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1 **MULTIPLICITY OF NEUTRALLY STABLE PERIODIC ORBITS**
2 **WITH COEXISTENCE IN THE CHEMOSTAT SUBJECT TO**
3 **PERIODIC REMOVAL RATE**

4 THOMAS GUILMEAU* AND ALAIN RAPAPORT†

5 **Abstract.** We identify a taxonomic property on the growth functions in the multi-species
6 chemostat model which ensures the coexistence of a subset of species under periodic removal rate.
7 We show that proportions of some powers of the species densities are periodic functions, leading
8 to an infinity of distinct neutrally stable periodic orbits depending on the initial condition. This
9 condition on the species for neutral stability possesses the feature to be independent of the shape of
10 the periodic signal for a given mean value. We give also conditions allowing the coexistence of two
11 distinct subsets of species. Although these conditions are non-generic, we show in simulations that
12 when these conditions are only approximately satisfied, then the behavior of the solutions is close
13 from the non-generic case over a long time interval, justifying the interest of our study.

14 **Key words.** Chemostat model, Periodic removal rate, Coexistence, Poincaré map, Multiplicity
15 of periodic orbits, Neutral stability.

16 **MSC codes.** 34C25, 37C25, 92-10, 92D25, 92D40

17 **1. Introduction.** The mathematical model of the chemostat can represent a
18 vast array of natural phenomena where different living species compete for a common
19 limiting resource. In particular, it is widely used to model waste water bio-processes
20 or to capture competition for a single resource in ecological modeling [15, 5]. Recall
21 that the chemostat is originally an experimental device in which bacterial species grow
22 in a perfectly stirred vessel of constant volume, continuously removed and fed with
23 fresh substrate. Of course, the mathematical model of the chemostat reflects also the
24 behavior of this device.

25 When several species (of densities x_i , $i = 1, 2, \dots$) all consume a single substrate
26 that is fed in the ecosystem at a constant rate, then the mathematical theory of the
27 chemostat claims that the *Competitive Exclusion Principle* holds, meaning that all the
28 species will asymptotically disappear from the system, except the fittest one [15, 5].
29 However, in more complex environments, this property does not always hold. This is
30 for instance the case of periodic operation of bioreactors [13] or temporal fluctuations
31 in ecology [6, 4, 10]. If the environment favors for some time one species and then
32 another one in a balanced way, then one may expect the two species to coexist. A
33 large part of the literature is dedicated to the study of the asymptotic behavior of
34 these dynamics, with two or more species, under periodic removal rate [16, 1, 7, 9]
35 or periodic nutrient input [6, 14, 4, 17] or both [18, 11].

36 Indeed, when a vessel with two species of concentrations $x_i(t)$ at time t ($i = 1, 2$)
37 is fed with a periodic removal rate, the system can exhibit the following different
38 behaviors :

- 39 • The two species are washed out, that is $\lim_{t \rightarrow +\infty} x_i(t) = 0$, for $i = 1, 2$.
- 40 • One species only is washed out while the other survives.
- 41 • The two species coexist, that is $x_i(t) > \epsilon > 0$, for $t \geq 0$ and $i = 1, 2$, for some
42 $\epsilon > 0$.

43 Those behaviors can be predicted using the Floquet theory. Namely, the Flo-

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44 quiet exponents allow to determine if the periodic solutions with only one species are
 45 unstable. If both of these single-species periodic solutions are hyperbolic unstable,
 46 then the theory of competitive planar systems [2] applied to the chemostat model
 47 shows that any positive solution converges asymptotically to a periodic solution with
 48 species coexistence (a complete description of this theory is given for instance in [15]).
 49 However, the possibility of having several attracting periodic orbits remains an open
 50 problem. Although there is no theoretical obstruction for this, no such example has
 51 been yet exhibited in the literature. Let us underline that for a given set of species,
 52 the condition for the single-species periodic solutions to be unstable depends on the
 53 periodic removal rate function, and not only on its mean value. Differently to the sta-
 54 tionary environment for which the single break-even concentrations determine which
 55 species can survive, the shapes of the growth functions come into play in periodic
 56 environments.

