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Coexistence of species with different dispersal across landscapes: a critical role of spatial correlation in disturbance

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Supplementary Figure S1

Figure S1. Effect of disturbance periodicity (T) on the competitive outcome of a local disperser interacting with a global disperser (red dashed line at $\rho_d = q_{dd}$ indicating randomly structured disturbance), while simultaneously varying disturbance extent $\rho_d$ and spatial aggregation $q_{dd}$.

(a) T=50, (b) T=100, (c) T=150 and (d) T=200. Other parameters: see figure 3 except mortality rate $m_2=0.014$ (global disperser). Inaccessible region: see equation (2).
Supplementary Methods

Constructing a closed dynamical system for two dispersers

In this model, we choose \( \rho_1, \rho_2, q_{1/1}, q_{2/2}, q_{1/2} \) as independent variables so as to construct a closed dynamical system for two competitors. According to the definition of local density [1], we have

\[
q_{i/j} = \frac{\rho_j}{\rho_i} \quad (i,j \in \{0, 1, 2\})
\]  

(S1)

where local density \( q_{i/j} \in [0,1] \) is the conditional probability of a neighbouring site for a randomly chosen individual \( j \) being occupied by an individual \( i \), and pair density \( \rho_{ij} \) represents the probability when choosing a pair of neighbouring sites at random that one of them is species \( i \) while another one is species \( j \). Based on equation (S1), we can further derive the dynamics of \( q_{i/j} \) as

\[
\frac{dq_{i/j}}{dt} = -q_{i/j} \frac{d\rho_j}{\rho_j} + \frac{1}{\rho_j} \frac{d\rho_j}{dt}.
\]  

(S2)

Therefore, we obtain

\[
\begin{align*}
\frac{dq_{1/1}}{dt} & = -q_{1/1} \frac{d\rho_j}{\rho_j} + \frac{1}{\rho_j} \frac{d\rho_j}{dt} \\
\frac{dq_{2/2}}{dt} & = -q_{2/2} \frac{d\rho_j}{\rho_j} + \frac{1}{\rho_j} \frac{d\rho_j}{dt} \\
\frac{dq_{2/1}}{dt} & = -q_{2/1} \frac{d\rho_j}{\rho_j} + \frac{1}{\rho_j} \frac{d\rho_j}{dt}
\end{align*}
\]  

(S3)

For the transition rate of pair density \( \rho_{11} \), we have

\[
\frac{d\rho_{11}}{dt} = 2\rho_{10} \left( \frac{1}{z} \alpha \cdot q_{1/01} \right) - 2\rho_{11} \left( m_1 + \frac{1}{z} \gamma_{11} q_{1/11} + \frac{z-1}{z} \gamma_{12} q_{2/11} \right).
\]  

(S4)
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in which the first term on the right hand describes the transition of the pair 0-1 (or 1-0) becoming 1-1 due to local dispersal. The empty site in the pair 0-1 can be colonized by two pathways:

local dispersal from the individual 1 in the pair of 0-1 (with the probability 1/z) or the potential presence of individual 1 from other z-1 neighbours of the target 0-site (z=4). The second term is the transition of the pair 1-1 becoming 1-0 (or 0-1) because of species mortality. Besides species intrinsic morality \( m_1 \), the death of a target individual 1 in the pair 1-1 is also influenced by both the already presence of a neighbouring individual 1 in the pair of 1-1 sites and the potential presence of conspecific individual 1 from its remaining z-1 neighbours (i.e. intraspecific competition), as well as the potential presence of heterospecific individual 2 in the z-1 neighbours (i.e. interspecific competition). The parameter \( q_{i,j,k} \) (e.g. \( q_{1/01} \), \( q_{1/11} \) and \( q_{2/11} \)) is the triplet conditional probability for an \( i \)-site which is another neighbour of a \( j \)-site in the pair of \( j-k \).

