Modeling Competition in Motionless Populations

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1 Introduction

A key factor when modelling community dynamics consists in the way interactions take place. The vast majority of the research on community models, that follow in the wake of Lotka and Volterra [23], assumes that individuals are well mixed and that any one of them can interact with all the rest. Interestingly, epidemic and eco-epidemic models do take into account such a major feature distinguishing the type of transmission [4, 21], that is closely related to the way individuals interact. Recently, [1–3, 18] addressed a series of community models that implement a social structure determining how populations interact with each other. Some cases of predator-prey interactions of this type are instead discussed in [17].

In this paper we consider interference competition between two motionless populations, for which individual interaction dynamics is definitely different from mobile living beings [24]. Plants, of course, do belong to this category. Sessile species competition has been also reported in fungi [25], sponges [31], corals [5, 12, 14], giant clams, barnacles [10] or most of bivalves [27] are other examples, along with microorganism that grow up in colonies [20].

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We thus consider two populations that homogeneously occupy two neighboring territories, but do not mix with each other, at least not significantly. Interactions among the two species populations can only occur through the common boundaries of the two cultures in consideration, that border each other. Note that these different domains occupied by the two populations may well consist also of islands or other more complicated geometrical shapes.

Thus, these considerations lead us to replace the classical 1–1 interactions among individuals of the same species with just those with the most immediate neighbors of a single individual [18]. In the model we thus must prevent that one individual may compete with all other individuals of the population that are in far away locations.

When the model is written in terms of *explicit carrying capacities*, the dynamics of interference competition is driven by the balance between intra- and interspecific competition [24, 32], or, if the model is formulated with *emerging carrying capacities*, by competitive strengths [6, 15, 26]. We prefer the latter approach, see [16]. In any case, the early theory of competition [11, 19, 30] understands coexistence as the result of the common interplay of inter- and intraspecific interactions. Specifically coexistence is obtained when intraspecific competition limits species density more strongly than interspecific competition. In the present model competition is by far different than in the classical model, since 1–1 interactions among all individuals are precluded. In particular, both intra- and interspecific competition are relaxed. Therefore, we expect competition outcomes to be different than in the classical model as in the recent extensions [8, 9]. Indeed, interactions seem to be milder in the model we present herein, so that we expect to find that species are more likely to coexist.

From a mathematical point of view, the model we present belongs to the general class of *competitive systems* in the positive cone, see [13] and the references therein. This fact precludes the existence periodic solutions and guarantees that solutions converge to an equilibrium point.

Our main results are the following. When a sessile population competes with a mobile population, all the competitive outcomes of the classical model are possible. Besides, conditional bi-stable coexistence in favor of the sessile population is possible, meaning that both a semi-trivial equilibrium and a coexistence equilibrium are (locally) asymptotically stable. Thus, whether the sessile population wins or both populations coexist depends on the system's initial conditions, i.e. the initial amount of individuals of each population.

When both competing populations are sessile only species exclusion, with outcome determined just by the system's initial conditions, or conditional tri-stable coexistence, i.e. coexistence, are possible, as it was already shown in [22].

The manuscript is organized as follows: in the next section we compare the classical logistic single population evolution with the corresponding one of a motionless population. In Sect. 3, we set the features of non-mobile populations for which the interactions occur only at the boundary of their respective domains into a mathematical formulation. Subsequently, we analyze the competition among mobile and motionless populations in Sect. 4. The interactions of two motionless

populations are instead analysed in Sect. 5. Finally, we discuss the results achieved 64
for the various cases in Sect. 6. 65

2 The Single Population Case 66

The single population case has been briefly examined also in [18], as a motivation 67
for further changes in the formulation of herd behavior models. Here however we 68
focus on a population that does not move, which therefore has its own specific 69
features, distinguishing it from the more commonly considered mobile populations. 70
The starting point for a single population is represented by the classical logistic 71
(or Verhulst) model, namely 72

$$x' = \widehat{r}x - ax^2, \tag{1}$$

for which the the population settles at the equilibrium 73

$$x^c = \frac{\widehat{r}}{a}. \tag{2}$$

For one single plant living in a plantation, therefore surrounded just by other 74
plants of the same species, because the interactions occur only with possibly a 75
fraction $b \leq 1$ of the closest neighbors, the model becomes instead: 76

$$x' = \widehat{r}x - bax\sqrt{x}. \tag{3}$$

Equation (3) is a modification of the well known logistic growth that takes into 77
account that sessile living beings stand still and interact only with their most 78
immediate neighbors. Thus, a given individual competes with the nearby ones, that 79
we assume are located at the boundary layer of its "vital space", that is, a circle area 80
around the individual. Assuming that individuals are homogeneously distributed, 81
the boundary of each individual's *vital space* is proportional to the boundary of 82
the territory occupied by this species, i.e., proportional to $\sqrt{x}$. Clearly, of the two 83
possible equilibria of (3), the origin is unstable while the population thrives at level 84

$$x^* = \frac{\widehat{r}^2}{b^2a^2}. \tag{4}$$

Thus, qualitatively, the two models (1) and (3) behave in the same way. However, 85
recalling that $b \leq 1$, whether a single plant living in a wood or plantation is better off 86
than a corresponding animal individual living amidst his own consimilars, depends 87
on the ratio between its net reproduction rate and the intraspecific competition rate. 88
If the former exceeds the latter, the level at which the vegetable species settles is 89
certainly higher than the corresponding animal population. 90

3 The Competing Sessile Populations Model 91

The departure model in this case is the classical Lotka-Volterra competition model 92
the with *emergent carrying capacities* [6, 15, 26] rather than explicit carrying 93
capacities [23, 32]: 94

$$\begin{cases} x_1' = r_1 x_1 - a_{11} x_1^2 - a_{12} x_1 x_2 \\ x_2' = r_2 x_2 - a_{22} x_2^2 - a_{21} x_1 x_2 \end{cases} \tag{5}$$

where x_i and $r_i > 0$ stand for the amount of individuals and the intrinsic growth 95
rate of species $i = 1, 2$, respectively. Coefficients $a_{ij} > 0$ account for intra- ($i = j$) 96
and interspecific ($i \neq j$) competition, for $i, j = 1, 2$. 97

The modeling of sessile populations is rather different from the classical 98
interacting populations of animals that can move around. As assumed in other 99
investigations concerning herds of herbivores and their predators, [1, 2, 17] or 100
interference competition [22], we assume here that interactions among different 101
species, uniformly located in specific territories, occur through their common 102
boundaries, as stated above. They are assumed to be smooth, motivating the use 103
of the square root in the interaction terms. 104

Thus, we denote by x_1 and x_2 the densities of the populations, i.e., the number of 105
individuals per surface unit, occupying an area S. Thus the species of the population 106
i found in the periphery or neighborhood of their environment are proportional to 107
the perimeter of the patch where the culture is located, whose length depends on $\sqrt{S}$. 108
They are therefore proportional in number to the square root of the density, i.e. to 109
$\sqrt{x_i}$, $i = 1, 2$. In fact, different shapes could be accommodated by taking a different 110
exponent, other than one half, in the model formulation. However, in part based 111
also on the results of [7] for which no fundamentally different results arise, and for 112
simplicity sake, we confine ourselves to the assumption of a smooth boundary. This, 113
as mentioned, entails the use of the exponent one half in the model formulation. We 114
next examine in detail the intra- and inter- specific interaction terms: 115

- Inter-specific interactions take place on the boundary of each species domain. In 116
  view of the previous discussion, as individuals are assumed to be homogeneously 117
  distributed, the interaction between species x_i and x_j takes the following form: 118

$$- d_i a_{ij} \sqrt{x_i} \sqrt{x_j}, \tag{6}$$

where the minus sign denotes interactions harming the population i under 119
consideration, a_{ij} stands for the competition interaction coefficient of species 120
j on population i; $1 \geq d_i \geq 0$ is a constant that scales competition to the 121
fraction of the common perimeter. If species do not interact, i.e. there is no 122
common boundary, then $d_i = 0$. Therefore, $d_i a_{ij}$, $i \neq j$ stands for interspecific 123
competition and includes information on the fraction of the boundary where 124

competition takes place, so that its interpretation is slightly different from the interaction coefficients of the classical model. In general $d_i \neq d_j$.

- For intraspecific dynamics, we must include the growth rate and possibly intraspecific competition and therefore use replicas of (3):

$$x_i' = \widehat{r}_i x_i - b_i a_{ii} x_i \sqrt{x_i}, \tag{7}$$

where $\widehat{r}_i$ stands for the net intrinsic growth rate, a_{ii} is the intraspecific competition rate. In this context, b_i in (7) stands for the proportion between the local boundary and the perimeter occupied by the entire population, so that $1 \geq b_i \geq 0$. It is assumed to be the same for all individuals of the same species.

