On the Principle of Competitive Exclusion in Metapopulation Models

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Abstract: In this paper we present and analyse a simple two populations model with migrations among two different environments. The populations interact by competing for resources. Equilibria are investigated. A proof for the boundedness of the populations is provided. A kind of competitive exclusion principle for metapopulation systems is obtained. At the same time we show that the competitive exclusion principle at the local patch level may be prevented to hold by the migration phenomenon, i.e. two competing populations may coexist, provided that only one of them is allowed to freely move or that migrations for both occur just in one direction.

Keywords: populations, competition, migrations, patches, competitive exclusion

1 Introduction

In this paper we consider a minimal metapopulation model with two competing populations. It consists of two different environments among which migrations are allowed.

As migrations do occur indeed in nature, [6], the metapopulation tool has been proposed to study populations living in fragmented habitats, [16, 25]. One of its most important results is the fact that a population can survive at the global level, while becoming locally extinct, [9, 10, 11, 15, 20, 21, 31, 32]. An earlier, related concept, is the one of population assembly, [14], to account for heterogeneous environments containing distinct community compositions, providing insights into issues such as biodiversity and conservation. As a result, sequential slow invasion and extinction shape successive species mixes into a persistent conguration, impenetrable by other species, [17], while, with faster invasions, communities change their compositions and each species has a chance to survive.

A speciﬁc example in nature for our competition situation for instance is provided by Strix occidentalis, which competes with, and often succumbs to, the larger great horned owl, Bubo virginianus. The two in fact compete for resources, since they share several prey, [12]. If the environment in which they live gets fragmented, the competition cannot be analysed classically, and the metapopulation concept becomes essential to describe the natural interactions. This paper attempts the development of such an issue in this framework. Note that another recent contribution in the context of patchy environments considers also a transmissible disease affecting the populations, thereby introducing the concept of metaecoeplidemic models, [30].

An interesting competition metapopulation model with immediate patch occupancy by the strongest population and incorporating patch dynamics has been proposed and investigated in [19]. Patches are created and destroyed dynamically at different rates. A completely different approach is instead taken for instance in [3], where different competition models, including facilitation, inhibition and tolerance, are investigated by means of cellular automata.

The model we study bears close resemblance with a former model recently appeared in the literature, [23]. However, there are two basic distinctions, in the formulation and in the analysis. As for the model formulation, in [23] the populations are assumed to be similar species competing for an implicit resource. Thus there is a unique carrying capacity for both of them in each patch in which they reside. Furthermore their reproduction rates are the same. We remove both these assumptions, by allowing in each patch different carrying capacities for each population, as well different reproduction rates. Methodologically, the approach used

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in [23] uses the aggregation method, thereby reducing the system of four differential equations to a two-dimensional one, by assuming that migrations occur at a different, faster, timescale than the life processes. This may or may not be the case in real life situations. In fact, referring to the herbivores inhabiting the African savannas, this movement occurs throughout the lifetime, while intermingling for them does not constitute a "social" problem, other than the standard intraspecic competition for the resources, [26, 27]. The herbivores wander in search of new pastures, and the predators follow them. This behavior might instead also be inuenced by the presence of predators in the surrounding areas, [29]. Thus the structure of African herbivores and the savanna ecosystems may very well be in fact shaped by predators' behavior.

In the current classical literature in this context, it is commonly assumed that migrations of competing populations in a patchy environment lead to the situation in which the superior competitor replaces the inferior one. In addition, it is allowed for an inferior competitor to invade an empty patch, but the invasion is generally prevented by the presence of a superior competitor in the patch, [28]. Based on this setting, models investigating the proportions of patches occupied by the superior and inferior competitors have been set up, [13]. The effect of patch removal in this context is analysed in [22], coexistence is considered in [8, 2, 24, 1], and similarly let \( n_{ij} \) be the migration rate from \( j \) to \( i \) for the population \( Q_i \).

The resulting model has the following form:

\[
P_1 = r_1P_1 \left(1 - \frac{P_1}{K_1}\right) - a_1P_1Q_1 - m_{21}P_1 + m_{12}P_2 \quad (1)
\]

\[
Q_1 = s_1Q_1 \left(1 - \frac{Q_1}{H_1}\right) - b_1Q_1P_1 - n_{21}Q_1 + n_{12}Q_2 \equiv F_1(P_1, P_2, Q_1, Q_2),
\]

\[
P_2 = r_2P_2 \left(1 - \frac{P_2}{K_2}\right) - a_2P_2Q_2 - m_{12}P_2 + m_{21}P_1 \equiv F_2(P_1, P_2, Q_1, Q_2),
\]

\[
Q_2 = s_2Q_2 \left(1 - \frac{Q_2}{H_2}\right) - b_2Q_2P_2 - n_{12}Q_2 + n_{21}Q_1 \equiv F_3(P_1, P_2, Q_1, Q_2).
\]

Note that a very similar model has been presented in [23]. But (1) is more general, in that it allows different carrying capacities in the two patches for the two populations, while in [23] only one, \( K \), is used, for both environments and populations. Further, the environments do not affect the growth rates of each individual population, while here we allow different reproduction rates for the same population in each different patch. Also, competition rates in [23] are the same in both patches, while here they are environment-dependent. The analysis technique used in [23] also makes the assumption that there are two time scales in the model, the fast dynamics being represented by migrations and the slow one by the demographics, reproduction and competition. Based on this assumption, the system is reduced to a planar one, by rst calculating the equilibria of the fast part of the system using the aggregation method, and then the aggregated two-population slow part is analysed.

Here we thus remove the assumption of a fast migration, compared with the longer lifetime population dynamics because for the large herbivores the migration process is a lifelong task, being always in search of new
Table 1: All the possible equilibria of the three ecosystems: Y means that the equilibrium is possible. We indicated also the unconditional instability, and with a star the instability verified just numerically. Critical means that stability is achieved only under very restrictive parameter conditions, i.e. in general the corresponding point must be considered unstable. P column is for the model in which only P migrates, 1→2 for unidirectional migrations model, full for the complete model; unst means unstable equilibrium, crit denotes critical equilibrium.

