

COMPETITION AND DISPERSAL DELAYS IN PATCHY ENVIRONMENTS

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ABSTRACT. Dispersal delays are introduced into a competition model for two species that disperse among n identical patches. The model is formulated as a system of integro-differential equations with an arbitrary distribution of dispersal times between patches. By identifying steady states and analyzing local stability, conditions for competitive exclusion, coexistence or extinction are determined in terms of the system parameters. These are confirmed by numerical simulations with a delta function distribution, showing that all solutions approach a steady state and that high dispersal is generally a disadvantage to a species. However, if the two species have identical local dynamics, then small dispersal rates (with certain parameter restrictions) can be an advantage to the dispersing species. If the number of species is increased to three, then oscillatory coexistence with dispersal delay is possible.

1. Introduction. Lotka (1932) and Volterra (1926) developed a classical model of competition; see, for example, [4, Section 3.5]. Realistically, most species exist in patchy environments; thus, dispersal needs to be incorporated into the classical Lotka-Volterra competition model. For two species competing on two patches, ordinary differential equation (ODE) models have been studied by several authors; see, for example, Levin [3], Takeuchi [7, Chapter 5, Section 5.6], Gourley and Kuang [1].

In Takeuchi [7] a four-dimensional ODE system model is formulated for two species that compete on two non-identical patches. Let N_{ij} (for $i, j = 1, 2$) denote the density of species i on patch j , r_{ij} and K_{ij} denote the growth rate and carrying capacity for species i on patch j , respectively, and α_{12j} and α_{21j} denote the interspecific competition parameters on patch j . Furthermore, let D_i be the dispersal rate for species i (the model given in [7, page 121] assumes that dispersal is both species and patch dependent). All parameters are assumed to be positive. The model equations [7, page 121] are

$$\frac{dN_{ij}}{dT} = \frac{r_{ij}}{K_{ij}} N_{ij} (K_{ij} - N_{ij} - \alpha_{ikj} N_{kj}) + D_i [N_{il} - N_{ij}], \quad (1)$$

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in which $i, j, k, \ell = 1, 2$, where $i \neq k$ and $j \neq \ell$. Note that in the absence of dispersal ($D_i = 0$), system (1) reduces to the classical competition model on each patch. Possible boundary steady states of (1) are $E_0 = (0, 0, 0, 0)$, $E_{N_1} = (\bar{N}_{11}, \bar{N}_{12}, 0, 0)$, $E_{N_2} = (0, 0, \bar{N}_{21}, \bar{N}_{22})$, which exist for any $D_i > 0$. The boundary steady state E_{N_i} is globally stable with respect to the positive N_i subspace. In addition, there may also exist a unique positive equilibrium point for (1), in which case it is globally stable; see [7, page 121]. For the case in which the patches are identical (i.e., $r_{ij} = r_i$, $K_{ij} = K_i$, $\alpha_{ikj} = \alpha_{ik}$), the condition $\alpha_{21} < 1 < 1/\alpha_{12}$ ensures a positive equilibrium point exists for each patch [7, page 124]. This is equivalent to $\alpha_{12} < 1$ and $\alpha_{21} < 1$ as in the classical case of competition between two species. Hence, species that compete on two identical patches have a globally asymptotically stable equilibrium point for any $D_i > 0$, $i = 1, 2$, provided the above condition holds.

Another approach to analyzing competition models with dispersal was taken by Levin [3], who analyzed the case of two species on two patches; see also [9, Section 5.4.1]. As a special case of (1), identical local dynamics and dispersal rates for the two species between the two patches are assumed. Therefore, $r_{ij} = r$, $K_{ij} = K$, $\alpha_{ikj} = \alpha$ and $D_i = D$. The assumption is made that the two species cannot coexist locally within one patch, i.e., $\alpha > 1$. With $D = 0$, the model is the classical case of competition between two species; thus only one species will be present in each patch. Due to the clear symmetry of this system, an obvious assumption is made in the case $D > 0$, namely, $N_{11} = N_{22}$ and $N_{21} = N_{12}$, thus reducing system (1) to two dimensions, namely

$$\frac{dN_{i1}}{dT} = \frac{r}{K} N_{i1} (K - N_{i1} - \alpha N_{k1}) + D [N_{k1} - N_{i1}],$$

for $i, k = 1, 2$, $i \neq k$. For sufficiently small dispersal rates, the two species can coexist in this coupled patch model. However, as dispersal rates increase, “complete mixing” occurs and the distinction between the two patches is lost, and coexistence is no longer possible [9, Section 5.4.1].

An ODE competition model is analyzed in a recent paper by Gourley and Kuang [1]. Species 1 and 2 have identical dispersal rates between the two patches, but have different birth rates within each patch. This is a special case of (1) with $r_{ij} = K_{ij}$, $D_i = D$ and $\alpha_{ikj} = 1$. If $r_{ij} > r_{i\ell}$ and if species k widens the disparity between these birth rates (i.e., if species k adopts a higher birth rate in patch j and a lower birth rate in patch ℓ , while maintaining the same average birth rate), then species k will outcompete species i , for a sufficiently large dispersal rate D .

Competition models in patchy environments discussed so far demonstrate the effect of dispersal on the outcome of competition but assume that dispersal is instantaneous. Realistically individuals that disperse take time to re-enter their patch. An arbitrary distribution of dispersal (travel) times between identical patches is now introduced. In this model, which is formulated in Section 2, both species disperse among an arbitrary number of identical patches. Local stability analysis of the spatially homogeneous steady states in which at least one species is absent (i.e., boundary steady states) is carried out in Section 3, and the results are summarized in Theorem 3.2. All analytical results are valid for an arbitrary distribution of dispersal times and can be applied to special cases of the general models, such as constant travel time (as in the case of a delta function distribution) and zero travel time (ODE models). To support analytical results for the models in which both species disperse, in Section 4 results of some numerical simulations are given. These

assume a delta function distribution for dispersal times (i.e., all dispersing individuals take the same traveling time). A similar model for three competing species can have oscillatory solutions (Section 5). A one-patch model with dispersal is briefly considered in Section 6, and concluding remarks are given in Section 7.