Merging (7) and (6) yields the competing sessile populations model

$$\begin{cases} x_1' = \widehat{r}_1 x_1 - b_1 a_{11} x_1 \sqrt{x_1} - d_1 a_{12} \sqrt{x_1} \sqrt{x_2}, \\ x_2' = \widehat{r}_2 x_2 - b_2 a_{22} x_2 \sqrt{x_2} - d_2 a_{21} \sqrt{x_1} \sqrt{x_2}. \end{cases} \tag{8}$$

Theorem 3.1 *The positive solutions of system* (8) *are bounded from above.*

Proof Note that

$$x_i' = \widehat{r}_i x_i - b_i a_{ii} x_i \sqrt{x_i} - d_i a_{ij} \sqrt{x_j} \sqrt{x_i} < \widehat{r}_i x_i - a_{ii} x_i \sqrt{x_i} < 0$$

for $x_i > (r/a_{ij})^2$. In particular, in the positive cone define a suitable box B with one corner located at the origin and the opposite one at the point $V = ((r_1/d_1 a_{12})^2, (r_2/d_2 a_{21})^2)$. The situation thus corresponds to the flow entering into B. ∎

Remark 3.1 System (8) is a *competitive system* (sensu [13]) in the positive cone $\mathbb{R}_+^2 := (0, +\infty) \times (0, +\infty)$, in view of the fact that

$$\frac{\partial}{\partial x_j} \left(\widehat{r}_i x_i - b_i a_{ii} x_i \sqrt{x_i} - d_i a_{ij} \sqrt{x_j} \sqrt{x_i} \right) < 0, \qquad j \neq i, \, i, j = 1, 2,$$

and the flow of the system belongs to class $C^1 (\mathbb{R}_+^2)$. Thus, Theorem 3.1 along with [13] imply that all the positive solutions of system (8) converge to an equilibrium point.

Remark 3.2 Note that as pointed out in [29], the right hand side of (8) does not satisfy the Lipschitz condition, with a consequent loss of uniqueness of the solution trajectories on the coordinate axes. Thus we need special care in treating vanishing populations when we change the variables of the system (8) to obtain the auxiliary system in order to eliminate the singularity. Therefore, to study the trivial and semi-

trivial equilibrium points, we have to turn to the original formulations (8), compare the approach of [3]. 150 151

Hence, we will study the trivial and semi-trivial equilibria directly using model (8). The trivial and semi-trivial equilibria are the following points: 152 153

$$E_0 = (0, 0), \quad E_1 = \left(\left(\frac{r_1}{b_1 a_{11}} \right)^2, 0 \right), \quad E_2 = \left(0, \left(\frac{r_2}{b_2 a_{22}} \right)^2 \right) \tag{9}$$

Note also that there are square root terms in system (8), so that the stability of the trivial and semi-trivial equilibrium points (9) cannot be assessed using the Jacobian matrix which, in turn, works when dealing with coexistence equilibria. However, square roots make the Jacobian matrix to be involved; we next introduce an equivalent singularity-free system to overcome such a problem. 154 155 156 157 158

4 Mobile and Sessile Populations Interactions 159

We consider here the interactions between a mobile population competing with a non-mobile one. Thus the system is a combination of both (5) and (7), giving: 160 161

$$\begin{cases} x_1' = r_1 x_1 - a_{11} x_1^2 - a_{12} x_1 x_2, \\ x_2' = r_2 x_2 - a_{22} b_2 x_2 \sqrt{x_2} - a_{21} x_1 x_2. \end{cases} \tag{10}$$

Proceeding as for system (8), it is easy to realize that the trajectories of (10) are bounded from above. To analyze the existence of equilibrium points and the long term behavior of the solutions of (10), we rewrite it in the following more convenient form: 162 163 164 165

$$\begin{cases} x_1' = r_1 x_1 \left(1 - \frac{a_{11}}{r_1} x_1 - \frac{a_{12}}{r_1} x_2 \right), \\ x_2' = r_2 x_2 \left(1 - \frac{a_{22}}{r_2} b_2 \sqrt{x_2} - \frac{a_{21}}{r_2} x_1 \right). \end{cases} \tag{11}$$

We rescale the above system with a special change of variables and parameters, namely $w_i = \frac{a_{ii}}{r_i} x_i$, $c_{ij} = \frac{a_{ij} r_j}{a_{jj} r_i}$, to obtain 166 167

$$\begin{cases} w_1' = r_1 w_1 \left(1 - w_1 - c_{12} w_2 \right), \\ w_2' = r_2 w_2 \left(1 - b_2 \sqrt{\frac{a_{22}}{r_2}} \sqrt{w_2} - c_{21} w_1 \right). \end{cases} \tag{12}$$

A further rescaling in system (12) given by $\widehat{w}_2 = \frac{a_{22}}{r_2} w_2$, $\quad \widehat{c}_{12} = \frac{r_2}{a_{22}} c_{12}$, yields the so-called special auxiliary system:

$$\begin{cases} w_1' = r_1 w_1 \left(1 - w_1 - \widehat{c}_{12}\widehat{w}_2\right), \\ w_2' = r_2 \widehat{w}_2 \left(1 - b_2\sqrt{\widehat{w}_2} - c_{21}w_1\right). \end{cases} \tag{13}$$

Let us recall that Theorem 3.1, as well as remarks 3.1 and 3.2 hold *mutatis mutandi*.

4.1 Equilibria

The trivial and semi-trivial equilibria of system (13) are:

$$E_0 = (0, 0) \quad E_1 = (1, 0) \quad \text{and} \quad E_2 = \left(0, \frac{1}{b_2^2}\right) \tag{14}$$

We consider the nullclines of system (13), that are given by

$$\widehat{w}_2 = f_1(w_1) = \frac{1 - w_1}{\widehat{c}_{12}}, \qquad \widehat{w}_2 = f_2(w_1) = \frac{(c_{21}w_1 - 1)^2}{b_2^2}.$$

The coexistence equilibria are denoted by $E_3^\pm = (w_1^\pm, f_1(w_1^\pm))$. They are given by the intersection of the nullclines, in this case a curve and a straight line. These solutions can be obtained from the roots of the following quadratic equation:

$$P_{sc}(w) = \frac{1}{\widehat{c}_{12}b_2^2}\left[-\widehat{c}_{12}c_{21}^2 w^2 + (2\widehat{c}_{12}c_{21} - b_2^2)w + (\widehat{c}_{12} - b_2^2)\right].$$
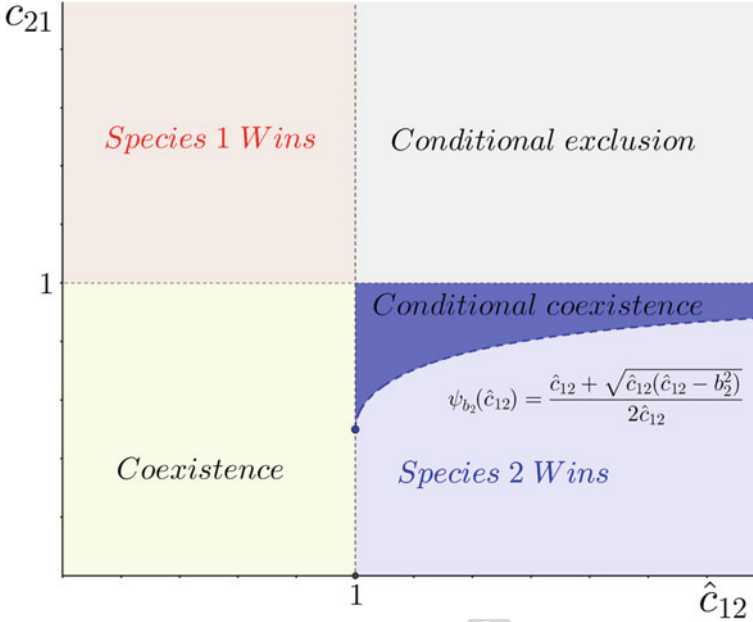
Thus

$$w_1 = \frac{2\widehat{c}_{12}c_{21} - b_2^2 \pm b_2\sqrt{4\widehat{c}_{12}c_{21}(c_{21} - 1) + b_2^2}}{2\widehat{c}_{12}c_{21}^2}. \tag{15}$$

Imposing that the discriminant of expression (15)

$$D := 4\widehat{c}_{12}c_{21}(c_{21} - 1) + b_2^2 \tag{16}$$

is nonnegative, we find the real roots in the positive cone. The following Lemma 4.1 and Theorem 4.1 summarize these conditions.