| P   | P1 | Q1 | P2 | Q2 | 1→2 | full |
|-----|----|----|----|----|------|------|
| E1  | 0  | 0  | 0  | 0  | Y (unst) | Y (unst) |
| E2  | 0  | 0  | 0  | +  | Y (unst) | Y (crit) |
| E3  | 0  | 0  | 0  | +  | Y (unst) | Y (crit) |
| E4  | 0  | 0  | 0  | 0  | Y (unst) | Y (unst) |
| E5  | +  | 0  | 0  | 0  | Y (crit) | Y (crit) |
| E6  | +  | 0  | 0  | 0  | Y (crit) | Y (crit) |
| E7  | +  | 0  | 0  | +  | Y (unst) | Y (crit) |
| E8  | +  | 0  | 0  | +  | Y (unst) | Y (unst) |
| E9  | 0  | +  | 0  | 0  | Y (unst) | Y (unst) |
| E10 | 0  | +  | 0  | 0  | Y (unst) | Y (unst) |
| E11 | 0  | +  | 0  | +  | Y (crit) | Y (crit) |
| E12 | 0  | +  | 0  | +  | Y (crit) | Y (crit) |
| E13 | +  | +  | 0  | 0  | Y (crit) | Y (crit) |
| E14 | +  | +  | 0  | 0  | Y (crit) | Y (crit) |
| E15 | +  | +  | 0  | +  | Y (crit) | Y (crit) |
| E16 | +  | +  | 0  | +  | Y (crit) | Y (crit) |

where P, and Q, denote the generic equilibrium point and

\[
J_{11} = r_1 \left( 1 - \frac{P_1}{K_1} \right) - a_1 P_1 + s_1 Q_1 \left( 1 - \frac{Q_1}{H_1} \right) - b_1 Q_1 P_1 \\
J_{22} = s_1 \left( 1 - \frac{Q_1}{H_1} \right) - b_1 P_1 - n_{21} \\
J_{33} = r_2 \left( 1 - \frac{P_2}{K_2} \right) - a_2 Q_2 - m_{12} \\
J_{44} = s_2 \left( 1 - \frac{Q_2}{H_2} \right) - b_2 P_2 - n_{12}.
\]

2.1 Boundedness of the trajectories

We will now show that the solutions of (1) are always bounded. We shall explain the proof of this assertion for the complete model, but the same method can be used on each particular case, with obvious modifications.

Let us set \( \phi = P_1 + Q_1 + P_2 + Q_2 \). Boundedness of \( \phi \) implies boundedness for all the populations, since they have to be non-negative. Adding up the system equations, we obtain a differential equation for \( \phi \), the right hand side of which can be bounded from above as follows

\[
\phi = r_1 P_1 \left( 1 - \frac{P_1}{K_1} \right) - a_1 P_1 Q_1 + s_1 Q_1 \left( 1 - \frac{Q_1}{H_1} \right) - b_1 Q_1 P_1 \\
+ r_2 P_2 \left( 1 - \frac{P_2}{K_2} \right) - a_2 P_2 Q_2 + s_2 Q_2 \left( 1 - \frac{Q_2}{H_2} \right) - b_2 P_2 Q_2 \\
\leq r_1 P_1 \left( 1 - \frac{P_1}{K_1} \right) + s_1 Q_1 \left( 1 - \frac{Q_1}{H_1} \right) \\
+ r_2 P_2 \left( 1 - \frac{P_2}{K_2} \right) + s_2 Q_2 \left( 1 - \frac{Q_2}{H_2} \right) \\
= r_1 P_1 \frac{r_1}{K_1} + s_1 Q_1 \frac{s_1}{H_1} + r_2 P_2 \frac{r_2}{K_2} + s_2 Q_2 \frac{s_2}{H_2} \\
+ s_2 Q_2 - \frac{s_2}{H_2} Q_2^2.
\]

Let

\[
\mu_i = \frac{v K_i}{r_i}, \quad \mu_2 = \frac{v H_i}{r_1}, \quad \mu_3 = \frac{v K_i}{r_2}, \quad \mu_4 = \frac{v H_i}{s_2}.
\]

Substituting in (3) we get

\[
\phi \leq v P_1 - \frac{P_1^2}{\mu_1} + v Q_1 - \frac{Q_1^2}{\mu_2} + v P_2 - \frac{P_2^2}{\mu_3} + v Q_2 - \frac{Q_2^2}{\mu_4} + v P_1 + v Q_1 + v P_2 + v Q_2 - \frac{P_1^2}{\mu_1} - \frac{Q_1^2}{\mu_2} - \frac{P_2^2}{\mu_3} - \frac{Q_2^2}{\mu_4}
\]

\[
= v \left( P_1 + Q_1 + P_2 + Q_2 - \frac{P_1^2}{\mu_1} - \frac{Q_1^2}{\mu_2} - \frac{P_2^2}{\mu_3} - \frac{Q_2^2}{\mu_4} \right).
\]

If we set

\[
\mu_+ = \max_i \{ \mu_i \}, \quad \mu_- = \min_i \{ \mu_i \}, \quad \tau = \frac{\mu_3}{4 \mu_+^3}
\]
we nd
\[ \phi \leq v \left( P_1 + Q_1 + P_2 + Q_2 - \frac{\mu^3}{\mu^2} (P_1^2 + Q_1^2 + P_2^2 + Q_2^2) \right) \]
\[ \leq v \left( P_1 + Q_1 + P_2 + Q_2 - \frac{\mu^3}{4\mu^2} (P_1 + Q_1 + P_2 + Q_2)^2 \right) \]
\[ = v\phi \left( 1 - \frac{\phi}{\tau} \right). \]

Let us now set
\[ P_1(0) + Q_1(0) + P_2(0) + Q_2(0) = \phi(0) = u_0 \]
and let u be the solution of the Cauchy problem
\[ u(t) = tv(t) \left( 1 - \frac{u(t)}{\tau} \right), \quad u(0) = u_0. \]

By means of the generalized Grönwall inequality we have that \( \phi(t) \leq u(t) \) for all \( t > 0 \), and so
\[ \limsup_{t \to +\infty} \phi(t) \leq \limsup_{t \to +\infty} u(t) = \tau < +\infty. \]
This implies at once that \( \phi \) is bounded, and thus the boundedness of the system's populations as desired.

Observe that the boundedness result obtained here for this minimal model is easily generalized to meta-populations living in \( n \) patches.

3 One population unable to migrate

Here we assume that the Q population cannot migrate between the two environments. This may be due to the fact that it is weaker, or that there are natural obstacles that prevent it from reaching the other environment, while these obstacles instead can be overcome by the population \( P \). Thus each subpopulation \( Q_1 \) and \( Q_2 \) is segregated in its own patch. This assumption corresponds therefore to setting \( m_{ij} = 0 \) into (1). In this case we will denote the system's equilibria by \( \hat{E}_k \), with \( k = 1, \ldots, 16 \). It is easy to show that equilibria \( \hat{E}_2, \hat{E}_4, \hat{E}_{10}, \hat{E}_{12} \) do not satisfy the rst equilibrium equation, and \( \hat{E}_5, \hat{E}_7, \hat{E}_{13}, \hat{E}_{15} \) do not satisfy the third one, so that all these points are excluded from our analysis since they are unfeasible.

At the origin, \( \hat{E}_1 \), the Jacobian (2) has the eigenvalues
\[ \lambda_\pm = \frac{1}{2}(m_{12} + m_{21} - r_1 - r_2) \pm \frac{\sqrt{\Delta}}{2}, \]
\[ \Delta = (m_{12} + m_{21} - r_1 - r_2)^2 - 4(m_{12}r_1 - m_{21}r_2) \]
and \( s_1 > 0, s_2 > 0 \), from which its instability follows.