According to the pair approximation principle [1], we have

\[
q_{i,j,k} \approx q_{i,j} \quad (i,j,k \in \{0, 1, 2\}).
\]  

(S5)

Similar to equation (S4), the change rate of the pair density \( \rho_{22} \) can be written as

\[
\frac{d \rho_{22}}{dt} = 2 \beta \rho_{22} - 2 \rho_{22} \left( m_2 + \frac{\gamma_{22}}{z} + \frac{z-1}{z} \gamma_{22} q_{2/22} + \frac{z-1}{z} \gamma_{21} q_{1/22} \right).
\]  

(S6)

where the only difference is the first term in which the vacant site in the pair of 0-2 sites becomes occupied by seed random dispersal across the whole landscape.

Following the same principle, we can derive the dynamics of the pair density \( \rho_{12} \) as

\[
\frac{d \rho_{12}}{dt} = \beta \rho_{12} \rho_{10} + \frac{z-1}{z} \alpha q_{1/02} \rho_{20} - \rho_{12} \left( m_1 + \frac{\gamma_{12}}{z} + \frac{z-1}{z} \gamma_{12} q_{2/12} + \frac{z-1}{z} \gamma_{11} q_{1/12} \right) - \rho_{12} \left( m_2 + \frac{\gamma_{21}}{z} + \frac{z-1}{z} \gamma_{21} q_{1/21} + \frac{z-1}{z} \gamma_{22} q_{2/21} \right).
\]  

(S7)

In order to form the closed system, we should consider the following constraints
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\[
\begin{align*}
\rho_0 + \rho_1 + \rho_2 &= 1 \\
q_{i,j} &= q_{j,i} \rho_i / \rho_j, \\
q_{i,j} &= 1 - q_{j,i} - q_{k,j}
\end{align*}
\]  
(S8)

with \(i,j,k \in \{0, 1, 2\}\).

Combining equations (1a,b) and (S3-S8), we obtain

\[
\frac{dq_{1n}}{dt} = -q_{1n} \left[ \alpha \left(1 - q_{1n} - q_{2n}\right) + m_1 + \frac{\gamma_{11}}{2} + \frac{1}{2} \gamma_{11}q_{1n} + \frac{1}{2} \gamma_{12}q_{2n} \right] + \left(1 - q_{1n} - q_{2n}\right) \left( \frac{\alpha}{2} + \frac{3}{2} \alpha \rho_1 \frac{1 - q_{1n} - q_{2n}}{1 - \rho_1 - \rho_2} \right),
\]

(S9)

\[
\frac{dq_{2n}}{dt} = -q_{2n} \left[ \beta \left(1 - \rho_1 - \rho_2\right) + m_2 + \frac{\gamma_{22}}{2} + \frac{1}{2} \gamma_{22}q_{2n} + \frac{1}{2} \gamma_{21}q_{2n}q_{1n} \right] + 2 \beta \rho_2 \left(1 - \rho_1q_{2n} \rho_2 - q_{2n}\right),
\]

(S10)

\[
\frac{dq_{2n}}{dt} = -q_{2n} \left[ \alpha \left(1 - q_{1n} - q_{2n}\right) - \frac{1}{4} \left( \gamma_{11}q_{1n} + \gamma_{12}q_{2n} \right) \right] + m_2 + \frac{\gamma_{21} + \gamma_{12}}{4} + \frac{3}{4} \left( \gamma_{21} \rho_1q_{2n} \rho_2 + \gamma_{22}q_{2n} \right) + \beta \rho_2 \left(1 - q_{1n} - q_{2n}\right) + \frac{3}{4} \alpha \rho_2 \frac{1 - q_{1n} - q_{2n}}{1 - \rho_1 - \rho_2} \left(1 - q_{2n} - \rho_1q_{2n} \rho_2\right),
\]

(S11)

Therefore, equations (1a,b) and (S9-S11) with five variables (\(\rho_1, \rho_2, q_{1n}, q_{2n} / \rho_2\)) form a closed mathematical system for two competitors with different dispersal modes in a homogeneous landscape.

