ON CARRYING-CAPACITY CONSTRUCTION, METAPOPULATIONS AND DENSITY-DEPENDENT MORTALITY

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Abstract. We present a mathematical model for competition between species that includes variable carrying capacity within the framework of niche construction. We make use the classical Lotka-Volterra system for species competition and introduce a new variable which contains the dynamics of the constructed niche. The paper illustrates that the total available patches at equilibrium always exceeds the constructed niche at equilibrium in the absence of species.

1. Introduction. This work presents a mathematical model for competition between species [4] that includes variable carrying capacity within the framework of niche construction [6]. We center on the characterization of the local dynamics of the model and the coexistence and competitive exclusion conditions as affected by the niche construction hypothesis, specifically, by carrying capacity construction as characterized by [3].

The classic model of population dynamics that considers a feedback due to population density is the logistic equation

\[ \dot{N} = rN \left( 1 - \frac{N}{K} \right), \]

where \( r \) is the intrinsic growth rate and \( K \) the so-called carrying capacity of the environment. Basically \( K \) is the maximum density of organisms that a given site can support before entering the stage of negative growth rate that occurs obviously, when \( N > K \). In the classical model \( K \) is a fixed constant. Several models have

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addressed the effect of density-dependence on population growth both in ecological and in epidemiological contexts [e.g., [4]; [5]; [3]].

As an extension of these ideas, one can attempt to generalize this model by making the identification of environment and carrying capacity. After all, the richer the environment the higher the $K$. If we take $K = \kappa z$ where $z$ is a variable that represents niche construction (in units of density) and $\kappa$ is a positive dimensionless constant specific to a given environment, then we can establish a new level of feedback between population growth and environment due to the variability of $K$.

The effect of variable $K$ on population dynamics is well known [2; 1] but, in our case, following the work by Krakauer et al. [3] the model aims to explore the role of niche construction associated with density-dependent mortality. The simplest model based upon these ideas is the following:

\[
\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right), \\
\frac{dz}{dt} = p + \omega N - dz,
\]

where $p$ is the background recruitment rate of niche production, $d$ the niche construction clearance rate and $\omega$ is the rate of niche construction due to the presence of $N$. It is straightforward to check that the unique equilibrium of this system is

\[
z^* = \frac{p}{d} + \frac{\omega}{d} N^*, \quad N^* = \frac{\kappa p}{d - \omega \kappa}.
\]

Several observations are in order: first the niche construction clearance rate $d$ must be sufficiently large so that niche construction can reduce it by the amount $\omega \kappa$; second, the equilibrium value of the population density satisfies $N^* > p/d$ where the RHS of the inequality is the niche constructed equilibrium value in the absence of a population; thirdly, the niche construction equilibrium value $z^*$ is the weighted average of its equilibrium value in the absence of species and the equilibrium density of the species. The corresponding weight is precisely the rate $\omega$ at which $N$ creates niche. The equilibrium is asymptotically stable under certain conditions straightforward to verify. In summary we see that at equilibrium, niche construction is an affine function of population density and that density is a constant multiple of the background niche construction with a restriction that allows the system to be self-regulated. If the clearance rate of niche construction is too low, then niche construction by the resident species would push the whole system into a positive feedback cycle with ever-growing carrying capacity.

In this work we study a generalization of the previous very simple model in the context of metapopulations or, with the adequate equivalences, infectious diseases. Our system consists of a number $N$ of patches available to colonization by either of two species $I_1$ and $I_2$, the second one competitively superior to the first so as to allow coexistence [5; 3; 7]. As in the simple model, the patches either empty or occupied have density dependent life-expectancy and the niche construction is embedded into the carrying capacity of each species and may be different.

2. Model setup. Consider the following model for a metapopulation system with two species that occupy patches labeled $I_1$ and $I_2$ where the total patch population has density dependent growth and therefore, a carrying capacity $K$. The density dependent mortality function is defined as

\[
\theta(N) = N(u + rN/K),
\]
where \( N \) is the total number of patches, \( S \) is the number of available patches, \( u \) is the density-independent mortality rate, \( b \) is the natality rate and \( r = b - u \) the intrinsic growth rate. The equations are as follows

\[
\begin{align*}
\dot{S} &= bN - \beta_1 S I_1 N - \beta_2 S I_2 N - \theta(N) \frac{S}{N}, \\
\dot{I}_1 &= \beta_1 S \frac{I_1}{N} - \sigma \beta_2 I_1 \frac{I_2}{N} - \theta(N) \frac{I_1}{N} - \nu_1 I_1, \\
\dot{I}_2 &= \beta_2 S \frac{I_2}{N} + \sigma \beta_2 I_1 \frac{I_2}{N} - \theta(N) \frac{I_2}{N} - \nu_2 I_2, \\
\dot{N} &= bN - \theta(N) - \nu_1 I_1 - \nu_2 I_2.
\end{align*}
\]