The point \( \hat{E}_3 = (0,0,0,H_2) \) is unconditionally feasible, but the eigenvalues of (2) evaluated at \( \hat{E}_3 \) turn out to be
\[ \lambda_\pm = \frac{1}{2}(-a_1H_1 - m_{12} - m_{21} + r_1 + r_2) \pm \frac{\sqrt{\Delta}}{2}, \]
\[ \Delta = (a_1H_1 + m_{12} + m_{21} - r_1 - r_2)^2 - 4(a_1H_1m_{12} - m_{21}r_1 - m_{12}r_2 + r_1r_2) \]

together with \( -s_2 < 0, s_1 > 0 \), so that also \( \hat{E}_3 \) is unconditionally unstable.

The point \( \hat{E}_{11} = (0,H_1,0,H_2) \) is always feasible. Two eigenvalues for (2) are easily found, \( -s_1 < 0, -s_2 < 0 \). The other ones come from a quadratic equation, for which the Routh-Hurwitz conditions reduce to
\[ r_1r_2 < a_1H_1 + a_2H_2 + m_{12} + m_{21}, \]
\[ r_1r_2 + m_{12}a_1H_1 + m_{21}a_2H_2 + a_1a_2H_1H_2 \]
\[ > r_1(m_{12} + a_2H_2) + r_2(m_{21} + a_1H_1). \]

For parameter values satisfying these conditions then, \( \hat{E}_{11} \) is stable.

Equilibrium \( \hat{E}_9 = (0,H_1,0,0) \) is always feasible, and the Jacobian (2) has eigenvalues
\[ \lambda_\pm = \frac{1}{2}(-a_1H_1 - m_{12} - m_{21} + r_1 + r_2) \pm \frac{\sqrt{\Delta}}{2}, \]
\[ \Delta = (a_1H_1 + m_{12} + m_{21} - r_1 - r_2)^2 - 4(a_1H_1m_{12} - m_{21}r_1 - m_{12}r_2 + r_1r_2) \]
again with \( -s_1 < 0, s_2 > 0 \) so that in view of the positivity of the last eigenvalue, \( \hat{E}_9 \) is always unstable.

Existence for the equilibrium \( \hat{E}_6 \) can be established as an intersection of curves in the \( P_1 - P_2 \) phase plane. The equations that define them describe the following two convex parabolaes
\[ \Pi_1: \quad P_2(P_1) = \frac{1}{m_{12}} \left[ r_1P_1(1 - \frac{P_1}{K_1}) - m_{21}P_1 \right], \]
\[ \Pi_2: \quad P_1(P_2) = \frac{1}{m_{21}} \left[ r_2P_2(1 - \frac{P_2}{K_2}) - m_{12}P_2 \right]. \]
Both cross the coordinate axes at the origin and at another point, namely
\[ X = \left( \frac{1}{r_1}(m_{21}K_1), 0 \right), \quad W = \left( \frac{1}{r_2}(r_2 - m_{12}K_2) \right) \]
respectively for \( \Pi_1 \) and for \( \Pi_2 \). Now by drawing these curves it is easily seen that they always intersect in the rst quadrant, independently of the position of these points, except when both have negative coordinates. The latter case need to be scrutinized more closely. To ensure a feasible intersection, we need to look at the parabolaes slopes at the origin. Thus, the feasible intersection exists if \( \Pi_1(0)[\Pi_2(0)]^{-1} < 1 \) or, explicitly when
\[ m_{12}m_{21} > (m_{21} - r_1)(m_{12} - r_2). \]
However, coupling this condition with the negativity of the coordinates of the above points \( X \) and \( W \), intersections of the parabolaes with the axes, the condition for the feasibility of \( \hat{E}_6 \) becomes simply
\[ r_1 < m_{21}, \quad r_2 < m_{12}, \]
which is exactly the assumption that the coordinates of the points \( X \) and \( W \) be negative. Hence it is automatically
satisfied. Further, in the particular case in which one or both such points coalesce into the origin, i.e. for either \( r_1 = m_{12} \) or \( r_2 = m_{12} \), it is easily seen that the corresponding parabola is tangent to the origin and a feasible \( \hat{E}_6 \) always exists. In conclusion, the equilibrium \( \hat{E}_6 \) is always feasible.

By using the Routh-Hurwitz criterion we can implicitly obtain the stability conditions as

\[
\begin{align*}
  s_2 &< b_2 P_2, \quad s_1 < b_1 P_1, \\
  r_1 \left( 1 - \frac{2}{K_1} P_1 \right) + r_2 \left( 1 - \frac{2}{K_2} P_2 \right) &< m_{12} + m_{21}, \\
  \left[ r_1 \left( 1 - \frac{2}{K_1} P_1 \right) - m_{21} \right] \left[ r_2 \left( 1 - \frac{2}{K_2} P_2 \right) - m_{12} \right] &> m_{12} m_{21}.
\end{align*}
\]

Numerical simulations reveal that the stability conditions are a nonempty set, we obtain \( \hat{E}_6 = (119.6503, 0, 167.4318, 0) \) for the parameter values \( r_1 = 90.5792, \quad r_2 = 97.0593, \quad s_1 = 3.5712, \quad s_2 = 3.1833, \quad K_1 = 119.0779, \quad K_2 = 167.9703, \quad H_1 = 112.7548, \quad H_2 = 212.7141, \quad a_1 = 41.5414, \quad a_2 = 2.6975, \quad b_1 = 39.7142, \quad b_2 = 4.1911, \quad m_{12} = 0.9619, \quad m_{21} = 0.9106, \quad n_{12} = 0, \quad n_{21} = 0.

For the equilibrium point \( \hat{E}_8 \) we can denote two parabola in the \( P_1 - Q_2 \) plane by solving the equilibrium equation for \( P_2 \):

\[
\begin{align*}
  \hat{P}_1 & = (r_2 P_1)(b_2 b_1 m_{12}^2) P_1 \left( r_1 - m_{21} \right) P_1 + H_2, \quad (6) \\
  \hat{P}_2 & = P_2 \left( \frac{b_2 b_1 m_{12} + 2 H_2 K_2}{b_2 K_2} \right) \left( r_2 s_2 - a_2 b_2 H_2 K_2 \right) Q_2^2 + \left( r_2 b_2 H_2 K_2 - 2 r_2 s_2 H_2 + a_2 b_2 H_2 K_2 - m_{12} b_2 H_2 K_2 \right) Q_2 + \left( r_2 s_2 H_2 - r_2 b_2 H_2 K_2 + m_{12} b_2 H_2 K_2 \right) \].
\]

The rst parabola intersects the \( Q_2 \) axis at the point \((0, H_2)\), it always has two real roots, one of which is positive and the other negative, and has the vertex with abscissa \( V = \frac{2}{b_2 H_2} (r_1 - m_{21}) \). The second parabola intersects the \( Q_2 \) axis at the points \( R_1 \equiv \left( 0, \frac{b_2 H_2 K_2 r_2 - H_2 r_2 s_2 + b_2 H_2 K_2 m_{12}}{a_2 b_2 H_2 K_2 - r_2 s_2} \right), \quad R_2 \equiv (0, H_2).