Fig. 1 Competition outcomes of system (10) in the $\widehat{c}_{12} - \widehat{c}_{21}$ parameter space as function of the competitive strengths as defined in Eq. (13). Species 1 (resp. 2) refers to the sessile (resp. mobile) population

Lemma 4.1 *Consider the function*   182

$$c_{21} = \psi_{b_2}(\widehat{c}_{12}) := \frac{\widehat{c}_{12} + \sqrt{\widehat{c}_{12}(\widehat{c}_{12} - b_2^2)}}{2\widehat{c}_{12}}, \qquad (17)$$

then, ψ_{b_2} is an unimodal function such that: 183

(1) its domain is the set $\{x \in \mathbb{R}^+ \mid 1 \leq x < \infty\}$ 184

(2) $c_{21}^* = \psi_{b_2}(1) = \frac{1+\sqrt{1-b_2^2}}{2}$ and $\lim\limits_{\widehat{c}_{12} \to +\infty} \psi_{b_2}(\widehat{c}_{12}) = 1$ 185

Proof It follows from direct calculations (Fig. 1). ∎   186

Whether there is none, one or two equilibrium points is determined by the sign of 187
the discriminant (16) of (15) and the quantities defined in the previous Lemma 4.1. 188

Theorem 4.1 *Consider the system* (13) *and the function* (17). *Recalling* (16) *we* 189
find 190

1. System (13) *has no equilibrium points in the positive cone if either* 191

   (a) $D < 0$, see the middle right panel in Fig. 2. 192
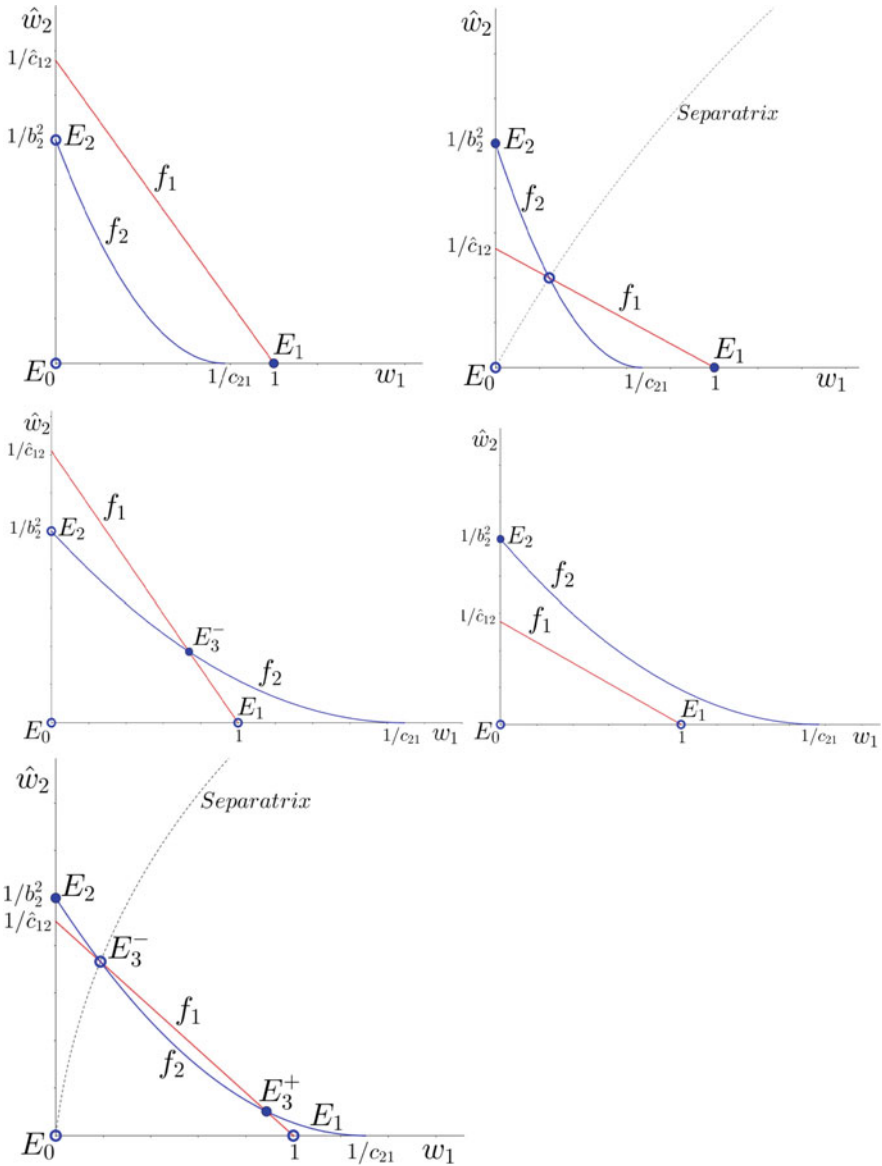   *(b) Both $1/c_{21} < 1$ and $1/\widehat{c}_{12} > 1/b_2^2$ hold, see top left panel in Fig. 2.* 193
   Alternatively we can require $\widehat{c}_{12} < 1$ and $c_{21} > 1$. 194

Fig. 2 Possible phase portraits of system (13). The horizontal (resp. vertical) axis refers to the sessile (resp. mobile) population. The curve f_1 (resp. f_2) stands for the nullcline of the sessile (resp. mobile) population. Solid points represent locally asymptotically stable equilibrium points while empty points represent unstable equilibria

2. *System* (13) *possesses a single equilibrium point in the positive cone (apart from the degenerated case $D = 0$) if either*

(a) Both $1/\widehat{c}_{12} < 1/b_2^2$ and $1/c_{21} < 1$ hold, see top right panel in Fig. 2. An alternative formulation of the above inequalities is $\widehat{c}_{12} > 1$ and $c_{21} > 1$.

(b) Both $1/\widehat{c}_{12} > 1/b_2^2$ and $1/c_{21} > 1$. An alternative formulation of the above inequalities is $\widehat{c}_{12} < 1$ and $c_{21} < 1$.

3. System (13) has two equilibrium points in the positive cone if $\widehat{c}_{12} > 1$ and $\psi_{b_2}(\widehat{c}_{12}) < c_{21} < 1$ hold, see the bottom panel of Fig. 2.

Proof It follows from direct calculations on (15) and (16) and geometrical considerations on the intersection of f_1 and f_2 with the axes. ∎

4.2 Stability

We focus now on the stability of the existing equilibrium points.

Theorem 4.2 *Consider system* (13)*, assuming that $r_1 > 0$ and $r_2 > 0$. Then,*

1. *The origin is always unstable.*
2. *Assume now $\widehat{c}_{12} > 1$ and $c_{21} > 1$. Then by condition 2.(a) of Theorem 4.1, there exists a single coexistence equilibrium point E_3^+, that is unstable. There exists a separatrix line connecting the origin with E_3^+ that defines the basins of attraction of E_1 and E_2.*
3. *E_1 is globally asymptotically stable if and only if $0 < \widehat{c}_{12} < 1$ and $c_{21} > 1$.*
4. *E_3^- is globally asymptotically stable if and only if $0 < \widehat{c}_{12} < 1$ and $0 < c_{21} < 1$.*
5. *Finally, assume now $0 < c_{21} < 1$ and $\widehat{c}_{12} > 1$. Then, by the condition 2.(b) of Theorem 4.1,*

   (a) *E_3^+ and E_2 are locally asymptotically stable while E_-^c is unstable. There exist a separatrix connecting the origin with E_-^c that defines the basins of attraction of E_2 and E_3^+, if and only if $\widehat{c}_{12} > 1$ and $\psi_{b_2}(\widehat{c}_{12}) < c_{21} < 1$.*
   (b) *E_2 is globally asymptotically stable if and only if $0 < c_{21} < \psi_{b_2}(\widehat{c}_{12})$ and $\widehat{c}_{12} > 1$.*

Proof Let us consider the Jacobian matrix of (10)

$$J_F(w_1, \widehat{w}_2) := \begin{pmatrix} r_1(1 - w_2 - \widehat{c}_{12}w_2) & -r_1\widehat{c}_{12}w_1 \\ -r_1c_{21}\widehat{w}_2 & r_2(1 - b_2\sqrt{\widehat{w_2}} - c_{21}w_1) - \frac{1}{2}r_2b_2\sqrt{\widehat{w_2}} \end{pmatrix}$$

We analyze the characteristic equation and apply the Routh-Hurwitz criterion to the equilibrium points for the various cases of the statement of the theorem:

1. It is easy to see that in the system (13), $w_i' > 0$ for $w_1, \widehat{w}_2 \sim 0$.
2. The statement holds because the eigenvalues of $J_F(E_1)$ are $\lambda_1 = -r1$, $\lambda_2 = r_2(1 - c_{21})$. Therefore, E_3^- is a saddle and E_2 and E_1 are locally asymptotically

stable; in such case, there exists a separatrix line through both E_3^- and the origin 228
that defines the basins of attraction of E_1 and E_2. 229

3. Direct calculations yield the eigenvalues of $J_F(E_2)$, $\lambda_1 = -r_2(1 - \frac{3}{2}b_2)$, $\lambda_2 =$ 230
$r_1(1 - \widehat{c}_{12})$. The statement implies that E_2 is stable while E_1 is unstable. Also 231
theorem 4.1 shows that no equilibrium points exist in the positive cone, and the 232
flow of the system makes E_2 globally asymptotically stable. 233