2. Model Formulation and Steady States. This model assumes that two species interact competitively and disperse between an arbitrary number $n \geq 2$ of identical patches. Let N_{ij} denote the density of species i on patch j , for $i = 1, 2$ and $j = 1, \dots, n$. Species i is assumed to have positive constant growth rate (the difference between birth and death rate) and carrying capacity, $r_i > 0$ and $K_i > 0$, respectively. The interspecific competition constant of species 2 on 1 is denoted by $\alpha_{12} > 0$, while that of species 1 on 2 is denoted by $\alpha_{21} > 0$.

Species i disperses at a rate $D_i \geq 0$, for $i = 1, 2$. Individuals of the same species have the same traveling time distribution between patches, and each patch is coupled to every other patch. Different individuals in a species may have different dispersal times, and also, for a single individual, the traveling time may vary between trips. For this reason, a general probability density function, as in [5], denoted by $G_i(S) \geq 0$, is used to account for the time it takes an individual of species i to disperse, given that the individual survives the trip. Hence, the product $G_i(S)dS$ is the probability that an individual disperses successfully, departing at time T and completing the trip between time $T + S$ and time $T + S + dS$. Consequently, $\int_0^\infty G_i(S)dS = 1$.

For species i , death during traveling is exponentially distributed with parameter $M_i \geq 0$. The probability of such an individual dying during a trip of duration S is represented by the cumulative distribution function $1 - e^{-M_i S}$. Thus the probability that this individual survives the trip is $e^{-M_i S}$, where M_i is the death rate during travel, for $i = 1, 2$. Note that mortality during travel is treated differently from mortality within a patch. Given that the patches are assumed to be identical, the parameters $r_i, K_i, \alpha_{12}, \alpha_{21}, D_i, G_i$ and M_i are assumed to be the same in each patch. Incorporating dispersal into the classical competition equations gives the model for $j = 1, \dots, n$ as

$$\begin{aligned} \frac{dN_{1j}}{dT} &= \frac{r_1}{K_1} N_{1j} (K_1 - N_{1j} - \alpha_{12} N_{2j}) \\ &\quad + D_1 \left[\frac{1}{n-1} \sum_{\ell=1, \ell \neq j}^n \int_0^\infty G_1(S) e^{-M_1 S} N_{1\ell}(T-S) dS - N_{1j} \right] \\ \frac{dN_{2j}}{dT} &= \frac{r_2}{K_2} N_{2j} (K_2 - N_{2j} - \alpha_{21} N_{1j}) \\ &\quad + D_2 \left[\frac{1}{n-1} \sum_{\ell=1, \ell \neq j}^n \int_0^\infty G_2(S) e^{-M_2 S} N_{2\ell}(T-S) dS - N_{2j} \right]. \end{aligned} \tag{2}$$

In these equations and in all that follow it is understood that if time dependence is omitted, then the variable is evaluated at the current time. For species i , the integral $\int_0^\infty G_i(S) e^{-M_i S} N_{i\ell}(T-S) dS$ realistically is $\int_0^{L_i} G_i(S) e^{-M_i S} N_{i\ell}(T-S) dS$, where L_i is the maximum life span of species i . The system is assumed to be closed; i.e., individuals must have left one patch in order to enter another. For all $t \geq 0$, existence and uniqueness of the solution of the initial value problem follow from standard results; see, for example, [2, Chapter 2, Section 2.2].

The following result shows that the region

$$X_{2n} = \{(N_{11}, \dots, N_{1n}, N_{21}, \dots, N_{2n}) : 0 \leq N_{ij} \leq K_i\}$$

is positively invariant and attracts all solutions, so it suffices to consider the dynamics on X_{2n} . Note that biologically $N_{ij}(S) = 0$ for $S \in (-\infty, -L_i)$.

PROPOSITION 2.1. *If $0 \leq N_{ij}(S) \leq K_i$ for $S \in (-\infty, 0]$ with $N_{ij}(0) > 0$, then for system (2), $0 \leq N_{ij}(T) \leq K_i$ for all $T \geq 0$, for $i = 1, 2$ and $j = 1, \dots, n$.*

Proof: Assume that T_i is the first positive time that $N_{ij} = 0$ for any j . Then

$$\frac{dN_{ij}(T_i)}{dT} = D_i \left[\frac{1}{n-1} \sum_{\ell=1, \ell \neq j}^n \int_0^\infty G_i(S) e^{-M_i S} N_{i\ell}(T-S) dS \right] \geq 0,$$

and therefore, by [6, Theorem 2.1, page 81], $N_{ij}(T) \geq 0$ for all $T \geq 0$. Now suppose that T_i is the first positive time that $N_{ij} = K_i$ for any j . Then for $k \neq i$

$$\begin{aligned} \frac{dN_{ij}(T_i)}{dT} &= -r_i \alpha_{ik} N_{kj} \\ &\quad + D_i \left[\frac{1}{n-1} \sum_{\ell=1, \ell \neq j}^n \int_0^\infty G_i(S) e^{-M_i S} N_{i\ell}(T-S) dS - K_i \right] \\ &\leq 0, \end{aligned}$$

and therefore $N_{ij}(T) \leq K_i$ for all $T \geq 0$. □

The analysis of the model (2) is simplified by rescaling variables and parameters and setting $u_{ij} = \frac{N_{ij}}{K_{ij}}$, $d_i = \frac{D_i}{r_i}$, $m_i = \frac{M_i}{r_i}$, for $i = 1, 2$, and $a_{12} = \alpha_{12} \frac{K_2}{K_1}$, $a_{21} = \alpha_{21} \frac{K_1}{K_2}$, $t = r_1 T$, $s = r_1 S$, and $\rho = \frac{r_2}{r_1}$. This results in the non-dimensional system

$$\begin{aligned} \frac{du_{1j}}{dt} &= u_{1j}(1 - u_{1j} - a_{12}u_{2j}) \\ &\quad + d_1 \left[\frac{1}{n-1} \sum_{\ell=1, \ell \neq j}^n \int_0^\infty g_1(s) e^{-m_1 s} u_{1\ell}(t-s) ds - u_{1j} \right] \\ \frac{du_{2j}}{dt} &= \rho u_{2j}(1 - u_{2j} - a_{21}u_{1j}) \\ &\quad + \rho d_2 \left[\frac{1}{n-1} \sum_{\ell=1, \ell \neq j}^n \int_0^\infty g_2(s) e^{-\rho m_2 s} u_{2\ell}(t-s) ds - u_{2j} \right], \end{aligned} \tag{3}$$

where $g_i(s) = \frac{1}{r_i} G_i(\frac{s}{r_i})$, for $i = 1, 2$; thus $\int_0^\infty g_i(s) ds = 1$.