Given that the two parabola always have one intersection on the boundary of the rst quadrant, we can formulate a certain number of conditions ensuring their intersection in the interior of the rst quadrant. These conditions arise from the abscissa of the vertex of \( \hat{P}_1 \), of the leading coefficient of \( \hat{P}_2 \) and by the relative positions of the roots of \( \hat{P}_2 \). By denoting as mentioned by \( V \) the abscissa of vertex of \( \hat{P}_1 \), by \( L \) the leading coefficient of \( \hat{P}_2 \) and by \( R \) the ordinate of \( R_1 \), we have explicitly 8 sets of conditions:

1. \( V > 0, \quad L > 0, \quad R > H_2 \): the feasibility condition reduces just to the intersection between \( \hat{P}_2 \) and the \( P_1 \) axis being larger than the positive root of \( \hat{P}_1 \). Letting

\[
Z = b_2^2 K_2 m_{21} (b_2 K_2 (m_{12} r_1 + (m_{21} - r_1) r_2) + (r_1 - m_{21}) r_2 s_2),
\]

explicitly we have

\[
r_1 > m_{21}, \quad a_2 b_2 H_2 K_2 < r_2 s_2, \quad K_1 < \frac{r_2 s_2 (b_2 K_2 (m_{12} - r_2) + r_2 s_2)^2}{Z},
\]

together with either \( m_{12} \geq r_2 \) or

\[
a_2 H_2 + m_{12} \geq r_2 > m_{12}, \quad K_2 < \frac{r_2 s_2}{b_2 (-m_{12} + r_2)}.
\]

2. \( V > 0, \quad L > 0, \quad R < H_2 \): the feasibility condition is that the slope of \( \hat{P}_2 \) at the point \((0, H_2)\) be smaller than that of \( \hat{P}_1 \) at the same point. But the value of the population \( P_2 \) in this case would be negative, thus this condition is unfeasible;

3. \( V > 0, \quad L < 0, \quad R > H_2 \): the feasibility condition requires the slope of \( \hat{P}_2 \) at the point \((0, H_2)\) to be smaller than that of \( \hat{P}_1 \) at the same point. But the value of the population \( P_2 \) would then be negative, so that this condition is unfeasible;

4. \( V > 0, \quad L < 0, \quad R < H_2 \): in general there is no intersection point;

5. \( V < 0, \quad L > 0, \quad R > H_2 \): the feasibility condition states that the slope of \( \hat{P}_2 \) at the point \((0, H_2)\) be smaller than that of \( \hat{P}_1 \) at the same point; explicitly

\[
m_{21} > r_1, \quad r_2 > m_{12}, \quad a_2 H_2 + m_{12} > r_2.
\]

6. \( V < 0, \quad L > 0, \quad R < H_2 \): for feasibility, the intersection between \( \hat{P}_2 \) and the \( P_1 \) axis must be larger than the positive root of \( \hat{P}_1 \); in other words

\[
m_{21} > r_1, \quad r_2 > m_{12}, \quad a_2 H_2 + m_{12} < r_2, \quad K_1 < \frac{r_2 s_2 (b_2 K_2 (m_{12} - r_2) + r_2 s_2)^2}{Z}, \quad \frac{(m_{21} - r_1) r_2 s_2}{b_2 (m_{12} r_1 + (m_{21} - r_1) r_2)} < K_2 < \frac{r_2 s_2}{b_2 (-m_{12} + r_2)}.
\]

7. \( V < 0, \quad L < 0, \quad R > H_2 \): there can be no intersection point;

8. \( V < 0, \quad L < 0, \quad R < H_2 \): for feasibility the slope of \( \hat{P}_2 \) at the point \((0, H_2)\) must be smaller than that of \( \hat{P}_1 \) at the same point. In this case, explicitly we have the feasibility conditions

\[
m_{21} > r_1, \quad r_2 > a_2 H_2 + m_{12}, \quad a_2 b_2 H_2 K_2 > r_2 s_2.
\]
The stability conditions given by the Routh-Hurwitz criterion can be stated as \( s_1 < b_1 P_1 \) together with

\[
m_{12} + m_{21} + \frac{2P_1 r_1}{K_1} + P_2 \left( b_2 + \frac{2s_2}{K_2} \right) + Q_2 \left( a_2 + \frac{2s_2}{H_2} \right) > r_1 + r_2 + s_2,
\]

\[
b_2 H_2 P_2 (K_2 - 2P_2) (K_1 (r_1 - m_{21}) - 2P_1 r_1) r_2 - K_2 m_{12} (K_2 - 2P_2) r_1
\]

\[
> (H_2 - 2Q_2) (K_2 (a_2 K_1 m_{21} Q_2 - (K_1 - 2P_1) m_{12} + a_2 Q_2) r_1) - (K_2 - 2P_2) (K_1 (m_{21} - r_1) + 2P_1 r_1) r_2) s_2
\]

and nally

\[
(H_2 (2K_2 P_1 r_1 + K_1 (2P_2 r_2 + K_2 (m_{12} + m_{21} + b_2 P_2 + a_2 Q_2 - r_1 - r_2 - s_2)))) + 2K_1 K_2 Q_2 s_2 (H_2 (K_2 (a_2 K_1 m_{21} Q_2 - (K_1 - 2P_1) r_1) - (K_2 - 2P_2) (K_1 (m_{21} - r_1) + 2P_1 r_1) r_2 + b_2 H_2 P_2 (2K_2 P_1 r_1 + K_1
\]

\[
\times (K_2 (m_{12} + m_{21} - r_1 - r_2 + 2P_2 r_2)) - (K_2 - 2P_2) (K_1 (m_{21} - r_1) + 2P_1 r_1) r_2)
\]

\[
(H_2 - 2Q_2) (2K_2 P_1 r_1 + K_1
\]

\[
\times (K_2 (m_{12} + m_{21} + a_2 Q_2 - r_1 - r_2 + 2P_2 r_2)) s_2)
\]

\[
> H_2 K_2 K_1 (b_2 H_2 P_2 (-K_2 m_{12} (K_1 - 2P_1) r_1 + (K_2 - 2P_2) (-2P_1 r_1 + K_1 (m_{21} - r_1)) r_2 - (H_2 - 2Q_2) (K_2 (a_2 K_1 m_{21} Q_2 - (K_1 - 2P_1) r_1) - (K_1 - 2P_1) (m_{12} + a_2 Q_2) r_1) - (K_2 - 2P_2) (K_1 (m_{21} - r_1) + 2P_1 r_1) r_2) s_2,
\]

where the population values are those at equilibrium. Also in this case the simulations show that this equilibrium \( \bar{E}_8 = (220.0633, 0.00176, 247.9334) \) can be achieved for the parameter values \( r_1 = 148.9386, r_2 = 97.3583, s_1 = 162.3161, s_2 = 94.1847, K_1 = 221.5104, K_2 = 260.2843, H_1 = 240.0507, H_2 = 252.1136, a_1 = 91.3287, a_2 = 49.4174, b_1 = 50.0022, b_2 = 88.6512, m_{12} = 0.0424, m_{21} = 0.9730, n_{12} = 0, n_{21} = 0 \), see Figure 1.