The extinction rates from patches \( I_1 \) and \( I_2 \) are \( \nu_1 \) and \( \nu_2 \) respectively; \( \beta_i \) are the effective propagule production rates. The parameter \( \sigma \) is a free parameter \( 0 \leq \sigma \leq 1 \) that represents the proportional change of the colonization rate when in the presence of two species, one of which is competitively superior (\( I_2 \) in this case) to the other (\( I_1 \)). If \( \sigma = 0 \) we have the classic Lotka-Volterra competition equations as treated in Krakauer \textit{et al.} \cite{3}. Now let \( K_i \) be the carrying capacity dependent on the so-called niche construction hypothesis with

\[
K_i = \kappa_i z
\]

where \( z \), the constructed niche variable, satisfies the following differential equation

\[
\dot{z} = p + (1 - c_1) \frac{e I_1}{N} + (1 - c_2) \frac{e I_2}{N} - dz.
\]

Observe that in the absence of occupied patches of either class we have the total number of available patches given by

\[
K_i = \kappa_i \frac{p}{d}.
\]

The niche-construction parameter of species \( i \) and the efficiency of niche construction are given by \( c_i \) and \( e \) respectively. As in the reference paper (Krakauer \textit{et al.}) we have \( 0 \leq c_i \leq 1 \), and \( 0 < e \leq 1 \). With these definitions of \( K_i \) (\( i = 1 \) empty patches, \( i = 2 \) occupied by species 1, \( i = 3 \) occupied by species 2) and defining

\[
\theta_i(N) = N \left( u + \frac{rN}{\kappa_i z} \right).
\]

we obtain summing the differential equations for \( S \), \( I_1 \) and \( I_2 \)

\[
\dot{N} = rN \left( 1 - \left[ \frac{S}{\kappa_1 z} + \frac{I_1}{\kappa_2 z} + \frac{I_2}{\kappa_3 z} \right] \right) - \nu_1 I_1 - \nu_2 I_2
\]

and, furthermore,

\[
\begin{align*}
\dot{S} &= bN - \beta_1 S \frac{I_1}{N} - \beta_2 S \frac{I_2}{N} - \theta_1(N) \frac{S}{N}, \\
\dot{I}_1 &= \beta_1 S \frac{I_1}{N} - \sigma \beta_2 I_1 \frac{I_2}{N} - \theta_2(N) \frac{I_1}{N} - \nu_1 I_1, \\
\dot{I}_2 &= \beta_2 S \frac{I_2}{N} + \sigma \beta_2 I_1 \frac{I_2}{N} - \theta_3(N) \frac{I_2}{N} - \nu_2 I_2, \\
\dot{z} &= p + (1 - c_1) \frac{e I_1}{N} + (1 - c_2) \frac{e I_2}{N} - dz.
\end{align*}
\]

System 1 constitutes a metapopulation model with density-dependent mortality alternative to the Lotka-Volterra ecological model of Krakauer \textit{et al.} \cite{3}.
3. Existence of a nontrivial equilibrium point with both species present.
In this section we determine, for various cases, the necessary conditions for the existence of equilibrium points with one or two species present. For all cases we use the condition \( r = b - u > 0 \).

3.1. Case 1. This case takes \( \sigma = 0 \), \( \kappa_j = \kappa \) for all \( j \), and \( \nu_j = 0 \), that is no colonization induced extinction rate. Obviously \( N = k z \) and then we obtain the following two equations determining the existence of equilibria \( \beta_i > r + u \) provided:

\[
\begin{align*}
z &= \frac{\beta_1 I_1 + \beta_1 I_2}{\kappa (\beta_1 - (r + u))}, \\
z &= \frac{\beta_2 I_1 + \beta_2 I_2}{\kappa (\beta_2 - (r + u))}.
\end{align*}
\]

These equations imply that no equilibrium solution exist with two different species present (i.e. \( \beta_1 \neq \beta_2 \)).