4. This statement follows by a standard analysis of the flow of the system. 234

5. We focus first in assessing the stability in case of two coexistence equilibrium 235
points. This scenario in the system dynamics may arise, when coefficients 236
vary, essentially in two different ways. On one hand, when D changes from 237
being negative to positive. On the other hand, already there exits a single 238
coexistence equilibrium point and the x_2-nullcline f_2 crosses one of the semi- 239
trivial equilibrium points in such a way that a second one appears. The dynamical 240
scenario is the same, no matter how it arises. 241

Let us rewrite the Jacobian matrix in a more convenient form. System (13) 242
is of the form $w_i' = w_i f_i(w_i, w_j)$, so that at any coexistence equilibrium point 243
$E = (E_1, E_2)$ it follows that $f_1(E) = 0 = f_2(E)$. Thus: 244

$$J_F(E) := \begin{pmatrix} -r_1 E_1 & -r_1 \widehat{c}_{12} E_1 \\ -r_2 c_{21} E_2 & -\frac{1}{2} r_2 b_2 \sqrt{E_2} \end{pmatrix} \tag{18}$$

From expression (15) for $D = 0$, the characteristic polynomial of (18) at the 245
equilibrium point arising when f_1 and f_2 collide is 246

$$\lambda^2 + \left(\frac{b_2^2(c_{21} r_2 - 2r_1) + 4\widehat{c}_{12} c_{21} r_1}{4\widehat{c}_{12} c_{21}^2} \right) \lambda. \tag{19}$$

Thus, one eigenvalue is $\lambda_1 = 0$ and the other one, λ_2, because of the hypotheses 247
of this statement, is negative; in particular, both eigenvalues are simple. Thus, the 248
eigenvalues are continuous under small perturbations of the parameters involved 249
in expression (18). As E_3^- and E_3^+ appear, λ_2 keeps being negative in the 250
corresponding Jacobian matrices while λ_1 becomes negative for $J_F(E_3^-)$ and 251
positive for $J_F(E_3^+)$. This is shown by a standard analysis of the system flow 252
after the bifurcation takes place. 253

The second statement of 5. can be proved as 4. ∎ 254

5 Two Sessile Populations Interactions 256

System (8) can be rewritten in a more convenient form introducing new variables 257
and rescaling coefficients by setting 258

$$x_i = z_i^2, \quad r_i = \frac{\widehat{r}_i}{2}, \quad c_{ii} = b_i a_{ii}, \quad c_{ij} = \frac{d_i a_{ij}}{2}, \quad i, j = 1, 2. \tag{20}$$

This yields the so-called *auxiliary system*:

$$\begin{cases} z_1' = r_1 z_1 - c_{11} z_1^2 - c_{12} z_2 \\ z_2' = r_2 z_2 - c_{22} z_2^2 - c_{21} z_1 \end{cases} \tag{21}$$

It is apparent that the non-negative semi-axes are not invariant for the flow of system (21), so that this system does not help in assessing the stability of the trivial and semi-trivial equilibrium points.

As before we address first the existence of equilibrium points and then analyze their stability.

5.1 Equilibria

As mentioned earlier the trivial and semi-trivial equilibria of system (8) are given by (9). As for the coexistence equilibria, we consider the nullclines of the auxiliary system (21) corresponding to system (8), given by

$$z_2 = f_1(z_1) = z_1 \frac{r_1 - c_{11} z_1}{c_{12}}, \quad z_1 = f_2(z_2) = z_2 \frac{r_2 - c_{22} z_2}{c_{21}}.$$

The nullclines cross each other at the origin and their curvature and location imply that they meet up to three times or none on the positive cone, see Fig. 3, the discussion below and the discussion and conclusion Sect. 6.

However, system (8) may exhibit two additional coexistence states in the positive cone. Substituting the second equation into the first one we obtain a fourth-degree equation:

$$Q_c(z_1) = \frac{1}{c_{12}^2} z_1 P_c(z_1) = 0, \tag{22}$$

where $Q_c(z_1) = f_2(f_1(z_1))$ and

$$P_c(z_1) = c_{22} c_{11}^2 z_1^3 - 2 c_{22} c_{11} r_1 z_1^2 + (c_{11} c_{12} r_2 + c_{22} r_1^2) z_1 + c_{12} (c_{12} c_{21} - r_1 r_2).$$

The geometry of the phase portrait implies that the coexistence equilibrium lies in the box with the origin and $(r_1/c_1, r_2/c_2)$ as opposite vertices. Therefore, we use Sturm's Theorem to account for the number of positive roots of equation $P_c(z_1) = 0$. Let us recall that the Sturm's sequence of equation $P_c(z_1) = 0$ is given by
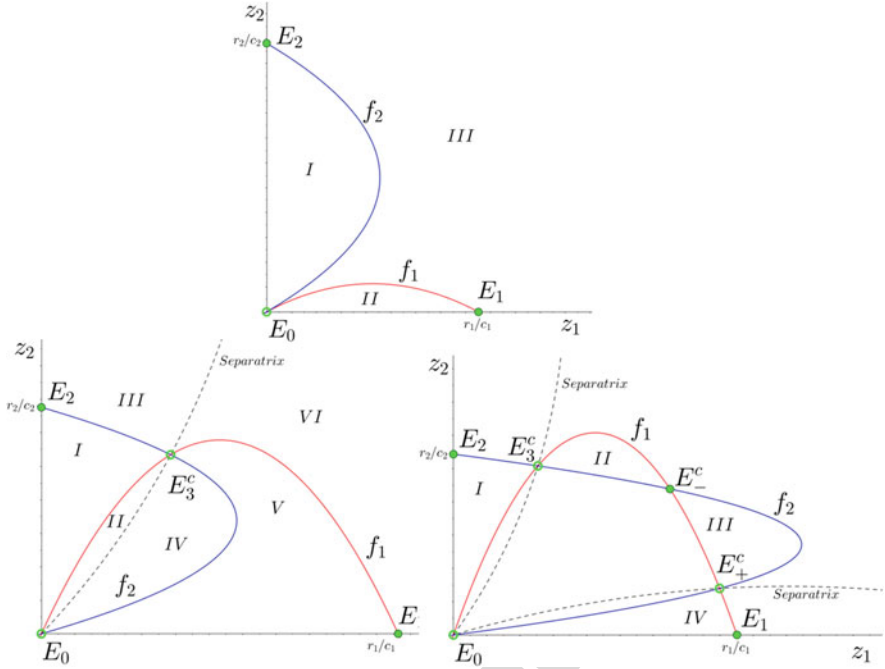
Fig. 3 Possible phase portrait of the corresponding auxiliary competition model (21). The horizontal (resp. vertical) axis refers to the sessile (resp. mobile) population. The curve f_1 (resp. f_2) stands for the nullcline of the sessile (resp. mobile) population. Solid points are locally asymptotically stable equilibria while non solid points are unstable equilibria. Left panel: for the parameter values $r_1 = 0.8$, $r_2 = 0.6$, $c_{12} = 1.2$, $c_{21} = 0.95$, $c_{11} = 0.47$, $c_{22} = 0.74$ condition (26) holds. Central panel: the parameter values $r_1 = 1$, $r_2 = 1$, $c_{12} = 1.51$, $c_{21} = 0.52$, $c_{11} = 0.66$, $c_{22} = 1.24$ fulfill conditions (27) and (28). Thus, the system exhibits the competitive exclusion principle, as for the classical competition model. Right panel: this scenario represents the tri-stable scenario. It is obtained for the parameter values $r_1 = 1$, $r_2 = 1$, $c_{12} = 0.28$, $c_{21} = 0.13$, $c_{11} = 0.47$, $c_{22} = 0.74$. In this case either one of the population could outcompete the other one, or both may coexist. In any case, the ultimate outcome of the system is determined just by the initial values

$$Seq_c(z_1) = \left\{ P_c(z_1), P_c'(z_1), R_1(z_1), R_2(z_1) \right\},$$

where the second term is its derivative of $P_c(z_1)$, and the remaining terms $R_i(z_1)$, $i = 1, 2$, are the remainders of the Euclidean divisions:

$$R_1(z_1) = -\text{rem}(P_c(z_1), P'(z_1)), \quad R_2(z_1) = -\text{rem}(P'(z_1), R_1(z_1)).$$

Then, evaluating each term of the Seq_c at the ends of interval $[0, r_1/c_{11}]$ we get the number of positive roots of $P_c(z_1) = 0$ as the number of changes of sign in $Seq_c(0)$ minus the number of change of signs in $Seq_c(\frac{r_1}{c_{11}})$. Thus, the actual Sturm's sequence is calculated on $P_c(z_1)$ instead of on $Q_c(z_1)$. Direct calculations lead to

$$P'_c(z_1) = 3c_{11}^2 c_{22} z_1^2 - 4c_{11} c_{22} r_1 z_1 + c_{11} c_{12} r_2 + c_{22} r_1^2 \tag{23}$$

$$R_1(z_1) := - \left(\frac{2r_2 c_{11} c_{12}}{3} - \frac{2c_{22} r_1^2}{9} \right) z_1 - \frac{9c_{11} c_{12}^2 c_{21} - 7c_{11} c_{12} r_1 r_2 + 2c_{22} r_1^3}{9c1} \tag{24}$$

$$R_2(z_1) := - \frac{9c_{11} c_{12}^2}{4(3c_{11} c_{12} r_2 - c_{22} r_1^2)^2} [4c_{11}^2 c_{12} r_2^3 + 27c_{11} c_{12}^2 c_{22} c_{21}^2 \tag{25}$$

$$- 18c_{11} c_{12} c_{22} c_{21} r_1 r_2 - c_{11} c_{22} r_1^2 r_2^2 + 4c_{22}^2 c_{21} r_1^3]$$