For the equilibrium \( \bar{E}_{14} \) the same above analysis can be repeated, with only changes in the parabolae and in the subscripts of the above explicit feasibility conditions. The details are omitted, but the results provide a set of feasibility conditions

\[
m_{12} > r_2, \quad r_1 > a_1 H_1 + m_{21}, \quad a_1 b_1 H_1 K_1 > r_1 s_1,
\]

and the following stability conditions given by the Routh-Hurwitz criterion \( s_2 < b_2 P_2 \) together with

\[
m_{12} + m_{21} + P_1 \left( b_1 + \frac{2r_1}{K_1} \right) + 2P_2 r_2 + Q_1 \left( a_1 + \frac{2s_1}{H_1} \right) > r_1 + r_2 + s_1,
\]

\[
b_1 H_1 P_1 \left( (K_2 - 2P_2) (K_1 (r_1 - m_{21}) - 2P_1 r_1) r_2 - K_2 m_{12} (K_2 - 2P_2) r_1\right)
\]

\[
> (H_1 - 2Q_1) (K_2 m_{12} (a_1 K_1 Q_1 - (K_1 - 2P_1) r_1) - (K_2 - 2P_2) (K_1 (m_{21} + a_1 Q_1 - r_1) + 2P_1 r_1) r_2) s_1,
\]

and nally

\[
(H_1 (2K_2 P_1 r_1 + K_1 (2P_2 r_2 + K_2 (m_{12} + m_{21} + b_2 P_2 + a_2 Q_2 - r_1 - r_2 - s_2)))) + 2K_1 K_2 Q_2 s_1 (H_1 (K_2 m_{12} (a_1 K_1 Q_1 - (K_1 - 2P_1) r_1) - (K_2 - 2P_2) (K_1 (m_{21} + a_1 Q_1 - r_1) + 2P_1 r_1) r_2 + b_1 H_1 P_1 (2K_2 P_1 r_1 + K_1 (K_2 (m_{12} + m_{21} - r_1 - r_2 + 2P_2 r_2)) - (H_1 - 2Q_1) (K_2 m_{12} (a_1 K_1 Q_1 - (K_1 - 2P_1) r_1) + 2K_2 P_1 r_1 + 2P_2 r_2) s_1\)
\]

\[
> H_1 K_1 K_2 (b_2 H_2 P_2 (-K_2 m_{12} (K_1 - 2P_1) r_1 + (K_2 - 2P_2) (-2P_1 r_1 + K_1 (m_{21} - r_1)) r_2 - (H_2 - 2Q_2) (K_2 m_{12} (a_1 K_1 Q_1 - (K_1 - 2P_1) r_1) - (K_2 - 2P_2) (K_1 (m_{21} + a_1 Q_1 - r_1) + 2P_1 r_1) r_2) s_1,
\]

with population values evaluated at equilibrium. Again, the whole set of conditions can be satisfied to lead to a stable conjugation for the following parameter choice:

\[
r_1 = 19.5081, \quad r_2 = 28.3773, \quad s_1 = 151.5480, \quad s_2 = 164.6916, \quad K_1 = 224.4882, \quad K_2 = 249.8364, \quad H_1 = 247.9646, \quad H_2 = 234.9984, \quad a_1 = 28.5839, \quad a_2 = 12.9906, \quad b_1 = 60.1982, \quad b_2 = 82.5817, \quad m_{12} = 0.8687, \quad m_{21} = 0.1361, \quad n_{12} = 0, \quad n_{21} = 0, \quad \text{with initial conditions} \quad (7.5967, 48.9253, 13.1973, 16.8990).
\]

The equilibrium coordinates are \( E_{14} = (0.0301, 244.9973, 242.1885, 0) \), see Figure 2.

The coexistence equilibrium \( \bar{E}_{16} \) has been deeply investigated numerically. It has been found to be always feasible, but never stable for all the sets of parameters used.

### 4 Unidirectional migration only

In this case, we assume that it is not possible to migrate from patch 2 back into patch 1, so that the coefficients \( m_{12} \) and \( n_{12} \) vanish. The reasons behind this statement can be found in natural situations. For instance it can be observed that freshwater shes swim downstream much more easily than upstream. In particular obstacles like dams and waterfalls may hinder the upstream migrations. In any case the overcoming of these obstacles requires a sizeable effort, for which suficient energy must be allocated. This however may not always be available.
We denote the equilibria here by $\tilde{E}_k$, $k = 1, \ldots, 16$. Equilibria $\tilde{E}_5, \tilde{E}_7, \tilde{E}_9, \tilde{E}_{10}, \tilde{E}_{13}, \tilde{E}_{14}, \tilde{E}_{15}$ are found to be all infeasible.

The origin $E_1$ has two positive eigenvalues $r_2 > 0$ and $s_2 > 0$, so that it is unstable.

The points $\tilde{E}_2 = (0, 0, K_2, 0)$ and $\tilde{E}_3 = (0, 0, 0, H_2)$ are feasible. For the former, the eigenvalues of the Jacobian are $-r_2, -m_{21} + r_1, -n_{21} + s_1, -b_2K_2 + s_2$, giving the stability conditions

$$r_1 < m_{21}, \quad s_1 < n_{21}, \quad s_2 < b_2K_2. \tag{8}$$

For the latter instead, the eigenvalues are $-m_{21} + r_1, -a_2H_2 + r_2, -n_{21} + s_1, -s_2$, with the following conditional stability conditions

$$r_1 < m_{21}, \quad r_2 < a_2H_2, \quad s_1 < n_{21}. \tag{9}$$

**Equilibrium**

$$\tilde{E}_4 = \left(0, 0, \frac{K_2s_2 (H_2 a_2 - r_2) - H_2r_2 (b_2K_2 - s_2)}{a_2b_2H_2K_2 - r_2 s_2}, \frac{b_2r_2 (b_2K_2 - s_2)}{a_2b_2H_2K_2 - r_2 s_2}\right)$$

is feasible for either one of the two alternative sets of inequalities

$$a_2H_2 > r_2, \quad b_2K_2 > s_2; \tag{10}$$

$$a_2H_2 < r_2, \quad b_2K_2 < s_2. \tag{11}$$

The eigenvalues are $-m_{21} + r_1, -n_{21} + s_1, \lambda_+$, where

$$2(a_2b_2H_2K_2 - r_2 s_2) \lambda_+ = r^2_2 s_2$$

$$+ r_2 s_2 (-a_2H_2 - b_2K_2 + s_2) \pm \sqrt{\Delta},$$

$$\Delta = r^2_2 s_2 (r_2 s_2 (-a_2H_2 - b_2K_2 + s_2)) + 2 + 4(a_2H_2 - r_2) (b_2K_2 - s_2) (a_2 b_2 H_2 K_2 - r_2 s_2)).$$