3.2. Case 2. Parameter values as in Case 1 except \( \sigma \neq 0 \). In this case the system of equations is given by

\[
\begin{align*}
\beta_1 - \beta_1 \frac{I_1}{N} - (\beta_1 + \sigma \beta_2) \frac{I_2}{N} - (u + r) &= 0, \\
\beta_2 - \beta_2 (1 - \sigma) \frac{I_1}{N} - \beta_2 \frac{I_2}{N} - (u + r) &= 0, \\
p \frac{d}{d} + \omega_1 \frac{I_1}{N} + \omega_2 \frac{I_2}{N} + \frac{p}{d} &= z,
\end{align*}
\]

where \( \omega_j = (1 - c_j) e \) for all \( j \). From these we can obtain a unique solution for \( z \) and the proportion of the landscape occupied by each species, namely \( i_j^* = \frac{I_j^*}{N} \). Observe that since \( N^* = k z^* \) at equilibrium, then

\[
I_1^* = \kappa z^* i_1^*, \quad I_2^* = \kappa z^* i_2^*.
\]

3.3. Case 3. Here the parameters are as in Case 2 but now \( \kappa_j \) may be all different. Without loss of generality take \( \kappa_1 = 1 \). In this case

\[
N' = r N \left[ 1 - \frac{1}{z} \left( S + \frac{I_1}{\kappa_2} + \frac{I_2}{\kappa_3} \right) \right].
\]

Equating (2) to zero and using \( S = N - I_1 - I_2 \) then we have

\[
z = N - I_1 \left( 1 + \frac{1}{\kappa_2} \right) - I_2 \left( 1 + \frac{1}{\kappa_3} \right).
\]

Observe that since \( z \geq 0 \) then necessarily (3) implies \( N \geq I_1 + I_2 \) which is consistent with the biological meaning of the equations.

Now, for the equilibrium solutions, setting again \( S = N - I_1 - I_2 \), we have

\[
\begin{align*}
\frac{\beta_1}{N} (N - I_1 - I_2) - \sigma \beta_2 \frac{I_2}{N} - \left( u + \frac{r N}{\kappa_2^2 z} \right) &= 0, \\
\frac{\beta_2}{N} (N - I_1 - I_2) + \sigma \beta_2 \frac{I_2}{N} - \left( u + \frac{r N}{\kappa_3^2 z} \right) &= 0,
\end{align*}
\]

and

\[
p \frac{d}{d} + \omega_1 \frac{I_1}{N} + \omega_2 \frac{I_2}{N} - z = 0.
\]

Equating (3) and the last equation, we conclude that \( N^* > p/d \), that is, the number of available patches is always larger than the total density of constructed niche.
Using (3) and (6), we solve for \( I_j \) in terms of \( N \) and \( z \) obtaining

\[
I_1 = \frac{a_1 N - a_2 z - a_3 z N}{a},
\]

\[
I_2 = \frac{b_3 z N + b_2 z - b_1 N}{a},
\]

where \( a = \kappa_3 \omega_2 (1 + \kappa_2) - \kappa_2 \omega_1 (1 + \kappa_3) \) and

\[
a_1 = \kappa_2 (p(1 + \kappa_3) + \kappa_3 \omega_2),
\]

\[
a_2 = \kappa_2 \kappa_3 \omega_2,
\]

\[
a_3 = d \kappa_2 (1 + \kappa_3),
\]

\[
b_1 = \kappa_3 (p(1 + \kappa_2) + \kappa_2 \omega_1),
\]

\[
b_2 = \kappa_3 \kappa_2 \omega_1,
\]

\[
b_3 = d \kappa_3 (1 + \kappa_2).
\]

These two equations together with (4) and (5) give the non-trivial endemic equilibrium points of the system. This set of equations do not have an explicit analytic solution, however, some information can be extracted from them regarding the roles of \( z \) and \( N \) for their existence. For the moment assume \( a > 0 \). Using \( z \) as a parameter we see that, in order for \( I_1 \) to be biologically feasible it is necessary that

\[
z < \frac{a_1 N - a_2 z - a_3 z N}{a_2 + a_3 N} = \frac{(p + \kappa_3 (p + \omega_2)) N}{\kappa_3 \omega_2 + (1 + \kappa_3) d N}.
\]