The dynamics of the system in (3) are analyzed below in the region

$$Y_{2n} = \{(u_{11}, \dots, u_{1n}, u_{21}, \dots, u_{2n}) : 0 \leq u_{ij} \leq 1\}.$$

Define

$$\tilde{g}_1(m_1) = \int_0^\infty g_1(s) e^{-m_1 s} ds \quad \text{and} \quad \tilde{g}_2(\rho m_2) = \int_0^\infty g_2(s) e^{-\rho m_2 s} ds, \tag{4}$$

$$h_1 = 1 - d_1(1 - \tilde{g}_1(m_1)) \leq 1 \quad \text{and} \quad h_2 = 1 - d_2(1 - \tilde{g}_2(\rho m_2)) \leq 1. \tag{5}$$

Here \tilde{g}_i is the one-sided Laplace transform of the travel time distribution $g_i(s)$. Note that for $m_i \geq 0$, \tilde{g}_i is a positive, decreasing function with $\tilde{g}_i(0) = 1$. The

dimensionless parameter h_i is a measure of the difference between growth and dispersal; h_i decreases with increasing dispersal rate, and vice versa.

The non-dimensional system (3) may admit four non-negative spatially homogeneous steady states lying in Y_{2n} . These are of the form $(\bar{\mathbf{u}}_1, \bar{\mathbf{u}}_2)$ in which the n -dimensional vector $\bar{\mathbf{u}}_i = (\bar{u}_{i1}, \dots, \bar{u}_{in})$ represents the steady state densities of species i on all $n \geq 2$ patches, for $i = 1, 2$. With the n -dimensional vector $\mathbf{h}_i = (h_i, \dots, h_i)$ for $i = 1, 2$, these steady states are

$$\begin{aligned}
 &(\mathbf{0}, \mathbf{0}) \qquad (\mathbf{h}_1, \mathbf{0}) \text{ for } h_1 > 0 \qquad (\mathbf{0}, \mathbf{h}_2) \text{ for } h_2 > 0 \\
 &(\mathbf{u}_1^*, \mathbf{u}_2^*) \text{ for } \mathbf{u}_1^* = (u_1^*, \dots, u_1^*) \text{ and } \mathbf{u}_2^* = (u_2^*, \dots, u_2^*) \\
 &\text{where } u_1^* = \frac{h_1 - a_{12}h_2}{1 - a_{12}a_{21}} \text{ and } u_2^* = \frac{h_2 - a_{21}h_1}{1 - a_{12}a_{21}}, \tag{6}
 \end{aligned}$$

provided that u_1^* and u_2^* are positive. In biological terms, the steady states in (6) represent extinction of both species on all n patches, competitive exclusion of species 2 on all patches with species 1 below its carrying capacity (due to dispersal), competitive exclusion of species 1 on all n patches with species 2 below its carrying capacity (due to dispersal) and coexistence of both species with the same densities of each species on all n patches. Inhomogeneous steady states $(\mathbf{u}_1^*, \mathbf{u}_2^*)$ can occur for a small set of parameter values if $d_1 = d_2$ and $\tilde{g}_1(m_1) = \tilde{g}_2(\rho m_2)$, but have not been ruled out analytically for the general system (3) with $d_1 \neq d_2$ and $\tilde{g}_1(m_1) \neq \tilde{g}_2(\rho m_2)$.

3. Local Stability Analysis. When applying linear stability analysis to the steady states in (6), the following lemma involving $\tilde{g}_1(m_1)$ is used. Replacing m_1 with ρm_2 and interchanging subscripts 1 and 2 in all the other parameters yields an identical result for $\tilde{g}_2(\rho m_2)$.

LEMMA 3.1. *Let $\lambda - 1 + c + d_1 = \pm bd_1\tilde{g}_1(m_1 + \lambda)$ be a characteristic equation in λ , where $c > h_1$ is a non-negative constant and b is a constant with $0 < b \leq 1$. Then $Re(\lambda) < 0$ for all roots λ .*

Proof: Let $\lambda = x + iy$, where $y \in \mathcal{R}$, and suppose that $x \geq 0$. Then by taking the modulus of each side and squaring

$$\begin{aligned}
 |x + iy - 1 + c + d_1|^2 &= |bd_1\tilde{g}_1(m_1 + x + iy)|^2 \\
 &= \left| bd_1 \int_0^\infty g_1(s)e^{-m_1s}e^{-xs}e^{-iys}ds \right|^2 \\
 &\leq \left(bd_1 \int_0^\infty |g_1(s)e^{-m_1s}| ds \right)^2 \\
 &= b^2 d_1^2 \tilde{g}_1^2(m_1) \\
 \Rightarrow (x - 1 + c + d_1)^2 + y^2 &\leq b^2 d_1^2 \tilde{g}_1^2(m_1)
 \end{aligned}$$

$$\Rightarrow (x - 1 + c + d_1 - bd_1\tilde{g}_1(m_1))(x - 1 + c + d_1 + bd_1\tilde{g}_1(m_1)) \leq -y^2.$$

For $c > h_1 \geq 1 - d_1 \pm bd_1\tilde{g}_1(m_1)$, the product on the left-hand side of the above inequality is positive, whereas the right-hand side is non-positive, giving a contradiction and completing the proof. \square