In case (10) holds, we nd $\lambda_+ > 0$ so that $\tilde{E}_4$ is unstable. In case instead of (11) the stability conditions are

$$r_1 < m_{21}, \quad s_1 < n_{21}. \tag{12}$$

and simulations show that this point is indeed stably achieved, Figure 3, for the parameter values $r_1 = 0.15, r_2 = 0.9, s_1 = 0.55, s_2 = 0.61, K_1 = 250, K_2 = 300, H_1 = 120, H_2 = 500, a_1 = 12, a_2 = 0.06, b_1 = 3, b_2 = 0.015, m_{12} = 0, m_{21} = 0.9, n_{12} = 0, n_{21} = 0.8$, giving the equilibrium $\tilde{E}_4 = (0, 0.205, 2799, 474, 9398)$.

The next points come in pairs.

$$\tilde{E}_{6+} = \left(\frac{K_1 (r_1 - m_{21})}{r_1}, 0, \frac{K_2 r_1 r_2 \pm \sqrt{\Delta}}{2r_2}, 0\right),$$

$$\tilde{E}_{11+} = \left(0, \frac{H_1 (s_1 - n_{21})}{s_1}, 0, \frac{H_2 s_1 s_2 \pm \sqrt{\Delta}}{2s_1 s_2}\right),$$

where

$$A = K_2 r_1 r_2 (-4K_1 m^2_{21} + 4K_1 m_{21} r_1 + K_2 r_1 r_2),$$

$$B = H_2 s_1 s_2 (-4H_1 n^2_{21} + 4H_1 n_{21} s_1 + H_2 s_1 s_2),$$

and with respective conditions for the non-negativity of their rst components given by

$$r_1 \geq m_{21}, \tag{13}$$

$$s_1 \geq n_{21}. \tag{14}$$

Note further that if (13) and (14) hold, then $A, B > 0$. But then $\sqrt{A} > K_2 r_1 r_2$ and $\sqrt{B} > H_2 s_1 s_2$, so that $\tilde{E}_{6+}$ and $\tilde{E}_{11+}$ have the second component negative, i.e. they are infeasible. The feasibility conditions for $\tilde{E}_{6+}$ and $\tilde{E}_{11+}$ are then respectively given by (13) and (14). The eigenvalues for $\tilde{E}_{6+}$ are $m_{21} - r_1$ and

$$-n_{21} + \frac{b_1 K_1 (m_{21} - r_1)}{r_1} + s_1, \quad \frac{\sqrt{A}}{K_2 r_1},$$

$$b_2 (-K_2 r_1 r_2 - \sqrt{A}) + s_2,$$

giving the stability conditions

$$r_1 (n_{21} - s_1) > b_1 K_1 (m_{21} - r_1),$$

$$2r_1 r_2 s_2 < b_2 \left(K_2 r_1 r_2 + \sqrt{A}\right),$$

where we used (13).

Eigenvalues of $\tilde{E}_{11+}$ are $n_{21} - s_1$ and

$$-m_{21} + r_1 + \frac{a_1 H_1 (n_{21} - s_1)}{s_1} + \frac{\sqrt{B}}{H_2 s_1 s_2},$$

$$2r_1 r_2 s_2 < b_2 \left(H_2 s_1 s_2 + \sqrt{B}\right).$$

having again used (14).

For the next two equilibria, we are able only to analyse feasibility. We nd

$$\tilde{E}_8 = \left(-\frac{K_1 m_{21}}{r_1} + K_1 r_1, 0, B, A\right)$$

with

$$A = \frac{1}{2} \left[2(a_2b_2H_2K_2r_1 - r_1 r_2 s_2) \left(a_2H_2K_2r_1 s_2 - K_2 r_1 r_2 s_2\right) + \left[-4(K_1K_2 m_{21} s_2 - K_1K_2 m_{21} r_1 s_2) - a_2b_2H_2K_2r_1 + r_1 r_2 s_2\right] \left(a_2H_2K_2r_1 s_2 - K_2 r_1 r_2 s_2\right) / 2 \right]^{1/2},$$

$$B = \frac{1}{2} a_2K_2K_2 r_1 (r_1 - r_1 r_2 s_2) \left(a_2K_2K_2 r_1 s_2 + b_2H_2K_2 r_1 r_2 s_2 - 2(a_2b_2H_2K_2r_1 - r_1 r_2 s_2) \left[-b_2H_2 - 4(K_1K_2 m_{21} s_2 - K_1K_2 m_{21} r_1 s_2) - a_2b_2H_2K_2r_1 + r_1 r_2 s_2\right] + \left(a_2H_2K_2 r_1 s_2 - K_2 r_1 r_2 s_2\right) / 2 \right]^{1/2}.\]
and

$$\bar{E}_{12} = \left(0, -\frac{H_1 n_{21} + H_1 s_1}{s_1}, D, C\right)$$

where

$$D = \frac{1}{2(b_2 a_2 K_2 H_2 s_1 - s_1 s_2 r_2)} \{b_2 K_2 H_2 s_1 r_2 - H_2 s_1 s_2 r_2$$

$$+ \left[-4(H_1 H_2 s_1^2 r_2 - H_1 H_2 s_1 s_2 r_2) - b_2 K_2 H_2 s_1 r_2 - H_2 s_1 s_2 r_2 \right]^{1/2}\}$$

$$C = \frac{1}{2 r_2 (b_2 a_2 K_2 H_2 s_1 - s_1 s_2 r_2)} \left[K_2 r_2$$

$$- b_2 a_2 K_2 H_2 s_1 r_2 + a_2 K_2 H_2 s_1 s_2 r_2$$

$$- \left[a_2 K_2 (-4(H_1 H_2 s_1^2 r_2 - H_1 H_2 s_1 s_2 r_2)$$

$$\times (-b_2 a_2 K_2 H_2 s_1 + s_1 s_2 r_2)$$

$$+ (b_2 K_2 H_2 s_1 r_2 - H_2 s_1 s_2 r_2)^2 \right]^{1/2}\}.$$ 

Feasibility for \(\bar{E}_8\) is ensured by

$$r_1 > m_{21}, \quad A > 0, \quad B > 0,$$

while for \(\bar{E}_{12}\) by

$$s_1 > n_{21}, \quad C > 0, \quad D > 0.$$

(17)

(18)