Similar to equation (3), when the periodic pulse disturbance (occurring at \(t = nT, n \in \mathbb{N}\)) is incorporated into the PA model, we can derive the dynamics of species clumping by combining equations (8) and (S9-S11)
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\[
\begin{align*}
\frac{d\alpha_{12}(t)}{dt} &= -q_{12}(t) \left[ \alpha (1-q_{12}(t) - q_{22}(t)) + m_2 + \frac{\gamma_{12}}{2} q_{12}(t) \right] + (1-q_{12}(t) - q_{22}(t)) \left( \frac{\alpha}{2} + \frac{3}{2} \alpha \rho_1(t) \frac{1-q_{12}(t) - q_{22}(t)}{1-\rho_1(t) - \rho_2(t)} \right) \\
\frac{d\alpha_{22}(t)}{dt} &= -q_{22}(t) \left[ \beta (1-\rho_1(t) - \rho_2(t)) + m_2 + \frac{\gamma_{22}}{2} q_{22}(t) + \frac{1}{2} \gamma_{22} q_{22}(t) \rho_1(t) / \rho_2(t) \right] + 2 \beta \rho_1(t) (1-\rho_1(t) q_{22}(t) / \rho_2(t) - q_{22}(t)) \\
\frac{d\alpha_{23}(t)}{dt} &= -q_{23}(t) \left[ \alpha (1-q_{23}(t) - q_{33}(t)) - \frac{1}{4} (\gamma_1 q_{23}(t) + \gamma_2 q_{33}(t)) + m_2 + \frac{\gamma_{23} + \gamma_{12}}{4} \right] + \frac{3}{4} (\gamma_1 \rho_1(t) q_{23}(t) / \rho_2(t) + \gamma_2 q_{22}(t)) + \beta \rho_1(t) (1-q_{23}(t) - q_{22}(t)) \\
\alpha_{22}(t^+) &= q_{22}(t)(1-2\rho_d + \rho_d q_{22}) / (1-\rho_d) \\
\alpha_{23}(t^+) &= q_{23}(t)(1-2\rho_d + \rho_d q_{23}) / (1-\rho_d) \\
\alpha_{12}(t^+) &= q_{12}(t)(1-2\rho_d + \rho_d q_{12}) / (1-\rho_d)
\end{align*}
\]

\( t \neq nT, n \in \mathbb{N} \)  \hspace{2cm} \text{(S12)}

Consequently, equations (3) and (S12) construct a dynamical system of two competing species in the face of spatially correlated periodic disturbance.

References

Electronic supplementary material

Supplementary Model Analysis

A. Model analysis of mean-field approximation model (MFA)

According to the mean-field approximation with \( q_{ij} \approx \rho_i \), equation (1) can be rewritten as

\[
\begin{align*}
\frac{d\rho_1}{dt} &= \alpha \rho_1 (1 - \rho_1 - \rho_2) - (m_1 + \gamma_1 \rho_1 + \gamma_2 \rho_2) \rho_1 \\
\frac{d\rho_2}{dt} &= \beta \rho_2 (1 - \rho_1 - \rho_2) - (m_2 + \gamma_2 \rho_2 + \gamma_1 \rho_1) \rho_2
\end{align*}
\]

(S13)

In equation (S13), the semi-trivial equilibrium is given by \( E_1 = (0, \frac{\beta - m_2}{\beta + \gamma_{22}}) \), which exists and is non-trivial if and only if \( \beta > m_2 \), and \( E_2 = \left( \frac{\alpha - m_1}{\alpha + \gamma_{11}}, 0 \right) \), which exists and is non-trivial if and only if \( \alpha > m_1 \). There also exists a unique positive equilibrium \( E^* = (\rho_1^*, \rho_2^*) \) with

\[
\rho_1^* = \frac{(\alpha - m_1)(\beta + \gamma_{22}) - (\beta - m_2)(\alpha + \gamma_{12})}{(\alpha + \gamma_{11})(\beta + \gamma_{22}) - (\beta + \gamma_{21})(\alpha + \gamma_{12})}
\]

\[
\rho_2^* = \frac{(\beta - m_2)(\alpha + \gamma_{11}) - (\alpha - m_1)(\beta + \gamma_{21})}{(\alpha + \gamma_{11})(\beta + \gamma_{22}) - (\beta + \gamma_{21})(\alpha + \gamma_{12})}
\]

if and only if

\[
\frac{(\beta + \gamma_{22})}{(\alpha + \gamma_{12})} > \frac{(\beta - m_2)}{(\alpha - m_1)} > \frac{(\beta + \gamma_{21})}{(\alpha + \gamma_{11})}.
\]