Similarly, if we want \( I_2 > 0 \) we require

\[
z > \frac{b_1 N - b_2 z - b_3 z N}{b_2 + b_3 N} = \frac{(p + \kappa_2 (p + \omega_1)) N}{\kappa_2 \omega_1 + (1 + \kappa_2) d N}.
\]

For the case \( a < 0 \) we have

\[
z > \frac{a_1 N - a_2 z - a_3 z N}{a_2 + a_3 N} = \frac{(p + \kappa_3 (p + \omega_2)) N}{\kappa_3 \omega_2 + (1 + \kappa_3) d N},
\]

and

\[
z < \frac{b_1 N - b_2 z - b_3 z N}{b_2 + b_3 N} = \frac{(p + \kappa_2 (p + \omega_1)) N}{\kappa_2 \omega_1 + (1 + \kappa_2) d N}
\]

for \( I_1 > 0 \) and \( I_2 > 0 \) respectively. In Figure (2) we show the coexistence and no coexistence regions according to the above inequalities for the case \( a > 0 \). Observe that the condition \( a > 0 \) is equivalent to require

\[
Q = \frac{\kappa_3 \omega_2 (1 + \kappa_2)}{\kappa_2 \omega_1 (1 + \kappa_3)} > 1.
\]

This expression is plotted in Figure (1). Observe the effect on \( Q \) of the feedback for niche construction illustrated in Figure (2) for \( Q > 1 \) and Figure (6) when \( Q < 1 \).

We show the graphs of a metapopulation model with density-dependent mortality, where we incorporate patch dynamics into the niche construction framework. The following scenarios (Figures 3, 4, 5) represent when the balance between the constructed niche by each species and the parameters \( \omega_i, i = 1, 2 \) namely \( Q \), is greater than one.

Figure 6 illustrates the possible scenarios for coexistence and extinction for \( Q < 1 \), i.e. the relation between the niche construction capacities of each species and
Figure 1. Qualitative behavior of $Q$ as a function of $(\kappa_2, \kappa_3) \in [0, 5] \times [0, 5]$ for a) $\omega_2/\omega_1 > 1$, b) $\omega_2/\omega_1 < 1$. Note the narrowing of the range where $Q > 1$ when going from a) to b).

Figure 2. Possible scenarios for coexistence and extinction regions when $Q > 1$. These are regions where an equilibrium point is feasible. The conditions that define them are necessary but not sufficient for their existence. Region e) is dashed to indicate that it is not feasible, given that not exist one or two species.

their contribution to the overall constructed niche is less than 1, (see Figures 7, 8, 9).
Figure 3. Coexistence of two species for $Q > 1$. This scenario corresponds to the region $b)$ of the Fig. 2. The parameters are $\kappa_1 = 1$, $\kappa_2 = 3.5$, $\kappa_3 = 1.4$, $b = 0.2$, $\beta_1 = 3.4$, $\beta_2 = 1.6$ $\sigma = 0.1$, $p = 0.5$, $d = 1$, $e = 1$, $u = 0.18$, $c_1 = 0.9$, $c_2 = 0.2$

Figure 4. Colonization by the specie $I_1$ for $Q > 1$. This scenario corresponds to the region $a)$ of the Fig. 2. The parameters are $\kappa_1 = \kappa_2 = 1$, $\kappa_3 = 1.4$, $b = 0.8$, $\beta_1 = 3.8$, $\beta_2 = 0.5$ $\sigma = 0.5$, $p = 1$, $d = 1$, $e = 1$, $u = 0.4$, $c_1 = 0.5$, $c_2 = 0.5$

Figure 5. Colonization by the specie $I_2$ for $Q > 1$. This scenario corresponds to the region $c)$ of the Fig. 2. The parameters are $\kappa_1 = \kappa_2 = 1$, $\kappa_3 = 1.5$, $b = 0.8$, $\beta_1 = 3.8$, $\beta_2 = 3.4$ $\sigma = 0.5$, $p = 0.1$, $d = 1$, $e = 1$, $u = 0.4$, $c_1 = 0.5$, $c_2 = 0.5$
Figure 6. Possible scenarios for coexistence and extinction regions when $Q < 1$. These are regions where an equilibrium point is feasible. The conditions that define them are necessary but not sufficient for their existence. Region e) is dashed to indicate that it is not feasible, given that not exist one or two species.