Theorem 5.1 *System* (8) *has no equilibrium points in the positive cone if*

$$c_{12} c_{21} - r_1 r_2 > 0 \tag{26}$$

Proof Consider the Sturm's sequences $Seq(0)$

$$P_c(0) = c_{12} \left(c_{12} c_{21} - r_1 r_2 \right), \qquad P'_c(0) = c_1 c_{12} r_2 + c_{22} r_1^2,$$

$$R_1(0) = \frac{-1}{9} \left(\frac{9c_{11} c_{12}^2 c_{21} - 7c_{11} c_{12} r_1 r_2 + 2c_{22} r_1^3}{c_{11}} \right)$$

and $R_2(0)$ is given by (25). On the other hand, $Seq(r_1/c_{11})$ consists of

$$P_c \left(\frac{r_1}{c_{11}} \right) = c_{12}^2 c_{21}, \quad P'_c \left(\frac{r_1}{c_{11}} \right) = r_2 c_{11} c_{12},$$

$$R_1 \left(\frac{r_1}{c_{11}} \right) = \frac{-c_{12}(9c_{12} c_{21} - r_1 r_2)}{9}$$

and $R_2(r_1/c_{11})$ is, again, given by (25), since it does not depend on z_1. Rearranging
terms

$$R_2(0) = \frac{-9c_{11} c_{12}^2}{4(3c_{11} c_{12} r_2 - c_{22} r_1^2)^2} [4 \left(c_{11}^2 c_{12} r_2^3 + c_{22}^2 c_{21} r_1^3 \right)$$

$$+ c_{11} c_{22}(27c_{12}^2 c_{21}^2 - 18c_{12} c_{21} r_1 r_2 - r_1^2 r_2^2)].$$

Note that the sign of $R_2(0) = R_2(r_1/c_{11})$ does not matter, since it is the
same for $Seq(0)$ and $Seq(r_1/c_{11})$. Therefore, gathering signs yield $Seq(0) =$

$\{+, +, -, sign(R_2(0))\}$ and $Seq(r_1/c_{11}) = \{+, +, -, sign(R_2(0))\}$, which con- 295
cludes the proof. ∎ 296

Assume now that condition (26) fails. Solving Eq. (22) under the assumption that 297
$c_{12}c_{21} - r_1r_2 = 0$ yields two complex roots along with $z_1 = 0$ as unique real root 298
with multiplicity 2. Recall that an equilibrium point in the third quadrant exists when 299
(26) holds. This equilibrium collides with the origin when $c_{12}c_{21} - r_1r_2 = 0$ and 300
appears in the positive cone as $c_{12}c_{21} - r_1r_2$ becomes negative. Besides, from the 301
analysis of the Sturm's sequence for $c_{12}c_{21} - r_1r_2 < 0$ at least one, and up to three, 302
positive coexistence equilibrium points exist. 303

Criteria leading to each outcome can be stated assessing conditions that control 304
the change of sign of the terms of the Sturm's sequence. Determining general 305
conditions is a hard task, since the terms of $Seq(0)$ and $Seq(r_1/c_{11})$ depend on 306
up to 6 parameters. In any case, we equate to zero each term with undetermined 307
sign of the Sturm's sequence and solve each expression for one parameter to obtain 308
conditions on the sign of each term. Solving the equations for c_i (resp. c_{ij}) yield 309
conditions for the exclusion or conditional tri-stability that depend the so-called 310
handling time (resp., on the competition strength) of each species. 311

Theorem 5.2 *Consider system* (8) *and assume that* 312

$$c_{12}c_{21} - r_1r_2 < 0 \qquad (27)$$

Then, 313

1. Assume that 314

$$9 < \frac{r_1r_2}{c_{12}c_{21}} \qquad (28)$$

and consider the straight lines 315

$$c_{22}^{\pm}(c_{11}) = \frac{1}{8c_{21}r_1^3}c_{11}\left[18c_{12}c_{21}r_1r_2 - 27c_{12}^2c_{21}^2 + r_1^2r_2^2 \qquad (29)\right.$$
$$\left. \pm\sqrt{(c_{12}c_{21} - r_1r_2)(9c_{12}c_{21} - r_1r_2)^3}\right]$$

in the $c_{11} - c_{22}$ parameter space, arising by setting $R_2(0) = 0$, see (25). *These* 316
lines define a sector region in the positive cone, see Fig. 4. Then, 317

(a) *The slope of $c_2 = c_2^{\pm}(c_{11})$ is positive.* 318
(b) *If (c_{11}, c_{22}) lies in between $c_2 = c_2^{\pm}(c_{11})$ three nontrivial equilibrium points* 319
$E_{\pm}^c$, E_3 in the positive cone exist. Ordered by its first component, $E_-^c <$ 320
$E_3^c < E_+^c$. 321
(c) *If (c_{11}, c_{22}) does not lie in between $c_2 = c_2^{\pm}(c_{11})$ then there exists a single* 322
nontrivial equilibrium point E_3 in the positive cone. 323
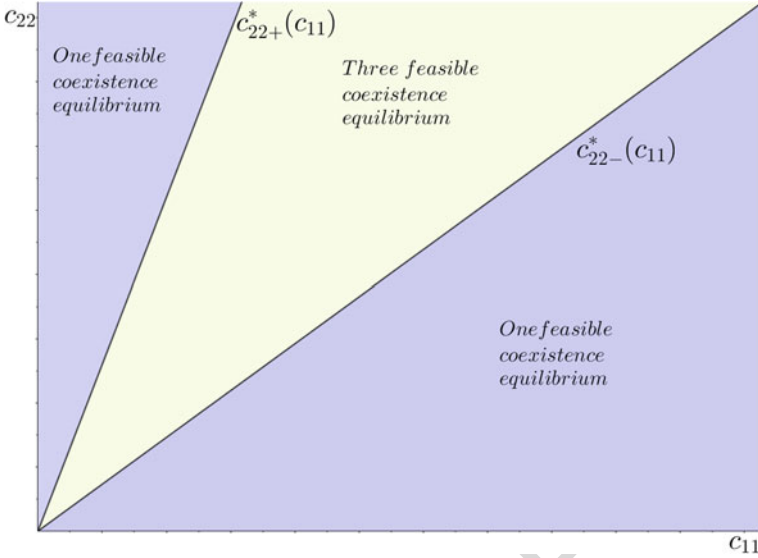
Fig. 4 Species competition outcomes in the $c_{11} - c_{22}$ parameter space, as function of the intraspecific competition $c_i, i, j = 1, 2$. The straight lines $c_{2+}^*(c_{11})$ show the thresholds values separating the regions where one or three coexistence equilibria exist in the positive cone. Namely, there exist three coexistence equilibria region consists of the (c_{11}, c_{22}) such that $c_{22-}^*(c_{11}) < c_{22} < c_{22+}^*(c_{11})$ (green colored area). Outside it, just one coexistence equilibrium is possible. The figure is generated with the parameter values $c_{12} = 0.5, c_{21} = 0.07, r_i = k_i = 1, i = 1, 2$

2. *Further, if condition*

$$9 > \frac{r_1 r_2}{c_{12} c_{21}} \tag{30}$$

holds, then there exists a single nontrivial equilibrium point E_3 in the positive cone. If condition (30) *is an equality, $c_2^{\pm}$ collide in a single straight line.*

Proof The equation $R_2(0) = 0$ is a second order equation in c_{22} of the form $-a(a_2 c_{22}^2 + a_1 c_{22} + a_0) = 0$. Solving it and rearranging terms we obtain expression (29). Note that condition (28), which, in particular, entails (27), ensures that the straight lines (29) are well defined, in the sense that the slopes are not complex but real numbers.

Note that a_0 and a_2 are positive; therefore, we need

$$a_1 = 27 c_{12}^2 c_{21}^2 - 18 c_{12} c_{21} r_1 r_2 - c_{12}^2 c_{21}^2$$

to be negative so that by solving $R_2(0) = 0$ in terms of c_{22} two positive roots are obtained. Rearranging terms, a_1 is equivalent to

$$a_1 = -(27 c_{12} c_{21}(c_{12} c_{21} - r_1 r_2) + r_1 r_2(9 c_{12} c_{21} - r_1 r_2))$$

therefore, conditions (27) and (28) imply that $a_1 > 0$, which proves 1.(a).