57 In the present work, we investigate how having species whose growth functions
 58 share similar shapes allow their coexistence and the multiplicity of neutrally stable
 59 periodic orbits (with two or more species). We do not assume the single-species
 60 periodic solutions to be hyperbolic, and generalize in a functional way the neutral
 61 stability condition in constant environment (which is given by the equality of break-
 62 even concentrations). The construction that we propose here is non-generic, relying
 63 on a relatively strong condition on the growth functions that is deemed as unfeasible
 64 in real life. However, one may face practical situations close from this non-generic
 65 case, which may provide a better understanding of the periodic chemostat over a long
 66 duration.

67 Our construction lies on the concept of "taxon", which in this paper, denotes a
 68 group of species whose growth functions share the same shape, in a sense which is
 69 made precise later on. We show that the fittest species from each taxon behave like
 70 one species to some extent, and when they can coexist, then there exists an infinite
 71 number of periodic orbits. Moreover, we also study the case when two taxa are present
 72 in the chemostat. In this situation, we show that the fittest species from each taxon
 73 can coexist all together, under an additional condition of instability of single-species
 74 periodic solutions chosen in each taxon.

75 The paper is organized as follows. In the next Section 2, we recall the equa-
 76 tions of the model with the usual assumptions and give some useful definitions and
 77 preliminary results. In Section 3, we present our new conditions with a concept of
 78 "taxon" and show some relevant properties. Sections 4 and 5 give our main results,
 79 first for a single taxon and then for competition between taxa. Finally, we presents
 80 and discusses several numerical simulations to illustrate our results Section 6, before
 81 drawing conclusions in Section 7.

82 **2. The setting.** We consider the multi-species chemostat model written as fol-
 83 lows

$$84 \quad (2.1) \quad \begin{aligned} \dot{s} &= u(t)(s_{in} - s) - \sum_{i=1}^n \frac{\mu_i(s)}{Y_i} x_i, \\ \dot{x}_i &= (\mu_i(s) - u(t))x_i, \quad 1 \leq i \leq n, \end{aligned}$$

85 (with $n \geq 2$) where s is the substrate concentration, s_{in} the input substrate concen-
 86 tration and x_i ($1 \leq i \leq n$) are the respective concentrations of the n populations. We
 87 recall the well-known fact that the yield coefficients Y_i , $1 \leq i \leq n$ can be taken equal
 88 to one without loss of generality, by a change of variables (x_i/Y_i replaced by x_i). As
 89 usual, the growth functions $\mu_i(\cdot)$ satisfy the following properties.

90 *Assumption 2.1.* For any $i = 1, \dots, n$, μ_i is a C^1 increasing function from \mathbb{R}_+ to
 91 \mathbb{R}_+ with $\mu_i(0) = 0$.

92 Under this assumption, we define classically the *break-even concentration* for each
 93 species $i = 1, \dots, n$ as the function

$$94 \quad \lambda_i(v) := \sup \{s \in \mathbb{R}_+; \mu_i(s) < v\}, \quad v > 0.$$

95 Note that when $\lambda_i(v)$ is finite, one has necessarily $\mu_i(\lambda_i(v)) = v$.

96 *Assumption 2.2.* The removal rate $u(\cdot)$ is a measurable function from $[0, +\infty)$ to
 97 $[u_-, u_+]$ with $0 < u_- \leq u_+$, which is T -periodic (with $0 < T < +\infty$). We posit

$$98 \quad \bar{u} = \frac{1}{T} \int_0^T u(t) dt.$$

99 Consider now the variable $b := s + \sum_{i=1}^n x_i$, whose dynamics is given by

$$100 \quad (2.2) \quad \dot{b} = u(t)(s_{in} - b).$$

101 Under Assumption 2.2, one has $u(t) \geq u_- > 0$ at any $t \geq 0$ and one can deduce that
 102 the solution of (2.2) converges exponentially to s_{in} , independently of the initial con-
 103 dition of (2.1). With Assumption 2.1, the solutions of (2.1) are uniquely defined and
 104 bounded for any non-negative initial condition. Therefore the asymptotic behavior of
 105 the $n + 1$ dimensional system (2.1) is determined by the n dimensional dynamics

$$106 \quad (2.3) \quad \dot{x}_i = \left[\mu_i \left(s_{in} - \sum_{j=1}^n x_j \right) - u(t) \right] x_i, \quad 1 \leq i \leq n,$$