Let $u_{ij} = \bar{u}_{ij} + v_{ij}$ with $|v_{ij}| \ll \bar{u}_{ij}$, for $i = 1, 2$ and $j = 1, \dots, n$. Thus

linearization of the system (3) in the neighbourhood of a non-negative steady state $(\bar{\mathbf{u}}_1, \bar{\mathbf{u}}_2)$ yields

$$\begin{aligned} \frac{dv_{1j}}{dt} &= v_{1j}(1 - 2\bar{u}_{1j} - a_{12}\bar{u}_{2j}) - a_{12}\bar{u}_{1j}v_{2j} \\ &\quad + d_1\left[\frac{1}{n-1} \sum_{\ell=1, \ell \neq j}^n \int_0^\infty g_1(s)e^{-m_1s}v_{1\ell}(t-s)ds - v_{1j}\right] \\ \frac{dv_{2j}}{dt} &= \rho v_{2j}(1 - 2\bar{u}_{2j} - a_{21}\bar{u}_{1j}) - \rho a_{21}\bar{u}_{2j}v_{1j} \\ &\quad + \rho d_2\left[\frac{1}{n-1} \sum_{\ell=1, \ell \neq j}^n \int_0^\infty g_2(s)e^{-\rho m_2s}v_{2\ell}(t-s)ds - v_{2j}\right] \end{aligned} \tag{7}$$

for $j = 1, \dots, n$. We now seek solutions to (7) of the form

$$v_{ij} = C_{ij}e^{\lambda t} \text{ for } i = 1, 2 \text{ and } j = 1, \dots, n,$$

where C_{ij} is an arbitrary constant. Substituting these assumed solutions into the linearized equations and setting $\bar{w}_{ij} = 1 - 2\bar{u}_{ij} - d_i$ for $i = 1, 2$ and $j = 1, \dots, n$ gives

$$\begin{aligned} 0 &= C_{1j}[\bar{w}_{1j} - a_{12}\bar{u}_{2j} - \lambda] \\ &\quad + \left[\frac{1}{n-1}d_1\tilde{g}_1(m_1 + \lambda)\right] \sum_{\ell=1, \ell \neq j}^n C_{1\ell} - C_{2j}[a_{12}\bar{u}_{1j}] \\ 0 &= -C_{1j}[a_{21}\bar{u}_{2j}] \\ &\quad + C_{2j}\left[\bar{w}_{2j} - a_{21}\bar{u}_{1j} - \frac{\lambda}{\rho}\right] + \left[\frac{1}{n-1}d_2\tilde{g}_2(\rho m_2 + \lambda)\right] \sum_{\ell=1, \ell \neq j}^n C_{2\ell}. \end{aligned}$$

Accordingly, the linearized coefficient matrix can be written as

$$B = \begin{pmatrix} C & D \\ E & F \end{pmatrix},$$

where C, D, E and F are $n \times n$ matrices. Let I denote the $n \times n$ identity matrix and J denote the $n \times n$ matrix with every entry equal to one. With $p_1 = \frac{1}{n-1}d_1\tilde{g}_1(m_1 + \lambda)$, $C = p_1J - (p_1 + \lambda)I + \text{diag}(\bar{w}_{1i} - a_{12}\bar{u}_{2i})$. Similarly, with $p_2 = \frac{1}{n-1}\rho d_2\tilde{g}_2(\rho m_2 + \lambda)$, $F = p_2J - (p_2 + \lambda)I + \rho \text{diag}(\bar{w}_{2i} - a_{21}\bar{u}_{1i})$. Matrices D and E are diagonal, $D = -a_{12}\text{diag}(\bar{u}_{1i})$ and $E = -\rho a_{21}\text{diag}(\bar{u}_{2i})$. The coefficient matrix B is now applied to each of the spatially homogeneous steady states in (6). Theorem 3.2 summarizes the local stability results.

THEOREM 3.2. *For system (3) with h_i defined as in (5), the stability properties of the extinction and the competitive exclusion steady states in (6) are given as follows:*

(a) *The steady state $(\mathbf{0}, \mathbf{0})$ is*

$$\begin{aligned} &\text{locally asymptotically stable if} && h_1, h_2 < 0, \\ &\text{unstable if} && h_1 > 0 \quad \text{or} \quad h_2 > 0. \end{aligned}$$

(b) *The steady state $(\mathbf{h}_1, \mathbf{0})$ is*

$$\begin{aligned} &\text{locally asymptotically stable if} && a_{21}h_1 > h_2, \\ &\text{unstable if} && a_{21}h_1 < h_2. \end{aligned}$$

(c) The steady state $(\mathbf{0}, \mathbf{h}_2)$ is

$$\begin{aligned} \text{locally asymptotically stable if} & \quad a_{12}h_2 > h_1, \\ \text{unstable if} & \quad a_{12}h_2 < h_1. \end{aligned}$$

Proof: The linearized coefficient matrix B has C , D , E and F as given above.

(a) At the steady state $(\mathbf{0}, \mathbf{0})$, B is a direct sum since $D(\mathbf{0}, \mathbf{0}) = E(\mathbf{0}, \mathbf{0}) = 0$, the $n \times n$ zero matrix. Thus all that remains is to find the sign of $Re(\lambda)$ for each of $detC = 0$ and $detF = 0$ at $(\mathbf{0}, \mathbf{0})$.

For $detC(\mathbf{0}, \mathbf{0}) = 0$, summing all rows, taking out the resulting common factor from row 1 and subtracting the first column from all other columns yields the following equation in λ :

$$(1 - d_1 + d_1\tilde{g}_1(m_1 + \lambda) - \lambda)(1 - d_1 - \frac{d_1\tilde{g}_1(m_1 + \lambda)}{n - 1} - \lambda)^{n-1} = 0. \tag{8}$$

Consider the first factor in (8). If $h_1 < 0$, then Lemma 3.1 for $c = 0$ implies $Re(\lambda) < 0$. On the other hand, suppose $h_1 > 0$ and let $\lambda = x \in \mathcal{R}$; then from (8)

$$f(x) = x - 1 + d_1 - d_1\tilde{g}_1(m_1 + x) = 0.$$

Then $f(0) = -h_1 < 0$, $f(1) > 0$ and $f'(x) = 1 - d_1\tilde{g}'_1(m_1 + x) > 0$. By the intermediate value theorem, there exists a positive x satisfying $f(x) = 0$, which implies that there is a λ for (8) with $Re(\lambda) > 0$, and so the steady state $(\mathbf{0}, \mathbf{0})$ is unstable. For the second factor in (8), by Lemma 3.1 with $b = \frac{1}{n-1}$, it follows that $Re(\lambda) < 0$ for all roots λ whenever $h_1 < 0$.