We now investigate the stability of the semi-trivial equilibria by separately linearizing the system (S13) near the equilibria \( E_1 \) and \( E_2 \), thus yielding the Jacobian matrices

\[
J(E_1) = 
\begin{bmatrix}
\alpha (1 - 2\rho_1 - \rho_2) - (m_1 + 2\gamma_1 \rho_1 + \gamma_1 \rho_2) & -\alpha \rho_1 - \gamma_{12} \rho_1 \\
-\beta \rho_2 - \gamma_{21} \rho_2 & \beta (1 - \rho_1 - 2\rho_2) - (m_2 + 2\gamma_{22} \rho_2 + \gamma_{21} \rho_1)
\end{bmatrix}
\]

and

\[
J(E_2) = 
\begin{bmatrix}
\alpha (1 - \rho_2) - (m_1 + \gamma_{12} \rho_2) & 0 \\
\beta \rho_2 (1 - 2\rho_2) - (m_2 + 2\gamma_{22} \rho_2) \rho_2
\end{bmatrix}
\]
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\[
\begin{bmatrix}
\alpha \left(1 - \frac{\beta - m_2}{\beta + \gamma_{22}}\right) - \left(m_1 + \gamma_{12} \frac{\beta - m_2}{\beta + \gamma_{22}}\right) & 0 \\
\beta \left(1 - 2 \frac{\beta - m_2}{\beta + \gamma_{22}}\right) - \left(m_2 + 2 \gamma_{22} \frac{\beta - m_2}{\beta + \gamma_{22}}\right)
\end{bmatrix}
\]

92

and

\[
J(E_2) = \begin{bmatrix}
\alpha (1 - 2 \rho_1) - (m_1 + 2 \gamma_{11} \rho_1) & 0 \\
0 & \beta (1 - \rho_1) - (m_2 + \gamma_{21} \rho_1)
\end{bmatrix}
\]

94

\[
= \begin{bmatrix}
\alpha \left(1 - 2 \frac{\alpha - m_1}{\alpha + \gamma_{11}}\right) - \left(m_1 + 2 \gamma_{11} \frac{\alpha - m_1}{\alpha + \gamma_{11}}\right) & 0 \\
0 & \beta \left(1 - \frac{\alpha - m_1}{\alpha + \gamma_{11}}\right) - \left(m_2 + \gamma_{21} \frac{\alpha - m_1}{\alpha + \gamma_{11}}\right)
\end{bmatrix}
\]

95

It is seen that $E_1$ is locally asymptotically stable if $\frac{\alpha - m_1}{\alpha + \gamma_{12}} < \frac{\beta - m_2}{\beta + \gamma_{22}}$, while $E_2$ is locally

96

asymptotically stable if $\frac{\beta - m_2}{\beta + \gamma_{21}} < \frac{\alpha - m_1}{\alpha + \gamma_{11}}$. But if the converse inequalities hold, then the respective

97

equilibria are unstable.

98

To investigate the stability of the unique positive equilibrium $E^* = (\rho_1^*, \rho_2^*)$, we assume that

99

the existence condition holds. Linearizing the system (S13) around the equilibrium $E^*$ yields the

100

Jacobian matrix

101

\[
J(E^*) = \begin{bmatrix}
-\alpha \rho_1 - \gamma_{11} \rho_1 & -\alpha \rho_1 - \gamma_{12} \rho_1 \\
-\beta \rho_2 - \gamma_{21} \rho_2 & -\beta \rho_2 - \gamma_{22} \rho_2
\end{bmatrix}
\]

102

If $\frac{(\beta + \gamma_{22})}{(\alpha + \gamma_{12})} > (\frac{(\beta + \gamma_{21})}{(\alpha + \gamma_{11})})$, $E^*$ is locally asymptotically stable.