Let us recall that conditions (27) and (28) imply that $Seq(0) = \{-, +, -, ?\}$ and $Seq(r_1/c_{11}) = \{+, +, ?, ?\}$, so that the only way of having three equilibrium points is that $R_2(0) > 0$ and $R_1(c_{11}/r_1) > 0$. Direct calculations show that the latter condition follows from (28) while the former holds for values of c_{11} and c_{22} that are between the straight lines $c_{22} = c_2^{\pm}(c_{11})$. This completes the proof of 1.(b).

The remaining statements follow in a similar way and the details are omitted. ■

In addition, solving the equations for c_{ij} (respectively c_i) yields conditions for exclusion or conditional tristability that depend on the so-called on the competition strength of each species (respectively the handling time). Recall that system (8) has no equilibrium points in the positive cone, independently of the parameter c_{ij} or c_i, in view of theorem 5.1.

Theorem 5.3 *Consider system* (8) *and assume that condition* (27) *holds. Then,*

1. *Assume further that condition* (28) *is fulfilled and*

$$\frac{2}{9}\frac{c_{22}r_1^2}{c_{11}r_2} < c_{12} < \frac{1}{4}\frac{c_{22}r_1^2}{c_{11}r_2} := \bar{c}_{12}, \tag{31}$$

Consider also the curves

$$c_{21}^{\pm}(c_{12}) = \frac{1}{27}\frac{c_{22}r_1(9c_{11}r_2c_{12} - 2c_{22}r_1^2) \pm 2\sqrt{c_{22}(c_{22}r_1^2 - 3c_{11}r_2c_{12})^3}}{c_{11}c_{22}c_{12}^2} \tag{32}$$

in the $c_{12}-c_{21}$ parameter space, obtained by setting $R_2(0)$ to zero, see expression (25). *These curves define a region in the positive cone, shown in Fig. 5. Then,*

   (a) *If (c_{12}, c_{21}) lies in between $c_{21} = c_{21}^{\pm}(c_{12})$ then there exist three nontrivial equilibrium points $E_{\pm}^c, E_3$ in the positive cone, ordered by their first component, $E_-^c < E_3^c < E_+^c$.*

   (b) *If (c_{12}, c_{21}) does not lie in between $c_{21} = c_{21}^{\pm}(c_{12})$ then there exists a single nontrivial equilibrium point E_3 in the positive cone.*

2. *Besides, if condition* (30) *holds, then there exists a single nontrivial equilibrium point E_3 in the positive cone. If condition $c_{12} = \frac{1}{3}\frac{c_{22}r_1^2}{c_{11}r_2}$, $c_{21}^{\pm}$ coalesce into a single curve. The outcome is also a single positive coexistence equilibrium point.*

Proof Let us consider $R_2(0) = 0$, again it is a second order equation of the form $-b(b_2c_{21}^2 + b_1c_{21} + b_0) = 0$. Solving such an equation in c_{21} and arranging terms yields expression (32). Note that the rightmost condition (31) ensures that the curves (32) are well defined, i.e. the expression under the square root is positive. Coefficient b_2 is positive, so that equation $R_2(0) = 0$ possesses two positive roots if

$$b_1 < 0 \Leftrightarrow c_{12} > \frac{2c_{22}r_1^2}{9c_{11}r^2}$$
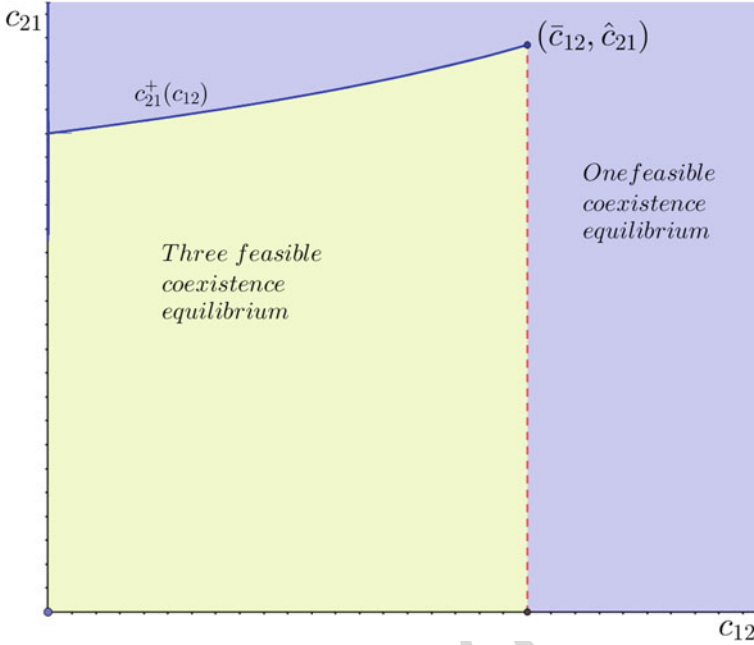
Fig. 5 Species competition outcomes as function of the intra-species competition parameter c_{ij}, $i, j = 1, 2$. The region in green delimited by $c_{21} = c_{21}^+(c_{12})$, the axes and $c_{12} = \bar{c}_{12}$ stands for the region in the parameter space where 3 positive (non trivial) equilibrium points arise. In the outer region (in purple) just one coexistence equilibrium is possible. The figure has been generated with the parameter values $c_{12} = 0.5$, $c_{21} = 0.07$, $r_i = k_i = 1$, $i = 1, 2$

and

$$b_0 > 0 \Leftrightarrow c_{12} < \frac{c_{22} r_1^2}{4 c_{11} r^2}.$$

Summing up, c_{12} fulfilling (31) ensures i) that $c_{21}^{\pm}$ are well defined and ii) $R_2(0)$ is positive if $c_{21}^-(c_{12}) < c_{21} < c_{21}^+(c_{12})$. Therefore, $Seq(0) = \{-, +, ?, +\}$ and $Seq(r_1/c_{11}) = \{+, +, +, +\}$, so that the only way of having three equilibrium points is that $R_1(0) < 0$, that is equivalent to:

$$c_{21} > \frac{r_1(7 c_{11} r_2 c_{12} - 2 c_{22} r_1^2)}{9 c_{11} c_{12}^2} := \tilde{c}_{21}(c_{12}).$$

Direct calculations show that $\tilde{c}_{21}(c_{12})$ crosses the c_{12} axis further away than $c_{21}^-(c_{12})$ does and that $\tilde{c}_{21}(c_{12}) < c_{21}^-(c_{12})$. Therefore, $c_{21}^-(c_{12}) < c_{21} < c_{21}^+(c_{12})$ implies $\tilde{c}_{21}(c_{12}) < c_{21}$, which completes the proof of 1.(b).

The remaining statement follows in the same way and is therefore omitted. ∎

5.2 Stability

We gather in the following theorem the stability conditions of the equilibrium points ^{375} found in the previous section. ^{376}

**Theorem 5.4** *Consider system* (8), *assuming that* $r_1 > 0$ *and* $r_2 > 0$. *Then,* ^{377}

1. *The origin is always unstable and the semi-trivial equilibrium points are always* ^{378} *locally asymptotically stable.* ^{379}
2. *Assume that condition* (26), $c_{12}c_{21} - r_1r_2 > 0$, *holds, so that there are no positive* ^{380} *equilibrium points. Then there is a separarix through the origin (which is a* ^{381} *saddle) delimiting the basins of attraction of the semi-trivial equilibrium points.* ^{382} *Thus, one of the species goes extinct depending on the system initial conditions.* ^{383}
3. *Assume now that conditions* (30) *hold. Then there exists a single coexistence* ^{384} *equilibrium point* E_3^c, *that is unstable. There exists a separatrix line passing* ^{385} *through* E_3^c *and the origin that defines the basins of attraction of* E_1 *and* E_2. ^{386}
4. *Finally, if conditions* (28) *and* (31) *hold, there exist three nontrivial equilibrium* ^{387} *points:* E_3^c *is locally asymptotically stable while* $E_\pm^c$ *are unstable. There exist* ^{388} *separatrices passing through the origin and each of* $E_\pm^c$ *that define a region were* ^{389} E_3^c *is located and define the basis of attraction of* E_1, E_2 *and* E_3^c. ^{390}

Proof

1. Keeping in mind remark 3.2, consider the nullclines of system (8), given by ^{392}

$$f_1 : x_2 = \frac{1}{a_{12}^2} \left[r_1 \sqrt{x_1} - b_1 a_{11} x_1 \right]^2,$$
$$f_2 : x_1 = \frac{1}{a_{21}^2} \left[r_2 \sqrt{x_2} - b_2 a_{22} x_2 \right]^2,$$
$$(33)$$