Figure 7. Colonization by the specie $I_1$ for $Q < 1$. This scenario corresponds to the region c) of the Fig. 6. The parameters are $\kappa_1 = 1$, $\kappa_2 = 1.0$, $\kappa_3 = 0.5$, $b = 0.8$, $\beta_1 = 3.8$, $\beta_2 = 0.5$ $\sigma = 0.5$, $p = 0.1$, $d = 1$, $e = 1$, $u = 0.4$, $c_1 = 0.9$, $c_2 = 0.9$

4. Local stability of the non-colonized state. We will refer to the non-colonized state as the NCS equilibrium. So looking for solutions with $I_1 = I_2 = 0$, we have

$$N' = rN \left( 1 - \frac{N}{NZ} \right)$$

$$z' = p - dz$$
Figure 8. Colonization by the specie $I_1$ for $Q < 1$. This scenario corresponds to the region $c)$ of the Fig. 6. The parameters are $\kappa_1 = \kappa_2 = 1$, $\kappa_3 = 0.5$, $b = 0.8$, $\beta_1 = 3.8$, $\beta_2 = 0.5$ $\sigma = 0.5$, $p = 1$, $d = 1$, $e = 1$, $u = 0.4$, $c_1 = 0.5$, $c_2 = 0.5$

Figure 9. Colonization by the specie $I_2$ for $Q < 1$. This scenario corresponds to the region $a)$ of the Fig. 6. The parameters are $\kappa_1 = \kappa_2 = 1$, $\kappa_3 = 1.1$, $b = 0.8$, $\beta_1 = 3.8$, $\beta_2 = 3.4$ $\sigma = 0.5$, $p = 1$, $d = 1$, $e = 1$, $u = 0.4$, $c_1 = 0.5$, $c_2 = 0.5$

The non-colonized equilibrium point, namely DFE is given by
\[(N^*, S^*, I_1^*, I_2^*, z^*) = (\kappa_1 \frac{P}{d}, \kappa_1 \frac{P}{d}, 0, 0, \frac{P}{d})\],
the Jacobian matrix evaluated at the DFE, has the eigenvalues
\[
\lambda_1 = -d \\
\lambda_2 = -\frac{\kappa_1 r + \kappa_2 (u - \beta_1)}{\kappa_2} \\
\lambda_3 = -\frac{\kappa_1 r + \kappa_3 (u - \beta_2)}{\kappa_3}
\]
and
\[
\lambda_{4,5} = \frac{(r + u)}{2} \pm \frac{\sqrt{\Delta}}{2}
\]
\[
\Delta = -(4br + 3r^2 - 2ru - u^2).
\]
For real roots we need
\[
4br + 3r^2 - 2ru - u^2 < 0
\]
since $r = b - u$ we equivalently require
\[ q(b, u) = -7b^2 + 12bu - 4u^2 > 0, \]
taking the above as a function of $u$
\[ b = \frac{6 + 2\sqrt{2}}{7} u \]
we have $q(b, u) = 0$. To satisfy the condition $q(b, u) = -7b^2 + 12bu - 4u^2 > 0$, we need to be in the shaded area (see Figure 10).

This is the region where real roots exist, to the left of the line $l(u)$ we have complex eigenvalues. For complex eigenvalues the real part is always positive.
\[ \text{Re}(\lambda_{4,5}) = \frac{r + u}{2} = \frac{b}{2}. \]

The last two eigenvalues may be complex conjugate (if $\Delta < 0$) with positive real part. We conclude that the NCS equilibrium is always unstable.

5. **Existence of boundary equilibria and their stability.** Boundary equilibria do exist and occur when either $I_1$ or $I_2$ equals zero. Here we show the existence of such points. Consider $I_1 > 0$ but $I_2 = 0$, $i \neq j$. From the equation for $I_i$ we obtain the relation
\[ \beta_i S - \theta_i(N) = 0 \]
which after substituting in the equation for $S$ gives that
\[ \beta_i \left( \frac{S}{N} \right)^2 - \beta_i \frac{S}{N} + b = 0 \]
rendering
\[ \left( \frac{S}{N} \right)^* = \frac{1}{2} \pm \sqrt{\frac{1 - 4b/\beta_i}{2}} < 1. \]
Since we seek real roots, then $1 > 1 - 4b/\beta_i > 0$ and thus we can have exactly two equilibrium points with $I_j = 0$. The condition $1 - 4b/\beta_i > 0$ implies that $\beta_i > 4b$ or, in other words, that the competition coefficient $\beta_i$ has to be significantly larger than the patch production rate. In summary, using the fact that $1 = S/N + I_1/N + I_2/N$ we can conclude that we have at most four boundary equilibria, at most two for $I_1 > 0$, $I_2 = 0$ and at most two for $I_1 = 0$ and $I_2 > 0$. 