103

Therefore, we can summarize the analytical results of the MFA model without considering

104

disturbance as follows (see Table S1).
Table S1 The local stability analysis of MFA model

<table>
<thead>
<tr>
<th>Equilibria</th>
<th>Existence</th>
<th>Local stability</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E_1 = (0, \frac{\beta - m_2}{\beta + \gamma_{22}})$</td>
<td>$\beta &gt; m_2$</td>
<td>$\frac{\beta + \gamma_{22}}{\alpha + \gamma_{12}} &lt; \frac{\beta - m_2}{\alpha - m_1}$</td>
</tr>
<tr>
<td>$E_2 = (\frac{\alpha - m_1}{\alpha + \gamma_{11}}, 0)$</td>
<td>$\alpha &gt; m_1$</td>
<td>$\frac{\beta - m_2}{\alpha - m_1} &lt; \frac{\beta + \gamma_{21}}{\alpha + \gamma_{11}}$</td>
</tr>
<tr>
<td>$E^* = (\rho_1^<em>, \rho_2^</em>)$</td>
<td>$\frac{\beta + \gamma_{22}}{\alpha + \gamma_{12}} &gt; \frac{\beta - m_2}{\alpha - m_1} &gt; \frac{\beta + \gamma_{21}}{\alpha + \gamma_{11}}$ and $\beta &gt; m_2$ and $\alpha &gt; m_1$</td>
<td>$\frac{\beta + \gamma_{22}}{\alpha + \gamma_{12}} &gt; \frac{\beta + \gamma_{21}}{\alpha + \gamma_{11}}$</td>
</tr>
</tbody>
</table>
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B. Model analysis of pair approximation (PA) model

The pair-approximation model allows us to derive some analytical conditions for successful invasion. We first summarize the PA system as follows:

\[
\begin{align*}
\frac{d\rho_1}{dt} &= \alpha\rho_1 \left(1 - q_{11} - q_{22}\right) - \left(m_1 + \gamma_{11} q_{11} + \gamma_{12} q_{21}\right) \rho_1 \\
\frac{d\rho_2}{dt} &= \beta\rho_2 \left(1 - \rho_1 - \rho_2\right) - \left(m_2 + \gamma_{22} q_{22} + \gamma_{21} q_{12}\right) \rho_2 \\
\frac{dq_{i1}}{dt} &= \frac{\alpha}{2} q_{i1} (1 + 3q_{i0} - q_{i1}) - q_{i1} \left[\alpha \left(1 - q_{11} - q_{22}\right) + m_1 + \frac{\gamma_{11}}{2} + \frac{\gamma_{12}}{2} q_{11} + \frac{\gamma_{22}}{2} q_{21}\right] \\
\frac{dq_{22}}{dt} &= 2\beta\rho_{20} - q_{22} \left[\beta \left(1 - \rho_1 - \rho_2\right) + m_2 + \frac{\gamma_{22}}{2} + \frac{\gamma_{21}}{2} q_{21}\right] \\
\frac{dq_{i2}}{dt} &= -q_{i2} \left[m_1 + \beta \left(1 - \rho_1 - \rho_2\right)\right] - \frac{q_{i2}}{4} \left[3 \left(\gamma_{11} q_{11} + \gamma_{12} q_{21}\right) + \gamma_{12} + \gamma_{21} - \gamma_{22} q_{22} - \gamma_{21} q_{12}\right] \\
&+ \beta\rho_{10} + \frac{3}{4} \alpha q_{10} q_{i0} 
\end{align*}
\]

in which \(q_{ij} = \rho_i \cdot q_{j|i} / \rho_j\) (\(i, j = 0, 1, 2\)).