   Condition (26) imply that the nullclines (33) divide the positive cone in three ^{393} different regions, as displayed in Fig. 6. Region I is characterized for $x_1' < 0$ ^{394} and $x_2' > 0$, and the flow points inward on the boundary of region I, so that ^{395} it is a trapping region and solutions starting within the closure of region I are ^{396} attracted by E_2, so that the origin is unstable. Proceeding as before, we find ^{397} that region III is a trapping region and any solution starting within the closure ^{398} of region III is attracted by E_1. It is immediate that E_1 and E_2 are locally ^{399} asymptotically stable just by considering the flow of the system on the straight ^{400} lines given by $\left\{ (z_1, v_{2z_2}), z_1 \geq v_{2z_1} \right\}$ and $\left\{ (v_{1z_1}, z_2), z_2 \geq v_{1z_2} \right\}$ respectively, ^{401} where (v_{1z_k}, v_{2z_k}) are the coordinates of the vertex of the nullcline of z_k, $k = 1, 2$. ^{402}
2. Consider a perfectly symmetric competition, i.e. $c_{12} = c_{21}$, $c_{11} = c_{22}$ and $r_1 =$ ^{403} r_2. Then, from the geometry of the phase portrait, the straight line $z_2 = z_1$ is ^{404} the *stable manifold*, i.e. a forward invariant curve such that solutions starting on ^{405} this line converge to the origin. Besides, it divides the positive cone on the basins ^{406} of attraction of the semi-trivial equilibrium points. Furthermore, because of the ^{407} continuity of the flow with respect to the system parameter and the uniqueness ^{408}
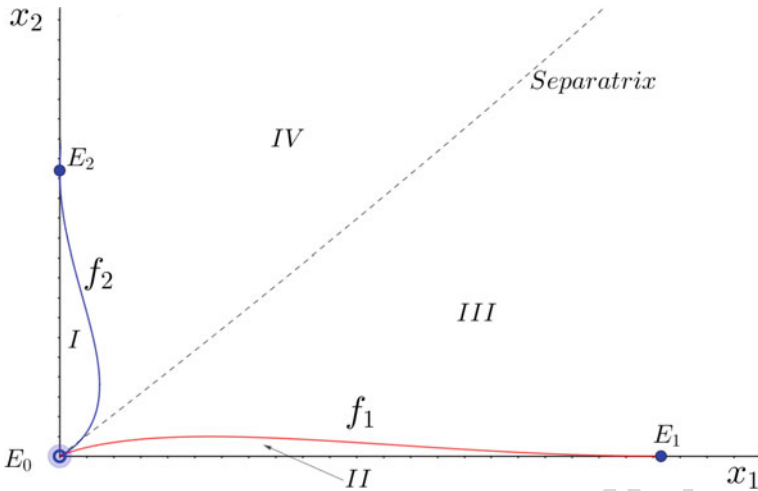
Fig. 6 The phase portrait for the competing populations. The figure is generated with the parameter values $a_{12} = 0.84$, $a_{21} = 1.10$, $a_{11} = 0.99$, $a_{22} = 0.75$, $r_i = 1$, $i = 1, 2$

of solutions on the positive cone, this invariant manifold changes continuously as the model parameters change as long as no positive equilibrium points appear in the positive cone.

3. This proof is an adaptation of the one of Theorem 4.2, item 2.a in [8]. Consider, as before, the perfectly symmetric case. Then the geometry of the phase plane ensures that E_3 is a saddle-node and that the straight line $z_2 = z_1$ is its stable manifold that defines the basins of attraction of the semi-trivial equilibrium points. As argued before, this setting remains qualitatively the same as the coefficients of the system vary continuously whenever no additional equilibrium points show up in the positive cone.

4. This statement follows *mutatis mutandi* from the previous one (see also the proof of Theorem 4.2, statement 2.a in [8]). ∎

6 Discussion and Conclusions

We now interpret the mathematical results from a biological point of view, comparing the new model with the classical one. A first and important remark concerns both intra- and interspecific competition coefficients. They are expressed in the same units, $1/(time \times individuals)$ for intra- and interspecific competition, respectively, in the classical model. However the units in the sessile populations model are: $1/(time \times individuals)$ and $1/time$. If populations are counted as number of individuals, there is no difference, as all these coefficients become frequencies. However, if the populations represent animals or plants, for instance, a possibility

is to count them using biomass. In such case there is a difference in the units. But even if units are different, nullclines can be qualitatively compared, as well as the structure of each model possible outcome.

The main results follow.

1. When a mobile and a sessile population compete, the dynamical outcomes are those of the classical model plus a bi-stable conditional coexistence.
2. Instead, when two sessile populations compete, the competition outcomes are reduced to competitive exclusion due to the system's initial conditions and tri-stable conditional coexistence.

Thus, sessility precludes global outcomes and puts the focus not only on the competitive abilities of each species, but also on the initial amount of individuals. Namely, there is neither global coexistence, for which species would coexist regardless of the initial amount of individuals of each one of them, nor global extinction where a "super-competitor" would rule out the other species independently of the initial composition of the community.

This is an interesting feature from the management point of view, since perturbations, whether human-driven or not, may drastically change the system outcome.

We next analyze in deeper detail each one of these features.

6.1 Sessile vs Mobile Species Competition

Theorem 4.2 concerns a mobile population 1 competing with a sessile population 2. It follows from this Theorem that all the dynamical outcomes of the classical model (5) are allowed and, in addition, bi-stable conditional coexistence in favor of the sessile population arises, except for a bi-stable conditional coexistence region that reduces the range in which the sessile species outcompetes the mobile one. The last dynamical outcome has already been observed in [8, 9] when modifying the classical competition model with Holling type II and IV competitive responses. Also in [1, 22] when considering social herd-induced behavior in one of the competing species.

The structure of the regions in the parameter space $\widehat{c}_{12} - c_{21}$ leading to each competitive outcome, see Fig. 2, is equivalent to the one of the classical model except for the bi-stable conditional coexistence in favor of the sessile species region. This region is set in the region where the classical model predicts that the mobile species would be excluded by the sessile species, and borders the species exclusion due to the system's initial conditions and (partially) the global coexistence regions, see Fig. 1. Therefore, in such a region the sessile species 2 cannot be eliminated by the mobile species 1. On the contrary, the mobile species has the chance of surviving via coexistence provided that the initial values are appropriate, see the bottom panel of Fig. 2. Thus, coexistence is more likely to occur than in the classical model.

Interestingly, consider interspecific competition coefficients $(\widehat{c}_{12}, c_{21})$ values belonging to the region where the sessile species 2 wins. Fixing $\widehat{c}_{12}$, as the effect of

the mobile species 1 on the sessile species 2, we find that $c_{21} < \phi_{b_2}(\widehat{c}_{12})$ increases and crosses the curve $c_{21} = \phi_{b_2}(\widehat{c}_{12})$, the mobile species 1 has the chance of surviving via coexistence with the sessile species. A further increment such that $c_{21} > 1$ makes the effect of the mobile species 1 on the sessile species 2 strong enough so that in the end only one species survives.

We summarize the results as follows:

- From a certain point of view, being sessile is not a serious handicap for a sessile species that faces competiton with a mobile population. This means that the sessile population will survive for the same parameter value ranges as for the classical model, although for the parameters in the dark-blue region in Fig. 2 the sessile species will share the environment with the mobile population.
- In contrast, the mobile population is more likely to survive when facing a sessile population than a mobile one. This fact is reflected by the above mentioned dark blue region in Fig. 1 that corresponds to the dynamical scenario depicted in the bottom panel of Fig. 2. Note that neither such a region nor nullclines configurations do exist in the classical model, when both populations are mobile.

6.2 The Intra- and Interspecific Competition Effect for Nullclines

We first analyze qualitatively the nullclines of system (8) versus the nullclines of the classical competition model (5). Let us note an important fact concerning both intra- and interspecific competition coefficients. These coefficients are somewhat non comparable since they are expressed in different units, in the classical/sessile population models. Therefore, even if we plot both nullclines on the same axes, as in Fig. 7, we do not know how these parameters vary together. Keeping this in mind, we focus on the x_1 nullclines given by

$$x_2 = f_1(x_1) = \frac{1}{a_{12}}(\widehat{r}_1 - a_{11}x_1) \qquad x_2 = \widehat{f}_1(x_1) = \frac{x_1}{d_1^2 \widehat{a}_{12}^2}(\widehat{r}_1 - b_1 \widehat{a}_{11}\sqrt{x_1})^2 \tag{34}$$

As mentioned earlier the nullcline of species 1 defines the values of population size of species 2 that allow species 1 to thrive. For instance, the f_1 nullcline of the classical model is a straight line with negative slope, see Fig. 7, blue dotted straight line, which means that the larger x_1 is, the less tolerant to the presence of x_2 it is. In other words, it means that x_1 continues growing only if x_2 decreases.

Figure 7 represents the possible relative positions of the x_1 nullcline in the classical and sessile populations models.