107 which leaves the set

$$108 \quad \Delta_0 := \left\{ x \in \mathbb{R}_+^n; \text{ such that } \sum_{i=1}^n x_i \leq s_{in} \right\}$$

109 forwardly invariant. In the remaining, we shall consider the asymptotic dynamic (2.3)
 110 on the set Δ_0 only (which is biology relevant in the chemostat framework).

111 Note that solutions of (2.3) with $x_i(0) = 0$ for some i are such that $x_i(t) = 0$ for
 112 any t . Therefore, by uniqueness of solutions of (2.3), we deduce that a solution $x(\cdot)$
 113 of (2.3) with a positive initial condition has to stay positive for any time.

114 We give below a Lemma that will be useful in the rest of the paper.

115 **LEMMA 2.3.** *There exists a number $\underline{s} \in (0, s_{in})$ such that the subset*

$$116 \quad \Delta := \left\{ x \in \Delta_0; s_{in} - \sum_{i=1}^n x_i > \underline{s} \right\}$$

117 *is forward invariant and attractive by the dynamics (2.3).*

118 *Proof.* Posit $s = s_{in} - \sum_{i=1}^n x_i$. Since x is a solution of (2.3) and the set Δ_0 is
 119 forward invariant, it comes

$$\begin{aligned}
 120 \quad \dot{s} &= - \sum_{i=1}^n \mu_i(s) x_i(t) + u(t)(s_{in} - s) \\
 121 \quad &\geq - \left(\max_{1 \leq i \leq n} \mu_i(s) \right) \sum_{i=1}^n x_i(t) + u(t)(s_{in} - s) \\
 122 \quad &\geq - \left(\max_{1 \leq i \leq n} \mu_i(s) \right) s_{in} + u(t)(s_{in} - s) \\
 123 \quad &\geq g(s) := - \left(\max_{1 \leq i \leq n} \mu_i(s) \right) s_{in} + u_-(s_{in} - s). \\
 124
 \end{aligned}$$

125 The function g is continuous and decreasing with $g(0) = u_- s_{in} > 0$ and $g(s_{in}) < 0$.
 126 By the intermediate value Theorem, there exists a number $s_m \in (0, s_{in})$ such that
 127 $g(s_m) = 0$ with $g(s) > 0$ for $s < s_m$. Therefore, for any $\underline{s} \in (0, s_m)$, the domain
 128 $\{s > \underline{s}\}$ is forwardly invariant and attractive by the dynamics of s , which amounts to
 129 claim that the subset Δ is forward invariant and attractive by the dynamics (2.3). \square

130 **3. A taxonomic assumption and its consequences.** We shall consider sub-
 131 sets $I \subset \{1, \dots, n\}$ of at least two species, whose growth functions μ_i ($i \in I$) share a
 132 common property, defining what we propose to call a *taxon* in the present context.

133 **DEFINITION 3.1.** *A subset of populations $I \subset \{1, \dots, n\}$ belong to a same taxon if*
 134 *there exists a C^1 increasing function φ with $\varphi(\underline{s}) < u_-$ and $\varphi(s_{in}) > u_+$, and numbers*
 135 *$\alpha_i > 0$, $\beta_i \in \mathbb{R}$ for $i \in I$ such that*

$$136 \quad (3.1) \quad \mu_i(s) = \alpha_i \varphi(s) + \beta_i, \quad s \in [\underline{s}, s_{in}], \quad i \in I.$$

137 *We shall say that such a function φ is a generating growth function of the taxon. We*
 138 *also define the subset $I^* \subset I$, which is such that*

$$139 \quad I^* := \{i \in I; \lambda_i(\bar{u}) = \min_{j \in I} \lambda_j(\bar{u})\}.$$