Here we consider the case in which the population is near the equilibrium where only species 1 (or species 2) exists, and explore whether the rare species 2 (or species 1) can increase in the PA system.
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Case I: Invasion by species 2 to a population dominated by species 1

We first calculate the equilibrium global and local densities of species 1 with local dispersal by neglecting the rare invasive species 2 ($\rho_2 = 0, q_{2/1} = 0$), consequently simplifying equation (S14) as

$$\begin{align*}
\frac{d \rho_1}{dt} &= \alpha \rho_1 (1 - q_{1/1}) - \rho_1 (m_1 + \gamma_{11} q_{1/1}) \\
\frac{d q_{1/1}}{dt} &= \frac{\alpha}{2} q_{1/1} (1 + 3 q_{1/0}) - q_{1/1} \left[ \alpha (1 - q_{1/1}) + m_1 + \frac{\gamma_{11}}{2} (1 + q_{1/1}) \right].
\end{align*}$$

(S15)

Therefore, we obtain the non-trivial equilibrium $E^* = (\rho_1^*, q_{1/1}^*)$ with

$$\begin{align*}
\rho_1^* &= \frac{3\alpha^2 - m_1 (4\alpha + \gamma_{11})}{(3\alpha - m_1) (\alpha + \gamma_{11})} \\
q_{1/1}^* &= \frac{\alpha - m_1}{\alpha + \gamma_{11}}.
\end{align*}$$

As a result, $E^*$ exists and is locally asymptotically stable if and only if $\alpha > m_1$ and

$$3\alpha (\alpha - m_1) / (\alpha + \gamma_{11}) > m_1.$$

Next, combined with $\rho_2 = 0$ (so $\rho_{20} = 0$) and $E^* = (\rho_1^*, q_{1/1}^*)$, and if we abbreviate $x = q_{2/2}$ and $y = q_{1/2}$, equation (S14) become

$$\begin{align*}
\frac{dx}{dt} &= -2m_2 x - \frac{x}{2} (\gamma_{22} + 3 \gamma_{21} x + 3 \gamma_{21} y) - x \left[ \frac{3\alpha \beta (m_1 + \gamma_{11})}{(3\alpha - m_1) (\alpha + \gamma_{11})} - (m_2 + \gamma_{22} x + \gamma_{21} y) \right] \\
\frac{dy}{dt} &= \beta \rho_{10}^* \frac{3\alpha}{4} (1 - x - y) q_{1/0}^* - \beta (1 - \rho_1^*) y - m_1 y - \frac{y}{4} \left( 3 \gamma_{11} \frac{\alpha - m_1}{\alpha + \gamma_{11}} + \gamma_{12} + \gamma_{21} - \gamma_{22} x - \gamma_{21} y \right),
\end{align*}$$

where $q_{1/0}^* = \frac{\rho_1^*}{1 - \rho_1^*} (1 - q_{1/1}^*) = q_{1/1}^* - \frac{m_1}{3\alpha}$ and $\rho_{10}^* = \rho_0 q_{1/0}^* = (1 - \rho_1^*) q_{1/0}^*$. 

11
This autonomous dynamical system has a single non-negative equilibrium \((0 \leq x \leq 1; 0 \leq y \leq 129)\) that is stable and obtained by letting \(\frac{dx}{dt} = 0\) and \(\frac{dy}{dt} = 0\), so

\[
\begin{align*}
-2m_2x - \frac{x}{2}(\gamma_{22} + 3\gamma_{22}x + 3\gamma_{21}y) &= x\left[ \frac{3\alpha\beta(m_1 + \gamma_{11})}{(3\alpha - m_1)(\alpha + \gamma_{11})} - (m_2 + \gamma_{22}x + \gamma_{21}y) \right], \\
4\beta\rho_{10}^* + 3\alpha q_{l/0}^* (1 - y) &= 4\beta(1 - \rho_{1}^*)y + (4m_1 + 3\gamma_{11}q_{l/1}^* + \gamma_{12} + \gamma_{21} - \gamma_{21}y)y.
\end{align*}
\]  