A first claim is that at low x_1 population size the sessile model is highly tolerant to an increase of the number of individuals for both species 1 and species 2. This feature, which is at odds with the classical model, can be explained by

considering the peculiarities of the sessile model. Indeed, interactions take place
at the boundary of either the vital surroundings of each individual (intraspecific
case) or the region occupied by each population (interspecific case). On one hand,
at low population size intraspecific competition does not play a major role as the
population grows, since individuals only interact with the nearby ones and there
are only a few of them. At the same time, interspecific interactions take place only
at the boundary of the area occupied by species 1. Thus, population growth is the
main driver of population dynamics at low densities. This trend is maintained at
low densities, while $\widehat{f}_1$ is increasing. Direct calculations yield that the maximum of

$$\widehat{x}_2 := \widehat{f}_1(\widehat{x}_1) = \frac{1}{4^2} \frac{r_1^4}{b_1^2 a_{11}^2 a_{12}^2} \text{ is reached at } \widehat{x}_1 := \frac{1}{4} \left(\frac{r_1}{b_1 a_{11}} \right)^2.$$

A second claim is that from $\widehat{x}_1$ onwards the nullcline decreases, meaning that if
x_1 increases slightly, so that intraspecific competition pressure increases, species 1
can keep growing only if species 2 reduces the interspecific competition pressure.
That is, the trend is similar to that of the classical model,

A third feature is that nullclines $\widehat{f}_1$ and f_1 may not cross the horizontal axis at
the same point. Indeed, the crossing points can be ordered in any way, as shown in
Fig. 7.

Finally, note that both nullclines can meet essentially in four different ways, as
shown in Fig. 7. Let us give an interpretation for instance to panel (A1). In the region
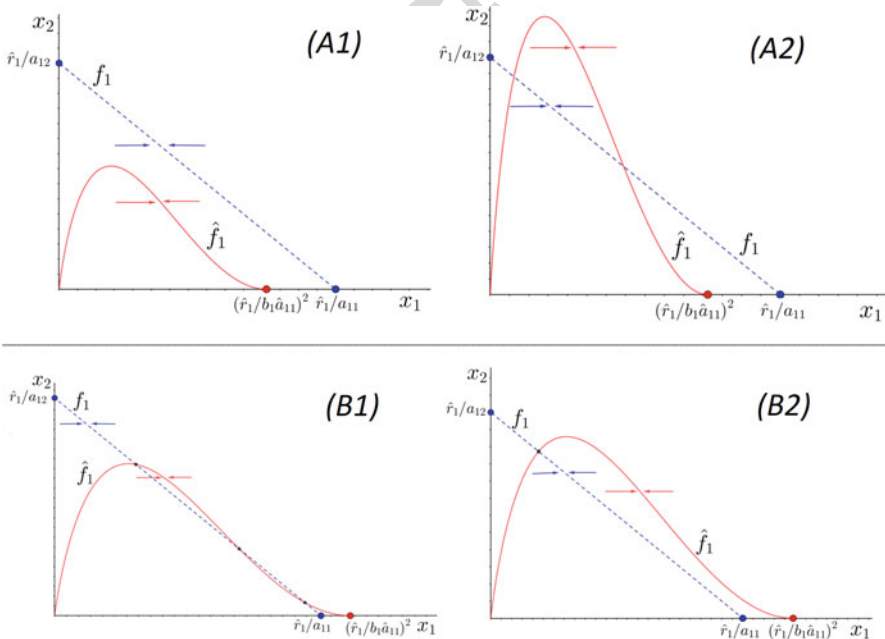

Fig. 7 The nullclines $x_1' = 0$ of systems (8) and classical model (5)

below $\widehat{f_1}$ (above f_1) x_1 increases (decreases) in both models. On the contrary, in the region between $\widehat{f_1}$ and f_1 species 1 would keep growing if represented by the classical model but would decrease if represented by the sessile populations model.

Note that the maximum of $\widehat{f_1}$ can be below (panel (A1)) or above (panel (A2)) f_1.

6.3 The Intra- and Interspecific Interaction and Coexistence Equilibria

Finally, we examine competition outcomes taking into account intra- and interspecific competition, that yield conditions for species exclusion or conditional tri-stability due to the system's initial conditions.

We may let either the intraspecific competition parameters c_{ii} vary for fixed values of the interspecific competition parameters c_{ij} or the other way around. Note that coefficient c_{ii} is a conglomerate of different factors that include intraspecific interaction a_{ii} and b_i, the relation between the perimeter of both the "vital space" around each individual and the perimeter of the area occupied by the whole population.

6.4 Varying Intra- Specific Competition Coefficients for Fixed Values of Interspecific Competition Coefficients

Theorem 5.2 indicates that under conditions (27) and (28) two possible outcomes are possible: either both species can coexist via tri-stable conditional coexistence or one of them goes extinct via the system's initial conditions.

In particular, with (c_{11}, c_{22}) lying between $c_{22} = c_{22}^{\pm}(c_{11})$, namely the straight lines defined in (29), there is tri-stable coexistence. Thus, consider fixed values of c_{ij} and r_i fulfilling the hypotheses of Theorem 5.2. Then, for each fixed value c_2^*:

- There is species coexistence via conditional tri-stability for $c_{11} \in (c_{11}^-, c_{11}^+)$ where $c_{22}^* = c_{22}^+(c_{11}^-)$ and $c_{22}^* = c_{22}^-(c_{11}^+)$.
- There is one species exclusion due to the system's initial conditions if $c_{11} \notin (c_{11}^-, c_{11}^+)$.

Everything works symmetrically if c_{11} is fixed and c_{22} varies. We may conclude that for each value of c_{ii} coexistence is possible for moderate values of c_{jj}, $i \neq j$. However, either low or large enough values of c_{ii} or c_{jj} would break coexistence.

Consistently with the classical model, numerical experiments show that the basin of attraction of E_1 is larger than the basin of attraction of E_2 for $c_{11} < c_{11}^-$. The result is reversed as $c_{11} > c_{11}^+$. This feature strongly suggests that the trade-
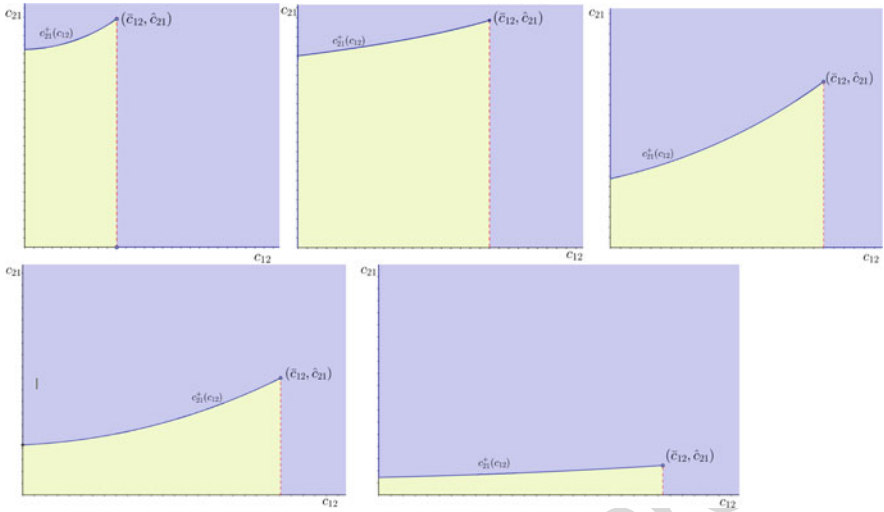
Fig. 8 Competition outcomes of system (8) as function of the interspecific competitive interaction c_{12}, c_{21} for a fixed value of c_{11} and increasing values of c_{22}. The figure is based analytic the expression or numerical calculations depending on each respective case and has been edited to improve it. Numerically fixed values of the parameters: $r_1 = 7.5$, $r_2 = 8$ $c_{11} = 0.9$ and of $c_{22} = 0.3, 1.1, 2.75, 3.3,$ and 16.7

off between intra- and interspecific competition forces works differently in sessile populations and in mobile populations.

6.5 *Inter-Specific Competition*

We fix now $c_{ii} > 0$ for $i = 1, 2$ and assume that condition (31) in Theorem 5.3 holds. Then, in a similar way as in the previous paragraph, there are conditions on the model coefficients that lead either to coexistence via conditional tri-stability or to species exclusion due to the system's initial conditions . In contrast, the curves defining the combination of interspecific competition coefficients leading to each outcome are nor straight lines and define a closed region on the positive cone, see Fig. 8. Inside such a region there is conditional coexistence while outside the competitive exclusion principle rules the system's outcome. Note that the shape of such a region changes as the other parameters change (in this case c_{22} changes as shown in the caption of Fig. 8). Note that the tri-stability region starts dropping towards the axis c_{12} as c_{22} increases.

Fixing c_{ii} and varying c_{ij}, this viewpoint is consistent with the classical model, meaning that a pair (c_{12}, c_{21}) close to the horizontal c_{12}-axis, i.e., $c_{12} > c_{21}$, makes the basin of attraction of E_2 larger than the one of E_1 and conversely.

Similarly, when we fix c_{ii}, moderate values of c_{ij} seem to promote species coexistence.

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