Θ is uniformly weakly ρ-persistent. By Lemma 1, Θ has a compact attracting set A, the assumptions of Theorem 2.6 in Thieme [2000] are satisfied, and Θ is uniformly strongly ρ-persistent. This implies that solutions of the model with nonnegative initial data and $Z_0 > 0$ satisfies

$$\liminf_{t \to \infty} C(t) \geq \mu,$$

for some small $\mu > 0$. Hence, the species is uniformly strongly persistent.

4. Discussion. In this paper we have generalized the model in Keymer et al. [2000]. Specifically, we have introduced age structure into the metapopulation model and studied the effects on metapopulation persistence of colonization and extinction rates that vary with patch age. Metapopulation models with similar types of age-dependence have been studied previously only for the case when landscapes are static, i.e., there is no patch destruction or creation, see Hastings and Wolin [1989], Metz and Diekmann [1986]. We derived an expression for the reproductive quantity $\mathcal{R}_d$ which determines whether the metapopulation will go extinct or maintain itself in a patch network in which habitable patches have a destruction rate δ. Of course if patches can be treated as static, i.e., $\delta = 0$, then $\mathcal{R}_d$ simplifies to the basic reproduction number $\mathcal{R}_0$ ($= \mathcal{K}_2$). In keeping with the findings of Keymer et al. [2000], we have shown that the incorporation of age structure does not alter the qualitative predictions of their model. Namely, the metapopulation either goes extinct (if $\mathcal{R}_d < 1$) or persists (if $\mathcal{R}_d > 1$) for all age distributions of colonization and all nonincreasing age distributions of extinction.

To illustrate how information on age-related changes in colonization and extinction can provide additional insight into predictions regarding persistence, we considered the following example in which both $c(a)$ and $\varepsilon(a)$ are simple step functions. We assumed that populations were incapable of producing colonists until their local population had attained some critical age (and corresponding size), referred to as a^*. From a^* onwards, colonization was assumed to occur at rate $\tilde{c}$. Similarly, the extinction rate of patches was assumed to be m_1 for all patch ages less than some threshold age, $\hat{a}$ and m_2 thereafter, based on the logic that young populations are more prone to demographic
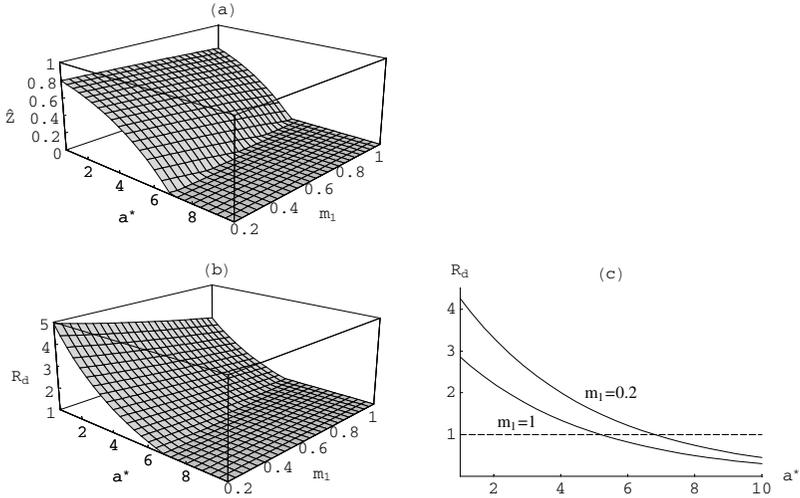
FIGURE 1.   (a) is a plot of the fraction of occupied patches $\widehat{Z}$ versus the critical age of colonization a^* and extinction rate of young patches m_1. (b) and (c) illustrate how the reproductive number $\mathcal{R}_d$ changes with a^* and m_1.

stochasticity. Consequently, we further assumed that $m_1 > m_2$. For demonstration purposes, we only considered the case in which $a^* > \hat{a}$. For these specific functions $c(a)$ and $\varepsilon(a)$, using the formula given in (21) we obtain

$$\mathcal{R}_d = \frac{\bar{s}\tilde{c}}{1/\tau + m_2}\left(e^{-(1/\tau + m_2)a^* - (m_1 - m_2)\hat{a}}\right).$$

We adopted the parameters $\bar{s}$ and $\bar{\tau}$ of Keymer et al. [2000], where $\bar{s}$ is the expected fraction of suitable habitat in the landscape, i.e., $\bar{s} = \gamma/(\delta + \gamma)$, and $\bar{\tau}$ is the expected patch life time, i.e., $\bar{\tau} = 1/\delta$. We also adopted the notation $\widehat{Z}$ to denote the proportion of suitable habitat occupied ($\hat{p}$ in Keymer et al. [2000]), i.e., $\widehat{Z} = Z^*/\bar{s}$ where Z^* is given in (18). From (18) we can derive a formula that relates $\mathcal{R}_d$ and $\widehat{Z}$. That is,
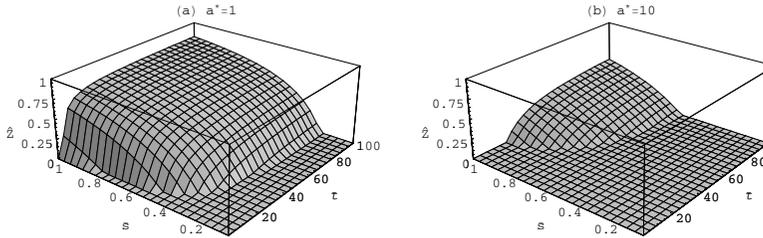
$$\widehat{Z} = 1 - \frac{1}{\mathcal{R}_d}.$$

FIGURE 2. Plots of the fraction of occupied patches $\widehat{Z}$ versus the expected fraction of suitable habitat $\bar{s}$ and the expected patch life time $\bar{\tau}$ for different values of the critical age of colonization a^*.

Figure 1 illustrates the joint importance of the age at which a patch first produces propagules and the extinction force acting on young populations. Lower extinction forces (m_1) enable populations to persist (in the region where $\widehat{Z} > 0$ in Figure 1(a) or $\mathcal{R}_d > 1$ in Figure 1(b)) even when the age of first propagule production (a^*) is delayed, Figure 1(c). This tradeoff is potentially of great importance to conservation efforts, as it suggests that species capable of rapidly producing potential colonists may fare better under environmental regimes that could heighten extinction risks for small populations.

In Figure 2 we depict the effect of age structure on the proportion of suitable habitat occupied. Clearly, early onset of propagule production, see Figure 2(a), results in a wider range of habitat suitability and patch lifetimes over which the metapopulation can persist. Note that, for any given level of $\bar{s}$, or $\bar{\tau}$, it is possible to compute the persistence threshold in terms of $\bar{\tau}$, or $\bar{s}$.

Our results suggest that future field studies of metapopulations would do well to address age-related changes associated with colonization and extinction processes. We have focused on simplistic age-dependent dynamics; richer relationships undoubtedly exist and await clarification by field biologists.

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