Numerical simulations show in fact their stability, as seen in Figures 4 and 5, respectively for the parameter values

$$r_1 = 148.8149, \quad r_2 = 95.9844, \quad s_1 = 121.9733,$$

$$s_2 = 171.8885, \quad K_1 = 228.8361, \quad K_2 = 223.9932,$$

$$H_1 = 201.4337, \quad H_2 = 216.7927, \quad a_1 = 71.2694,$$

$$a_2 = 47.1088, \quad b_1 = 68.1972, \quad b_2 = 7.1445, \quad m_{12} = 0,$$

$$n_{21} = 0.8175, \quad n_{12} = 0, \quad n_{21} = 0.$$

Equilibrium \(\bar{E}_8\) is given by

$$r_1 \left(1 - \frac{2}{K_1}\right) + r_2 \left(1 - \frac{2}{K_2}\right) < n_{12} + n_{21},$$

$$r_1 \left(1 - \frac{2}{K_1}\right) - m_{21} \left[r_2 \left(1 - \frac{2}{K_2}\right) - m_{12}\right] > m_{12} m_{21},$$

for the equilibrium \(\bar{E}_{12}\) we have the conditions

$$s_2 < b_2 P_2, \quad s_1 < b_1 P_1,$$

$$s_1 \left(1 - \frac{2}{H_1}\right) + s_2 \left(1 - \frac{2}{H_2}\right) < n_{12} + n_{21},$$

$$\left[s_1 \left(1 - \frac{2}{H_1}\right) - n_{12}\right]\left[s_2 \left(1 - \frac{2}{H_2}\right) - n_{12}\right] > n_{12} n_{21}.$$
(47.4215, 86.4803, 27.8785, 70.8909), as can be seen in Figures 7 and 8.

For the coexistence equilibrium $E_{16} = (10.7367, 10.7367, 15.0240, 15.0240)$ we have similar results as for the one of the one-migration only case. It is shown to exist and be stable in Figure 9, for the very specic parameter values $r_1 = 110, r_2 = 80, s_1 = 110, s_2 = 80, K_1 = 360, K_2 = 270, H_1 = 360, H_2 = 270, a_1 = 10, a_2 = 5, b_1 = 10, b_2 = 5, m_{12} = 0.5, m_{21} = 0.1, n_{12} = 0.5, n_{21} = 0.1$. Its stability however is easily broken under slight perturbations of the system parameters. Again, thus, the coexistence equilibrium $E_{16}$ is not generically stable.

6 Conclusions

6.1 Discussion of the possible systems’ equilibria

The metapopulation models of competition type here considered show that only a few populations congurations are possible at a stable level. First of all, in virtue of our assumptions, all these ecosystems will never disappear. Table 1 shows that equilibria $E_5, E_7, E_{10}, E_{13}, E_{15}$ cannot occur in any one of the models considered here. Of these, $E_2$ and $E_{10}$ are the most interesting ones. They show that one competitor cannot survive solely in one patch, while the other one thrives alone in the second patch. Thus it is not possible to reverse the outcome of a superior competitor in one patch in the other patch. Further, in the rst patch the two populations can coexist only in the model in which only one population is allowed to migrate back and forth into the other patch, equilibrium $E_{14}$. In that case, the migrating population thrives also alone in the second environment. The coexistence of all populations in both environments is “fragile”, it occurs only under very limited assumptions. Coexistence in the second patch can occur instead of the rst one empty at $E_4$, only in the following two cases. For the one-directional migration model, with immigrations into the second patch, the rst patch is left empty. When the rst patch is instead populated by one species only, at equilibria $E_{8}$ for both the one-population and unidirectional migrations models and at $E_{12}$, again for the one-directional migrations model. The equilibria in which one population is wiped out from the ecosystem instead, $E_6$ and $E_{11}$, occur in all three models. Finally, the three remaining equilibria contain only one population in just one patch. At $E_2$, only for the unidirectional migration model, the migrating population survives in the arrival patch. At $E_3$ it is the residential, i.e. the non-migrating, population that survives in its own patch, only for the one-population migrations model. At $E_3$ for both particular cases instead, the residential population survives in the “arrival” patch of the other migrating population.

6.2 Unrestricted migrations

Looking now more specically at each one of the proposed models, we draw the following inferences.

The model with unrestricted migration possibilities allows the survival of either one of the competing populations, in both patches, $E_6$ and $E_{11}$. Coupling this result with the fact that the interior coexistence has been numerically shown to be stable just for a specic parameter choice, but it is generally unstable, this result appears to be an extension of the classical competitive exclusion principle, [18], to metapopulation systems, in agreement with the classical literature in the eld, e.g. [1, 2, 8, 13, 20, 22, 24, 28]. It is apparent here, as well as in the classical case, that an information on how the basins of attraction of the two mutually exclusive boundary equilibria is important in assessing the nal outcome of the system, based on the knowledge of its present state. To this end, relevant numerical work has been performed for two and three dimensional systems, [4, 5]. An extension to higher dimensions is in progress.

6.3 Migration allowed for just one population

For the model in which only one population can migrate, two more equilibria are possible in addition to those of the full model, i.e. the resident, non-migrating, population $Q$ can survive just in one patch with the migrating one, and the patch can be either one of the two in the model, equilibria $E_{16}$ and $E_{14}$. The resident population cannot outcompete the migrating one, since the equilibria $E_{16}$ and $E_{14}$ are both unconditionally unstable. Thus, when just one population migrates, the classical principle of competitive exclusion does not necessarily hold neither at the wider metapopulation level, nor in one of the two patches, as shown by the nonvanishing population levels of patch 2 in equilibrium $E_8 = (220.0633, 0, 0.0176, 247.9334)$, Figure 1, and in patch 1 in equilibrium $E_{14} = (0.0301, 244.9973, 242.1885, 0)$, Figure 2. The coexistence in one of the two patches appears to be possible since the weaker species can migrate to the other competitor-free environment, thrive there and migrate back to reestablish itself with the competitor in the original environment. But the principle of competitive exclusion can in fact occur also in this model, since the numerical simulations reveal it, consider indeed the equilibrium $E_6 = (119.6503, 0, 167.4318, 0)$. However, restrictions in the interpatch moving possibilities of one population might prevent its occurrence. The coexistence of all the populations appears to be always impossible in view of the instability of the equilibrium $E_{16}$.

Using the algorithm introduced in [5], we have also explored a bit how the migration rates inuence the shape of the basins of attraction of the two equilibria $E_6$ and $E_{11}$.

For this model where just one population is allowed to migrate, keeping the following demographic parameters...
Fig. 1: The two top populations $P_1$ and $Q_1$ occupy the first patch, the bottom ones $P_2$ and $Q_2$ the second patch. The equilibrium $\tilde{E}_8 = (220.0633, 0.0.0176, 247.9334)$ is stable for the parameter values $r_1 = 148.9386$, $r_2 = 97.3583$, $s_1 = 162.3161$, $s_2 = 94.1487$, $K_1 = 221.5104$, $K_2 = 260.2843$, $H_1 = 240.0507$, $H_2 = 252.1136$, $a_1 = 91.3287$, $a_2 = 49.4174$, $b_1 = 50.0022$, $b_2 = 88.6512$, $m_{12} = 0.0424$, $m_{21} = 0.9730$, $n_{12} = 0$, $n_{21} = 0$.