Interchanging subscripts 1 and 2 and replacing λ in the matrix $F(\mathbf{0}, \mathbf{0})$ with $\rho\nu$, then factoring out the positive constant ρ , yields a matrix which is identical to $C(\mathbf{0}, \mathbf{0})$. Thus $Re(\lambda) > 0$ for some λ which is a root of the equation $detF(\mathbf{0}, \mathbf{0}) = 0$ whenever $h_2 > 0$, and $Re(\lambda) < 0$ for all λ if $h_2 < 0$. This proves part (a) of the theorem.

(b) At the steady state $(\mathbf{h}_1, \mathbf{0})$ for $h_1 > 0$, the matrix B is reducible since $E(\mathbf{h}_1, \mathbf{0}) = 0$ and $detC(\mathbf{h}_1, \mathbf{0}) = det((1 - 2h_1 - d_1 - \lambda - p_1)I + p_1J)$. Setting $detC(\mathbf{h}_1, \mathbf{0}) = 0$ yields the following equation in λ :

$$\begin{aligned} (1 - 2h_1 - d_1 + d_1\tilde{g}_1(m_1 + \lambda) - \lambda) \times \\ (1 - 2h_1 - d_1 - \frac{d_1\tilde{g}_1(m_1 + \lambda)}{n - 1} - \lambda)^{n-1} = 0. \end{aligned} \tag{9}$$

Since $2h_1 > h_1 > 0$, it follows from Lemma 3.1, using $b = 1$ and $b = \frac{1}{n-1}$, that $Re(\lambda) < 0$ for all roots λ of both factors in (9). Similarly setting $detF(\mathbf{h}_1, \mathbf{0}) = 0$ yields

$$\nu - 1 + a_{21}h_1 + d_2 - d_2\tilde{g}_2(\rho m_2 + \rho\nu) = 0, \tag{10}$$

$$\nu - 1 + a_{21}h_1 + d_2 + \frac{d_2\tilde{g}_2(\rho m_2 + \rho\nu)}{n - 1} = 0. \tag{11}$$

For $a_{21}h_1 > h_2$, Lemma 3.1 implies that $Re(\nu) < 0$ (i.e., $Re(\lambda) < 0$) for all roots ν of (10) and (11). Otherwise, if $a_{21}h_1 < h_2$, then, by using the intermediate value theorem as in (a) above, $Re(\lambda) > 0$ for some λ in (10) whenever $a_{21}h_1 < h_2$, and therefore, the steady state $(\mathbf{h}_1, \mathbf{0})$ is unstable.

(c) At the steady state $(\mathbf{0}, \mathbf{h}_2)$ for $h_2 > 0$, results follow from (b) by symmetry, thus completing the proof. \square

Note that if there is no mortality during travel ($m_1 = m_2 = 0$), then the steady states in (6) have $h_1 = h_2 = 1$. Thus in the results of Theorem 3.2 there is no dependence on the dispersal or delay.

Due to the difficulty of the expressions in the $2n \times 2n$ matrix B resulting from linearization about the positive steady state $(\mathbf{u}_1^*, \mathbf{u}_2^*)$, local stability analysis for this case has not been resolved. Existence and local stability conditions for the homogeneous steady states of the non-dimensional system (3) with $n = 2$ patches and $h_1, h_2 > 0$ are summarized in Table 1. For the case in which $h_1 > 0$ and $h_2 < 0$, species 1 outcompetes species 2 (as in *I*). Whereas if $h_1 < 0$ and $h_2 > 0$, then species 2 wins the competition (as in *IV*). If $h_1, h_2 < 0$, then the extinction steady state $(\mathbf{0}, \mathbf{0})$ is the only stable spatially homogeneous steady state, while all others cease to exist. As examples, some numerical simulations are presented in the next section for the case of two species dispersing among two and three patches. These show homogeneous coexistence is possible for some parameter values. Moreover, these simulations indicate that inhomogeneous coexistence steady states for (3) with $n = 2$ patches exist only in very restricted cases (see Figure 3).

For $h_1, h_2 < 0$, the linear stability result of Theorem 3.2(a) can be strengthened, as given in Theorem 3.3 below.

THEOREM 3.3. *If $h_1, h_2 < 0$, then the extinction steady state $(\mathbf{0}, \mathbf{0})$ of (2) is globally asymptotically stable.*

Proof: From (3) and the positivity of solutions, the following differential inequality results:

$$\frac{du_{ij}}{dt} \leq \rho_i u_{ij} + \rho_i d_i \left[\frac{1}{n-1} \sum_{\ell=1, \ell \neq j}^n \int_0^\infty g_i(s) e^{-\rho_i m_i s} u_{i\ell}(t-s) ds - u_{ij} \right],$$

for $i = 1, 2$ and $j = 1, \dots, n$, with $\rho_1 = 1$ and $\rho_2 = \rho$.

Consider this system with equality, namely,

$$\frac{d\tilde{u}_{ij}}{dt} = \rho_i \tilde{u}_{ij} + \rho_i d_i \left[\frac{1}{n-1} \sum_{\ell=1, \ell \neq j}^n \int_0^\infty g_i(s) e^{-\rho_i m_i s} \tilde{u}_{i\ell}(t-s) ds - \tilde{u}_{ij} \right],$$

for $t > 0$ and the same initial conditions on $(-\infty, 0]$ as for $u_{ij}(t)$. This system is linear, and thus its global dynamical behavior can be determined from the linear theory carried out in Theorem 3.2(a). For $h_1, h_2 < 0$, this implies that $(\mathbf{0}, \mathbf{0})$ is globally stable (not just locally stable) for the $\tilde{u}_{ij}(t)$ system. Moreover, since $u_{ij}(t) \leq \tilde{u}_{ij}(t)$, it follows by comparison using the quasimonotonicity property [6, Theorem 1.1, page 78] that $(\mathbf{0}, \mathbf{0})$ of (2) is globally asymptotically stable for $h_1, h_2 < 0$. \square

4. Numerical Simulations. To support and complement analytical results, numerical simulations are carried out by integrating the non-dimensional system (3) using MatLab (dde23). A delta function distribution for the probability density functions $g_i(s)$ is assumed, namely, $g_i(s) = \delta(s - \tau)$ for $i = 1, 2$. This implies that all dispersing individuals have the same traveling time out of the patch, and thus from (4) for some fixed τ (in dimensionless time) with $0 < \tau < \min \{r_1 L_i\}$,

$$\tilde{g}_1(m_1) = e^{-m_1 \tau} \quad \text{and} \quad \tilde{g}_2(\rho m_2) = e^{-\rho m_2 \tau}. \tag{12}$$

TABLE 1. Summary of existence and local stability conditions for all spatially homogeneous steady states of the two-patch model (3) for $n = 2$, with both species dispersing. The abbreviations DNE, UN and SN denote “does not exist,” “unstable numerically” and “stable numerically,” respectively.