140 In this definition, the choice of the generating function φ is not unique but it
 141 can typically represent a *canonical growth function* that verifies Assumption 2.1 so
 142 that the growth functions μ_i among a taxon differ only by an affine transformation
 143 away for 0 i.e. on the interval $[\underline{s}, s_{in}]$. Note that condition (3.1) cannot be imposed
 144 for any $s > 0$ if $\beta_i \neq 0$, because growth functions have to be equal to 0 at the origin
 145 (Assumption 2.1). Several examples of growth functions that satisfy Assumption 2.1
 146 and condition (3.1) will be given in Section 6. Let us point out that this condition
 147 does not prevent the graphs of the functions μ_i to cross on the domain $[\underline{s}, s_{in}]$.

148 The second part of Definition 3.1 concerns the subset $I^* \subset I$, which is made of all
 149 the species that share the same minimal break-even concentration. In some sense, the
 150 set I^* contains the fittest species, as these are the surviving species in the autonomous
 151 chemostat model [5]. Generically, the set I^* is reduced to a singleton, but we shall
 152 study in this work the non-generic situation where more than one species belong to
 153 I^* . Let us recall from [15] that sharing the same break-even concentration does not
 154 ensure in general the existence of periodic orbits with coexistence: the instability of
 155 periodic solutions with single species is required, which relies on an interplay between
 156 the shapes of the growth functions and the time-varying removal rate.

157 For convenience, we shall define some auxiliary numbers. The function φ being
 158 increasing with $\varphi(\underline{s}) < u_-$ and $\varphi(s_{in}) > u_+$, and as $\bar{u} \in [u_-, u_+]$, there exists an
 159 unique $\bar{s} \in (\underline{s}, s_{in})$ such that

$$160 \quad (3.2) \quad \varphi(\bar{s}) = \bar{u},$$

161 and for any $i \in I$ we define the numbers

$$162 \quad (3.3) \quad \gamma_i := \alpha_i^{-1}(\mu_i(\bar{s}) - \bar{u}) = \frac{\beta_i}{\alpha_i} + \bar{u}(1 - \alpha_i^{-1}).$$

163 *Remark 3.2.* We have for any $i \in I$ that $\mu_i(\lambda_i(\bar{u})) = \bar{u}$, which is equivalent to
 164 write

$$165 \quad \varphi(\lambda_i(\bar{u})) = \alpha_i^{-1}(\bar{u} - \beta_i) = \bar{u} - \gamma_i, = \varphi(\bar{s}) - \gamma_i.$$

166 Since the generating growth function φ is increasing, a higher value γ_i corresponds to
 167 a lower break-even concentration λ_i . In particular, we have that $i \in I^*$ exactly when
 168 $\gamma_i = \max_{j \in I} \gamma_j$.

169 The key point in our study will be to consider particular ratios of powers of species
 170 concentrations, for species that belong to I , defined as follows

$$171 \quad \rho_{ij} := \frac{\alpha_j \sqrt[\alpha_j]{x_i}}{\alpha_i \sqrt[\alpha_i]{x_j}}, \quad i, j \in I.$$

172 The dynamics of these variables present some particular properties, as shown in the
 173 next Proposition.

174 **PROPOSITION 3.3.** *Let I be a subset of populations that belong to a same taxon.*
 175 *For any solution positive solution in Δ , the dynamics of the ratios ρ_{ij} are as follows*

$$176 \quad (3.4) \quad \dot{\rho}_{ij} = \left(\gamma_i - \gamma_j + (\bar{u} - u(t))(\alpha_i^{-1} - \alpha_j^{-1}) \right) \rho_{ij}, \quad i, j \in I.$$

177 *Proof.* Let us first differentiate the equality $\alpha_j \sqrt[\alpha_j]{x_j} \rho_{ij} = \alpha_i \sqrt[\alpha_i]{x_i}$ with respect to t :

$$178 \quad \frac{1}{\alpha_j} x_j^{\frac{1}{\alpha_j} - 1} \dot{x}_j \rho_{ij} + x_j^{\frac{1}{\alpha_j}} \dot{\rho}_{ij} = \frac{1}{\alpha_i} x_i^{\frac{1}{\alpha_i} - 1} \dot{x}_i, \quad i, j \in I$$