Fig. 2: The two top populations $P_1$ and $Q_1$ occupy the first patch, the bottom ones $P_2$ and $Q_2$ the second patch. The equilibrium $\tilde{E}_{14} = (0.0301, 244.9973, 242.1885, 0)$ is stable for the parameter values $r_1 = 19.5081$, $r_2 = 28.3773$, $s_1 = 151.5480$, $s_2 = 164.6916$, $K_1 = 224.4882$, $K_2 = 249.8364$, $H_1 = 247.9646$, $H_2 = 234.9984$, $a_1 = 28.5839$, $a_2 = 12.9906$, $b_1 = 60.1962$, $b_2 = 82.5817$, $m_{12} = 0.8687$, $m_{21} = 0.1361$, $n_{12} = 0$, $n_{21} = 0$.

Fig. 3: The equilibrium $\tilde{E}_4$ is stable for the parameter values $r_1 = 0.15$, $r_2 = 90$, $s_1 = 0.55$, $s_2 = 61$, $K_1 = 250$, $K_2 = 300$, $H_1 = 120$, $H_2 = 500$, $a_1 = 12$, $a_2 = 0.06$, $b_1 = 3$, $b_2 = 0.015$, $m_{12} = 0$, $m_{21} = 0.9$, $n_{12} = 0$, $n_{21} = 0.8$, with initial conditions $(110, 80, 64, 250)$. The equilibrium coordinates are $\tilde{E}_4 = (0, 0.205, 2799, 474.9398)$.

The equilibrium $\tilde{E}_8$ remains unchanged, but we note instead that the point $\tilde{E}_6 = (9.3399, 0.5.4726, 0)$ has moved toward higher $P_1$ and lower $P_2$ population values. The separatrices are plotted in the bottom row of Figure 10. It is also clear that the basins of attraction in patch 1 hardly change, while in patch 2 the basin of attraction of the population $Q_2$ appears to be larger with a higher emigration rate from patch 2. Correspondingly, the one of $P_2$ becomes smaller in patch 2, according to what intuition would indicate.

6.4 Unidirectional migrations

When migrations are allowed from patch 1 into patch 2 only, a number of other possible equilibria arise, in part replacing some of the former ones. Granted that coexistence is once again forbidden for its instability, three new equilibria arise, containing either one or both populations in the patch toward which migrations occur, leaving the other one possibly empty. The principle of competitive exclusion in this case may still occur at the metapopulation level, but apparently coexistence at equilibrium $\tilde{E}_4$ might be possible in the patch toward which populations migrate if the stability conditions (12) coupled with the feasibility conditions (11) are satisfied. This appears to be also an interesting result.
Again exploiting the algorithm of [5], we investigated also the change in shape of the basins of attraction of the two equilibria $\tilde{E}_8$ and $\tilde{E}_{11}$. For this unidirectional migrations model. Using once again the demographic parameters (20), we take at rst the migration rates as follows

$$ m_{21} = 0.1, \quad m_{12} = 0, \quad n_{21} = 0.1, \quad n_{12} = 0, $$

obtaining equilibria $\tilde{E}_8 = (7.875, 0.8, 3.408, 0)$ and $\tilde{E}_{11} = (0.5, 5, 6.5860, 0.6, 6192)$. This result is shown in the top row of Figure 11, again patch 1 in the right frame and patch 2 in the left one. Instead with the choice

$$ m_{21} = 2.4, \quad m_{12} = 0, \quad n_{21} = 0.1, \quad n_{12} = 0, $$

allowing a faster rate for the population $P$, we again nd that the second equilibrium $\tilde{E}_{11}$ is unaffected, but the rst one lowers its population values, becoming $\tilde{E}_8 = (5, 0.9, 9907, 0)$, see bottom row of Figure 11. In this case the basins of attraction seem to have opposite behaviors. With a higher migration rate for $P$, its basin of attraction in patch 2 gets increased, while in patch 1 becomes smaller. This result is in agreement with intuition, in patch 1 the $P$ population become smaller and larger instead in patch 2.

### 6.5 Final considerations

We briey discuss also the model bifurcations for the unidirectional migration model. If $r_1 < m_{21}$ and $s_1 < n_{21}$,
Fig. 8: The coexistence equilibrium \( E_{11} \) is stable for the parameter values \( r_1 = 46.2191, r_2 = 191.5950, s_1 = 70.5120, \)
\( s_2 = 171.4748, K_1 = 240.3233, K_2 = 256.7841, H_1 = 244.9968, \)
\( H_2 = 263.8244, a_1 = 49.1146, a_2 = 43.3295, b_1 = 77.5334, \)
\( b_2 = 38.0149, m_{12} = 0.4620, m_{21} = 0.6463, n_{12} = 0.8896, n_{21} = 0.8370. \)

Fig. 9: The two top populations \( P_1 \) and \( Q_1 \) occupy the rst patch, the bottom ones \( P_2 \) and \( Q_2 \) the second patch. The coexistence equilibrium, \( E_{16} = (10.7367, 10.7367, 15.0240, 15.0240) \), is obtained just for a very specic parameter choice namely \( r_1 = 110, r_2 = 80, s_1 = 110, s_2 = 80, K_1 = 360, K_2 = 270, H_1 = 360, \)
\( H_2 = 270, a_1 = 10, a_2 = 5, b_1 = 10, b_2 = 5, m_{12} = 0.5, m_{21} = 0.1, \)
\( n_{12} = 0.5, n_{21} = 0.1. \)

The only feasible equilibria are \( \bar{E}_2, \bar{E}_3 \), which are stable under the additional conditions \( s_2 < b_2 K_2 \) and \( r_2 < a_2 H_2. \) When \( r_1 \) crosses the value \( m_{21} \) and similarly \( s_1 \geq n_{21}, \) the two previous equilibria become unstable, and transcritical bifurcations give rise respectively to the equilibria \( \bar{E}_6 \) and \( \bar{E}_{11}. \) The equilibrium \( \bar{E}_4 \) may coexist with each one of the previous equilibria, but in this case \( \bar{E}_2 \) and \( \bar{E}_3 \) must be unstable, whereas \( \bar{E}_6 \) and \( \bar{E}_{11} \) may be stable if their stability conditions hold.

In the two particular cases above discussed, of just one population allowed to migrate and of unidirectional migrations, our analysis shows that the standard assumptions used to study congurations in patchy environments may not always hold. Under suitable conditions, competing populations may coexist if only one migrates freely, or if migrations for both populations are allowed in the same direction and not backwards. This appears to be an interesting result, which might open up new research directions.
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