$h_1, h_2 > 0$	$a_{21}h_1 > h_2$	$a_{21}h_1 < h_2$
	<i>I: Competitive Exclusion</i> (Species 1 wins)	<i>II: Coexistence?</i>
$a_{12}h_2 < h_1$	(0, 0, 0, 0)-unstable ($h_1, h_1, 0, 0$)-STABLE (0, 0, h_2, h_2)-unstable ($u_{11}^*, u_{11}^*, u_{21}^*, u_{21}^*$)-DNE	(0, 0, 0, 0)-unstable ($h_1, h_1, 0, 0$)-unstable (0, 0, h_2, h_2)-unstable ($u_{11}^*, u_{11}^*, u_{21}^*, u_{21}^*$)-SN
	<i>III: Initial Condition</i> <i>Dependent Competitive</i> <i>Exclusion †</i>	<i>IV: Competitive Exclusion</i> (Species 2 wins)
$a_{12}h_2 > h_1$	(0, 0, 0, 0)-unstable ($h_1, h_1, 0, 0$)-STABLE (0, 0, h_2, h_2)-STABLE ($u_{11}^*, u_{11}^*, u_{21}^*, u_{21}^*$)-UN	(0, 0, 0, 0)-unstable ($h_1, h_1, 0, 0$)-unstable (0, 0, h_2, h_2)-STABLE ($u_{11}^*, u_{11}^*, u_{21}^*, u_{21}^*$)-DNE

† In special cases, two inhomogeneous steady states are found numerically and can be locally stable.

For all densities, constant initial values in the interval $(0, 1)$ for $t \in [-\tau, 0]$ are assumed. For the two-patch model with both species dispersing, Figure 1 illustrates stable coexistence, while Figure 2 illustrates initial condition dependent competitive exclusion.

As a special case of the two (identical) patch model, assume that the two competing species have identical local dynamics, $d = d_1 = d_2 < 0.1$, $m = m_1 = m_2$, $\tilde{g}_1(m_1) = \tilde{g}_2(\rho m_2)$ with $\rho = 1$ and $a_{12} \approx a_{21} > 1$. For a small set of parameter values, these restrictions can result in spatially inhomogeneous coexistence with small dispersal rates and travel delay (for some carefully chosen initial conditions). This is illustrated in Figure 3. For two species competing on three patches, an example of coexistence is illustrated in Figure 4. Numerical simulations for the case in which only species 1 disperses are qualitatively similar to the general cases discussed above with the restriction $h_2 = 1$ (since $d_2 = 0$). In the two-patch case, none of the new steady states introduced by $d_2 = 0$ are found to be stable.

5. More than Two Competitors: Oscillations Are Possible. For the case in which only two species compete between the patches, all found solutions approach a steady state. However increasing the number of competitors results in oscillations as a possible outcome for some parameter values. For three species competing among two patches, oscillatory coexistence is possibly due to a Hopf Bifurcation; see Kuang [2, page 60]. With a delta function distribution $\delta(S - T)$ for dispersal,

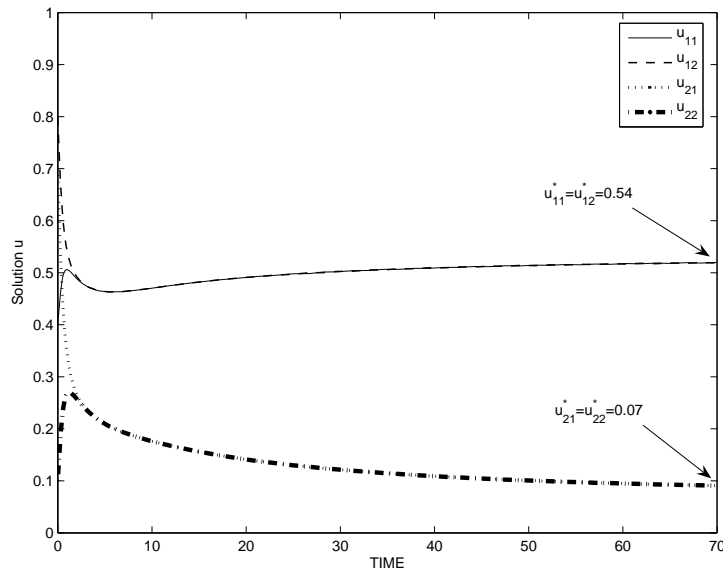


FIGURE 1. Coexistence steady state as in *II* of Table 1. The parameter values taken for illustration are $a_{12} = 0.5$, $a_{21} = 1.2$, $\rho = 1$, $m_1 = 1.5$, $m_2 = 1.3$ and $\tau = 0.3$. Here $d_1 = 1.2$ and $d_2 = 0.9$, implying $h_1 = 0.57$ and $h_2 = 0.71$. The coexistence steady state $(u_{11}^*, u_{12}^*, u_{21}^*, u_{22}^*) = (0.54, 0.54, 0.07, 0.07)$ is locally asymptotically stable.