(S16)

Thus, we can obtain \(x=0\), while the analytical solution of \(y \in [0,1]\) can be achieved from

\[
\gamma_{21}y^2 - 4\beta(1 - \rho_{1}^*) + \gamma_{12} + \gamma_{21} + 3\alpha \right] y + 4\beta\rho_{10}^* + 3\alpha q_{l/0}^* = 0.
\]

If invasive rare species 2 (seed global dispersal) with very small population \((\rho_2 \approx 0)\) is introduced into the system (S15), and if \(\frac{d\rho_2}{dt} > 0\), i.e. the discriminant

\[
\omega = \beta(1 - \rho_{1}^*) - (m_2 + \gamma_{22}q_{2/2} + \gamma_{21}q_{l/2}) = \beta(1 - \rho_{1}^*) - (m_2 + \gamma_{22}x + \gamma_{21}y) > 0,
\]

then the successful invasion by species 2 (with very small population) is possible, otherwise \((\omega < 0)\) it will be extinct and excluded by resident species 1.
139 **Case II: Invasion by species 1 to a population dominated by species 2**

Similarly, we first calculate the equilibrium densities of species 2 (\( \rho^*_2 \in [0,1] \) and 

\[
q^{*}_{2/2} = \rho^{*}_{22}/\rho^{*}_1 \in [0,1] \]

with seed global dispersal by neglecting the rare invasive species 1 

\( (\rho_1 = 0, q_{1/2} = 0) \), consequently obtaining the simplified version of equations (1) and (S6)

\[
\begin{align*}
\frac{d\rho_2}{dt} &= \beta \rho_2 (1 - \rho_2) - (m_2 + \gamma_{22} q_{2/2}) \rho_2 \\
\frac{d\rho_{22}}{dt} &= 2 \beta \rho_2 \rho_{20} - 2 \rho_{22} \left( m_2 + \frac{\gamma_{22}}{z} + \frac{z-1}{z} \gamma_{22} q_{2/2} \right).
\end{align*}
\]  

(S17)

Subsequently, we derive the non-trivial equilibrium \( E^* = (\rho^*_2, q^*_2) \) by letting \( \frac{d\rho_2}{dt} = 0 \) and

\[
\frac{d\rho_{22}}{dt} = 0, \text{ i.e.,}
\]

\[
\begin{align*}
\beta (1 - \rho^*_2) &= m_2 + \gamma_{22} q^*_2 \\
\beta \rho^*_2 (1 - q^*_2) &= m_2 q^*_2 + \frac{q_{2/2}^*}{4} (\gamma_{22} + 3 \gamma_{22} q_{2/2}^*),
\end{align*}
\]

obtaining

\[
\begin{align*}
\rho^*_2 &= \frac{\beta - m_2 - \gamma_{22} q_{2/2}^*}{\beta} \\
q_{2/2}^* &= \frac{5}{2} + \frac{2 \beta}{\gamma_{22}} - \frac{2}{\gamma_{22}} \sqrt{\left( \frac{5 \gamma_{22}}{4} + \beta \right)^2 - \gamma_{22} (\beta - m_2)}.
\end{align*}
\]

As a result, \( E^* \) exists and is locally asymptotically stable if and only if \( \beta > m_2 + \gamma_{22} q^*_{2/2} \),

\[
\begin{align*}
\left( \frac{5}{4} \gamma_{22} + \beta \right)^2 &> \gamma_{22} (\beta - m_2) \quad \text{and} \quad \frac{5 \gamma_{22}}{4} + \beta > \sqrt{\left( \frac{5 \gamma_{22}}{4} + \beta \right)^2 - \gamma_{22} (\beta - m_2)}.
\end{align*}
\]
Next, combined with $\rho_1 = 0$ (thus $\rho_{10} = 0$) and $E^*=(\rho_2^*, q_{2/2}^*)$, and if we abbreviate \[ x=(\alpha+\gamma_{11})q_{1/1} \quad \text{and} \quad y=(\alpha+\gamma_{12})q_{2/1}, \] we have $q_{1/1} = x/(\alpha+\gamma_{11})$ and $q_{2/1} = y/(\alpha+\gamma_{12})$. As a consequence, we can change the equations (S9) and (S11) as