179 and replace \dot{x}_k for $k = i, j$ by the expression $(\alpha_k \varphi(s(t)) + \beta_k - u(t))x_k$. One obtains

$$180 \quad x_j^{\frac{1}{\alpha_j}} \left(\varphi(s(t)) + \frac{\beta_j}{\alpha_j} - \alpha_j^{-1} u(t) \right) \rho_{ij} + x_j^{\frac{1}{\alpha_j}} \dot{\rho}_{ij} = x_i^{\frac{1}{\alpha_i}} \left(\varphi(s(t)) + \frac{\beta_i}{\alpha_i} - \alpha_i^{-1} u(t) \right)$$

181 for $i, j \in I$. Multiplying by $x_j^{\alpha_j}$, one can write

$$182 \quad \dot{\rho}_{ij} = \left(\frac{\beta_i}{\alpha_i} - \frac{\beta_j}{\alpha_j} - u(t)(\alpha_i^{-1} - \alpha_j^{-1}) \right) \rho_{ij}, \quad i, j \in I.$$

183 Finally, from the definition (3.3) of numbers γ_k , $k \in i, j$, one can also write

$$184 \quad \dot{\rho}_{ij} = \left(\gamma_i - \gamma_j + (\bar{u} - u(t))(\alpha_i^{-1} - \alpha_j^{-1}) \right) \rho_{ij}, \quad i, j \in I. \quad \square$$

185 The dynamics (3.4) of the ratios ρ_{ij} within a taxon presents thus the remarkable
 186 feature that the time evolution of each ratio depends only on its initial value and
 187 the function u , i.e. their dynamics are decoupled. As a consequence, one obtains the
 188 following properties of the solutions of (2.3).

189 PROPOSITION 3.4. *Let I be a subset of populations that belongs to a same taxon.*
 190 *For any positive solution in Δ , one has*

- 191 1. *For i, j in I^* , ρ_{ij} are periodic functions.*
- 192 2. *For $i \in I \setminus I^*$, x_i converges asymptotically to 0.*
- 193 3. *If $\liminf_{t>0} x_i(t) > 0$ for some $i \in I^*$, then $\liminf_{t>0} x_j(t) > 0$ for any other*
 194 *$j \in I^*$.*

195 *Proof.* From (3.4), one obtains the expression

$$196 \quad \frac{d}{dt} \log \rho_{ij} = (\gamma_i - \gamma_j) + (\bar{u} - u(t))(\alpha_i^{-1} - \alpha_j^{-1}), \quad t \geq 0$$

197 that we integrate between t and $t + T$:

$$198 \quad \log \rho_{ij}(t + T) = \log \rho_{ij}(t) + (\gamma_i - \gamma_j)T, \quad t \geq 0$$

199 which gives equivalently

$$200 \quad \rho_{ij}(t + T) = \rho_{ij}(t)e^{(\gamma_i - \gamma_j)T}, \quad t \geq 0.$$

201 Then, for $i, j \in I^*$, $\gamma_i = \gamma_j$ and the function ρ_{ij} is thus periodic. If $i \notin I^*$, for any
 202 $j \in I^*$, one has $\gamma_j > \gamma_i$ (see Remark 3.2) and thus $x_i(t) \rightarrow 0$ for $t \rightarrow +\infty$. The last
 203 point of the Proposition is a straightforward consequence of point 1. \square

204 This result states that the Competitive Exclusion Principle occurs within a taxon
 205 in the periodic chemostat. It also means that when one or several species of a same
 206 taxon persist in a periodic chemostat, it can be invaded by a new one belonging
 207 to the same taxon preserving the coexistence of all resident populations, under the
 208 condition that all species have the same minimal break even concentration (for the
 209 average removal rate). Diversity can be then (theoretically) augmented within a same
 210 taxon. Once one has shown that ratios are periodic functions, it is not surprising that
 211 one could obtain coexistence of species. However, one has to study the asymptotic
 212 behavior of the total biomass within a taxon to show the effective convergence of the
 213 solutions to a periodic orbit in \mathbb{R}_+^n , which is the matter of the next sections.