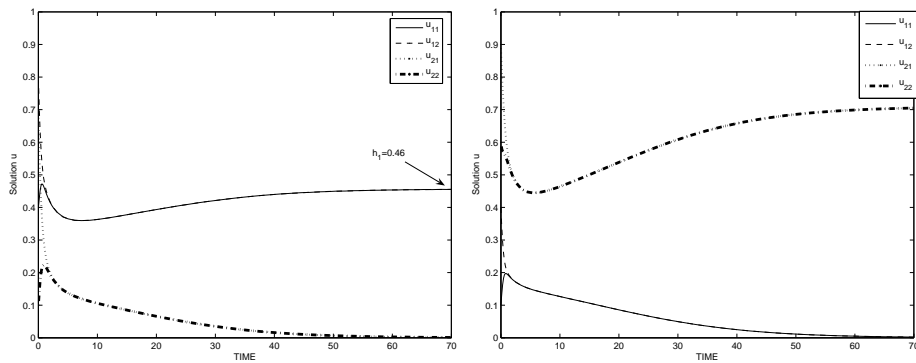


FIGURE 2. Initial condition dependent competitive exclusion as in *III* of Table 1, with $d_1 = 1.5$ and $d_2 = 0.9$, implying $h_1 = 0.46$ and $h_2 = 0.71$. The other parameter values taken are $a_{12} = 0.8$, $a_{21} = 1.8$, $\rho = 1$, $m_1 = 1.5$, $m_2 = 1.3$ and $\tau = 0.3$.

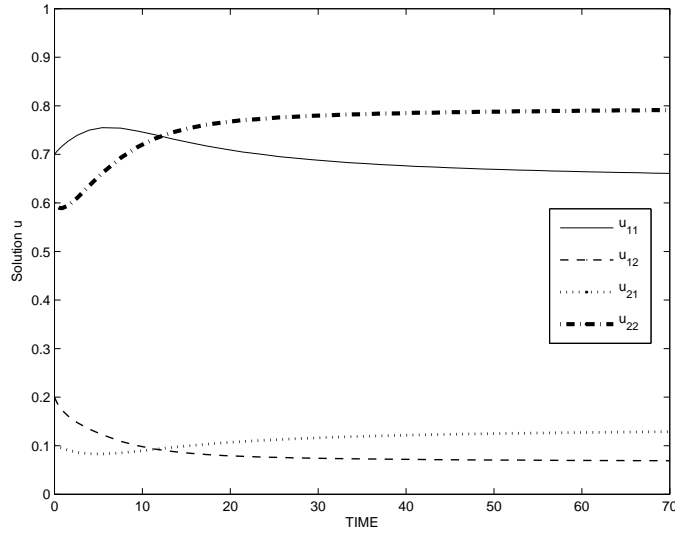


FIGURE 3. Stable inhomogeneous coexistence steady state for two competing species with identical local dynamics on two identical patches. Parameters taken are $d = 0.09$, $a_{12} = 2$, $a_{21} = 1.9$, $m = 0.5$ and $\tau = 0.3$.

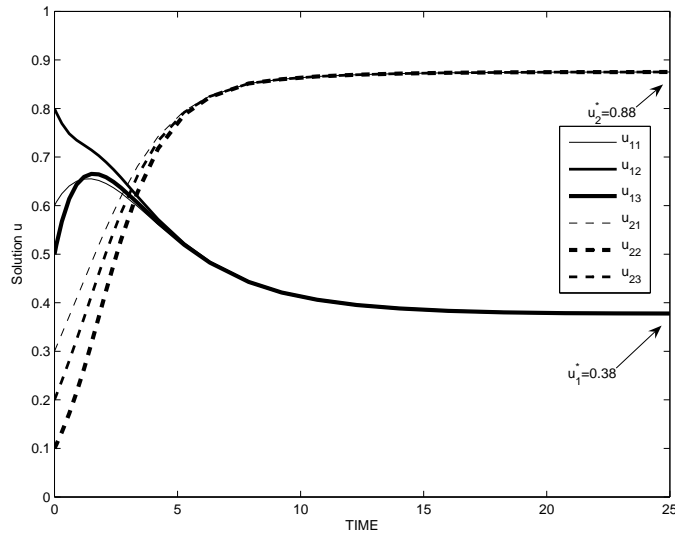


FIGURE 4. Coexistence of the two species on three patches as in (3) with $n = 3$, $d_1 = 0.7$ and $d_2 = 0.3$ ($h_1 = 0.902$ and $h_2 = 0.943$). Other parameters taken are $a_{12} = 0.6$, $a_{21} = 0.2$, $m_1 = 0.5$, $m_2 = 0.7$ and $\tau = 0.3$. Here $u_i^* = u_{ij}^*$ for $i = 1, 2$, $j = 1, 2, 3$.

the system of equations is

$$\begin{aligned} \frac{dN_{ij}}{dT} = & \frac{r_i}{K_i} N_{ij} (K_i - N_{ij} - \sum_{k=1, k \neq i}^3 \alpha_{ik} N_{kj}) \\ & + D_i \left[\frac{1}{n-1} \sum_{\ell=1, \ell \neq j}^n e^{-M_i T} N_{i\ell} (T - \mathcal{T}) - N_{ij} \right], \end{aligned} \quad (13)$$

where $i = 1, 2, 3$ and $j = 1, \dots, n$. Numerical simulation of (13) for $n = 2$ patches illustrates the oscillatory outcome for some carefully chosen parameter values [8, Example A] with $\mathcal{T} = 0.01$, as in Figure 5, in which the time axis is shown from 25 to 45.

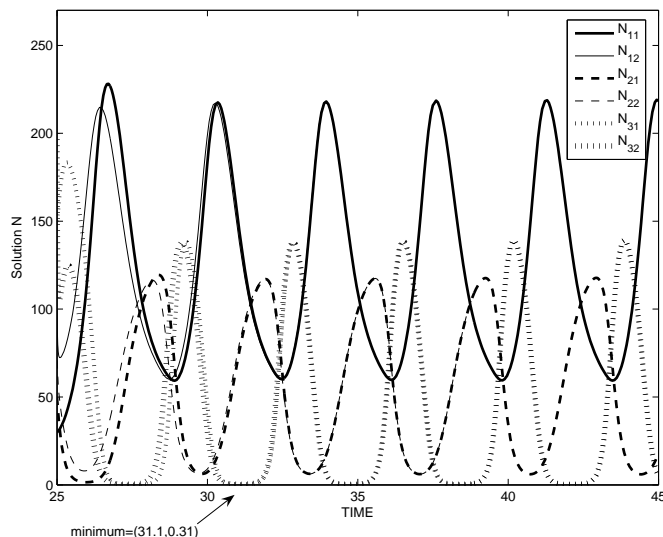


FIGURE 5. A two (identical) patch model in which three species disperse with small travel delay. The numerical data set used is: $D_1 = 0.3$, $D_2 = 0.4$, $D_3 = 0.1$, $M_1 = 0.5$, $M_2 = 0.4$, $M_3 = 0.6$, $\mathcal{T} = 0.01$, $r_1 = 25$, $r_2 = 16$, $r_3 = 60$, $K_1 = 250$, $K_2 = 160$, $K_3 = 240$, $\alpha_{12} = 1.5$, $\alpha_{21} = 0.5$, $\alpha_{13} = 1$, $\alpha_{31} = 1.1$, $\alpha_{23} = 1$ and $\alpha_{32} = 1.1$.