\[
\frac{dx}{dt} = \frac{\alpha}{2} \left( 1 - \frac{y}{\alpha+\gamma_{12}} \right) - \frac{x}{\alpha+\gamma_{11}} \left[ \frac{3\alpha}{2} + m_1 + \frac{\gamma_{11}}{2} - \left( \frac{\alpha - \gamma_{11}}{2} \right) \frac{x}{\alpha+\gamma_{11}} - \left( \frac{\alpha - \gamma_{12}}{2} \right) \frac{y}{\alpha+\gamma_{12}} \right]
\]

\[
\frac{dy}{dt} = \left( \beta \rho_2 + \frac{3}{4} a q_{2/0} \right) \left( 1\frac{x}{\alpha+\gamma_{11}} - \frac{y}{\alpha+\gamma_{12}} \right) - \frac{y}{\alpha+\gamma_{12}} \left[ \alpha + m_2 + \frac{\gamma_{12}}{2} + \frac{\gamma_{21}}{4} + \frac{3 \gamma_{22}}{4} q_{2/2} \right]
\]

This autonomous dynamical system has a single non-negative equilibrium $(x \in [0, \alpha + \gamma_{11}]$ and $y \in [0, \alpha + \gamma_{12}]$ and $\frac{x}{\alpha+\gamma_{11}} + \frac{y}{\alpha+\gamma_{12}} < 1$) that is stable and obtained by letting $\frac{dx}{dt} = 0$ and $\frac{dy}{dt} = 0$, so the analytical solutions of $x$ and $y$ can be obtained from

\[
\left[ \frac{\alpha}{2} \left( 1 - \frac{y}{\alpha+\gamma_{12}} \right) \right] \left[ \frac{3\alpha}{2} + m_1 + \frac{\gamma_{11}}{2} - \left( \frac{\alpha - \gamma_{11}}{2} \right) \frac{x}{\alpha+\gamma_{11}} - \left( \frac{\alpha - \gamma_{12}}{2} \right) \frac{y}{\alpha+\gamma_{12}} \right] = \left( \frac{y}{\alpha+\gamma_{12}} \right) \left[ \alpha + m_2 + \frac{\gamma_{12}}{4} + \frac{\gamma_{21}}{4} + \frac{3 \gamma_{22}}{4} q_{2/2} \right]
\]

If invasive rare species 1 (local dispersal) with very small population ($\rho_1 \approx 0$) is introduced into the system (S17), and if $\frac{d\rho_1}{dt}/\rho_1 > 0$, i.e., the discriminant ($\Delta > 0$)

\[
\Delta = \alpha \left( 1-q_{1/1}-q_{2/1} \right) - \left( m_1 + \gamma_{11} q_{1/1} + \gamma_{12} q_{2/1} \right)
\]

\[
= \alpha - m_1 - (\alpha + \gamma_{11}) q_{1/1} - (\alpha + \gamma_{12}) q_{2/1} = \alpha - m_1 - x - y > 0,
\]

then the successful invasion by species 1 (with very small population) is possible, otherwise (i.e., $\Delta < 0$) it will be extinct and excluded by resident species 2.

Finally, we summarize *Case I* and *Case II* in Table S2.
## Table S2 Invasibility analysis of PA model with two competing species

<table>
<thead>
<tr>
<th>( \Delta ) ( \omega )</th>
<th>( \Delta &gt; 0 )</th>
<th>( \Delta &lt; 0 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \omega &gt; 0 )</td>
<td>Coexistence</td>
<td>Species 2 (excluding species 1 with initial small density)</td>
</tr>
<tr>
<td>( \omega &lt; 0 )</td>
<td>Species 1 (excluding species 2 with initial small density)</td>
<td>Initial population density determining competitive outcome</td>
</tr>
</tbody>
</table>