![Figure 10. Eigenvalues region for non-colonized state.](image)
5.1. **The basic reproduction number.** The next-generation matrix for this system is

\[
N = \begin{pmatrix}
(b - \frac{r}{\kappa_1}) u & -u \left( \frac{r}{\kappa_2} + \nu_1 \right) & -u \left( \frac{r}{\kappa_3} + \nu_2 \right) \\
\frac{0}{\beta_1} & \frac{0}{\beta_1} & \frac{0}{\beta_2} \\
\frac{0}{\beta_2} & \frac{0}{\beta_2} & \frac{0}{\beta_2} \\
-\frac{qd}{p^2} & \left(\frac{1-c_1}{c_1} \right) & \left(\frac{1-c_2}{c_2} \right)
\end{pmatrix},
\]

and thus, the basic reproduction number is

\[
R_0 = \max \left\{ \frac{\beta_1}{u + \frac{r}{\kappa_2} + \nu_1}, \frac{\beta_2}{u + \frac{r}{\kappa_3} + \nu_2} \right\},
\]

implying a trade-off between growth \((r)\) and dispersal and competition \((\beta_i)\) that may result in poor or high invasion ability as measured by the reproduction number. Moreover, niche construction has no role in this trade-off (that occurs at the start of the invasion process).

6. **Conclusions.** The inclusion of explicit dynamics on the carrying capacity through the hypothesis of niche construction as we do it in this paper is a generalization of the pioneering work of [3]. These authors consider the classical Lotka-Volterra system for species competition and introduce a new variable \(z\) which contains the dynamics of the constructed niche. In our work we use instead a metapopulation approach where the total number of available patches is subdivided into three classes: empty patches and colonized patches for either of the two species involved in the interaction. Moreover, we impose a density dependent dynamics on the total patch population incorporating therefore patch dynamics into the niche construction framework.

Under the assumption of a constant niche generation rate independent of population dynamics (following the work of Krakauer et al. referred to above), we find that the total available patches at equilibrium always exceeds the constructed niche at equilibrium in the absence of species, i.e., \(N^* > p/d\). Also, one of our main results is that the conditions for coexistence or competitive exclusion of the species involved depends on \(z\) the amount of constructed niche. We found a threshold parameter \(Q\) that distinguishes cases (illustrated in Figures 2 and 6). The expression of \(Q\) is

\[
Q = \frac{\kappa_3 \omega_2 (1 + \kappa_2)}{\kappa_2 \omega_1 (1 + \kappa_3)},
\]

and represents a balance between the constructed niche by each species and the parameters \(\omega_i = (1-c_i)e\) which express the contribution of each species to the total constructed niche. This parameter expresses a rather delicate trade-off between the niche construction capacities of each species, given by \(\kappa_i\) and their contribution to the overall constructed niche \(\omega_i\) (see Figure 1). For example, assuming \(\omega_1 = \omega_2\), \(Q\) will be above or below 0 depending upon the values of the niche construction efficacies \(k_i\). Also note from Figures 2 and 6 that there exists an interval of values of \(z\), the constructed niche, that prevent the coexistence of the species and also that competitive exclusions occurs either for lower or higher values of \(z\); the middle ones having both species present. The region labeled \(e)\) in each of these Figures is not feasible since the local stability results of section 4 guarantee that extinction of both species is not feasible in this model. It is important to note that the diagrams
presented in Figures 2 and 6 represent only necessary but not sufficient conditions for competitive exclusion or coexistence.

As noted at the end of the previous section the expressions for the basic reproduction numbers of each species imply a trade-off between growth \((r)\) and dispersal and competition \((\beta_i)\) that may result in poor or high invasion ability as measured by the reproduction number where niche construction has no role in this trade-off (that occurs at the start of the invasion process).

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