6. One-Patch Model. The two species on two patches competition model (2) does not apply in the one-patch case ($n = 1$) in which it is assumed that individuals disperse out of the patch and then return (given that they survive). With $i, k = 1, 2$, $k \neq i$ and $\rho_1 = 1$, $\rho_2 = \rho$, the non-dimensional model equations for the one-patch model are

$$\begin{aligned} \frac{du_i}{dt} = & \rho_i u_i (1 - u_i - a_{ik} u_k) \\ & + \rho_i d_i \left[\int_0^\infty g_i(s) e^{-\rho_i m_i s} u_i(t-s) ds - u_i \right]. \end{aligned} \quad (14)$$

This situation is qualitatively similar to the general model (3). Coexistence is possible and locally stable for some parameter values. Existence and linear stability for the one-patch model with only species 1 dispersing ($h_2 = 1$) are summarized in Table 2, in which u_1^* and u_2^* are as stated in (6), with $h_2 = 1$. The coexistence steady state is proved analytically to be locally asymptotically stable in *II* and unstable in *III* by considering the characteristic equation and using techniques similar to those in the proof of Theorem 3.2. A case of coexistence is illustrated in Figure 6.

TABLE 2. Summary of existence and local stability conditions for all steady states of the one-patch model (14) with only species 1 dispersing.

$h_1 > 0$	$a_{21}h_1 > 1$	$a_{21}h_1 < 1$
	<i>I: Competitive Exclusion (Species 1 wins)</i>	<i>II: Coexistence</i>
$a_{12} < h_1$	(0, 0)-unstable ($h_1, 0$)-STABLE (0, 1)-unstable (u_1^*, u_2^*)-does not exist	(0, 0)-unstable ($h_1, 0$)-unstable (0, 1)-unstable (u_1^*, u_2^*)-STABLE
	<i>III: Initial Condition Dependent Competitive Exclusion</i>	<i>IV: Competitive Exclusion (Species 2 wins)</i>
$a_{12} > h_1$	(0, 0)-unstable ($h_1, 0$)-STABLE (0, 1)-STABLE (u_1^*, u_2^*)-unstable	(0, 0)-unstable ($h_1, 0$)-unstable (0, 1)-STABLE (u_1^*, u_2^*)-does not exist

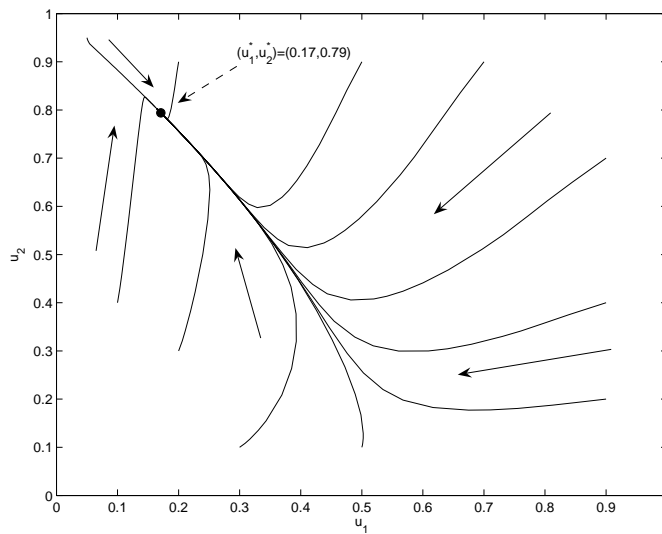


FIGURE 6. Phaseplane plot for *II* of Table 2 for (14), with $d_2 = 0$. The dispersal rate used is $d_1 = 1.2$, implying $h_1 = 0.57$. Other parameter values taken are $a_{12} = 0.5$, $a_{21} = 1.2$, $\rho = 1$, $m_1 = 1.5$ and $\tau = 0.3$. The coexistence steady state $(u_1^*, u_2^*) = (0.17, 0.79)$ is locally asymptotically stable.

7. Concluding Remarks. For the models formulated here, two competitors on a patchy environment with dispersal delay always approach a non-negative steady state (no periodic solutions are found). Linear stability and numerical simulation support this statement, but global asymptotic stability of steady states remains an

open problem. For the general n -patch model, Section 2, there are four possible outcomes: competitive exclusion of one species, coexistence, initial condition dependent competitive exclusion and extinction of both species. The dynamics of the system depends on the competition coefficients and the ratio $\frac{h_1}{h_2}$ measuring the ratio of the effects of dispersal on the linear increase of each species. For most parameter values, a dispersing species is at a disadvantage (i.e., a situation in which species 2 is extinct may be turned into a coexistence situation if species 1 disperses). As dispersal rates of one species increase, the other species eventually wins the competition. Extinction results when both species have positive dispersal mortality ($m_1, m_2 > 0$) and disperse at a very high rate ($h_1, h_2 < 0$). For a small range of parameter values, equal small dispersal rates can be an advantage to one of the species as exclusion is turned into coexistence (see Figure 3). Increasing the number of competitors to three may change the dynamics of the system, for then oscillatory coexistence is a possible outcome, as illustrated in Figure 5.

Some patchy environments are connected via a corridor in which the dispersing species compete for resources. In these and similar situations, competition during dispersal should be incorporated into the models, as this could change the overall outcome.

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