214 The (non-generic) property of having identical break-even concentrations that
 215 implies coexistence of species is already known in the classical chemostat model with
 216 constant removal rate (see for instance [5]). However, as we have recalled earlier, this
 217 property does not guarantee the coexistence under periodic removal rate. Instead,
 218 integral conditions which depends on the periodic function u have to be fulfilled
 219 [15]. Here, the remarkable feature within a taxon is that under the simple condition
 220 of equal break-even concentrations, coexistence can be guaranteed whatever is the
 221 periodic function u (provided that its average value is equal to the fixed value \bar{u}). This
 222 property presents thus a robustness with respect to the removal rate $u(\cdot)$ fluctuating
 223 about its mean value.

224 Now and for the rest of the paper, we shall assume that each species population
 225 can persist alone, which is ensured by the following hypothesis.

226 *Assumption 3.5.* One has $\mu_i(s_{in}) > \bar{u}$ for any $i = 1, \dots, n$.

227 **4. Multiplicity of periodic solutions within a single taxon.** In this sec-
 228 tion, we consider that all the species belong to a same taxon. Let us underline that we
 229 deal with dynamics in \mathbb{R}_+^n (with n possibly larger than 2), for which the mathematical
 230 tools for studying asymptotic periodic solutions that are specific to planar dynamics
 231 [2] do not apply here. In the proof of the coming results, we shall exploit the re-
 232 sults of Proposition 3.4 to rewrite the dynamics of each species as a non-autonomous
 233 dynamical system and use the theory of asymptotic periodic semi-flows [19].

234 PROPOSITION 4.1. *Assume that the whole set $I = \{1, \dots, n\}$ of populations belong*
 235 *to a same taxon. Then for any positive initial condition in Δ , the solution of (2.3)*
 236 *converges asymptotically to a periodic solution composed of all species in I^* , the other*
 237 *species being washout. Moreover, if I^* is not reduced to a singleton, the system (2.3)*
 238 *admits an infinite number of periodic solutions in Δ with distinct orbits, which depend*
 239 *on the initial proportions of species in I^* only.*

240 *Proof.* Let $x(\cdot)$ be a positive solution of (2.3) in Δ and $\rho_{ij}(\cdot)$, $i, j \in I$, be the
 241 corresponding solutions of (3.4). Take i^* in I^* such that

$$242 \quad \alpha_{i^*} = \min_{i \in I^*} \alpha_i.$$

243 We show that x_{i^*} converges asymptotically to a positive periodic solution.

244 The variable x_{i^*} can be written as the solution of the non-autonomous scalar
 245 dynamics

$$246 \quad \dot{x}_{i^*} = (f(t, x_{i^*}) - u(t))x_{i^*}$$

247 where

$$248 \quad f(t, y) := \mu_{i^*} \left(s_{in} - \sum_{i \in I^*} \rho_{ii^*}(t) \alpha_i y^{\frac{\alpha_i}{\alpha_{i^*}}} - \sum_{i \notin I^*} x_i(t) \right).$$

249 Let $\tilde{\mu}_{i^*}$ be a C^1 increasing extension of the function μ_{i^*} for negative arguments, and
 250 consider the dynamics

$$251 \quad (4.1) \quad \dot{y} = (\tilde{f}(t, y) - u(t))y$$

252 on \mathbb{R} , where \tilde{f} consists in replacing μ_{i^*} by $\tilde{\mu}_{i^*}$ in the expression of the function f . Note
 253 that the choice of x_{i^*} implies that one has $\alpha_i/\alpha_{i^*} \geq 1$ for any $i \in I^*$. Therefore, \tilde{f} is
 254 Lipschitz with respect to y and the solutions of (4.1) are well defined. At $y = s_{in}$, the
 255 argument of $\tilde{\mu}_{i^*}$ is negative, but as $\mu_{i^*}(0) = 0$ and $\tilde{\mu}_{i^*}$ is increasing, one has necessarily
 256 $\tilde{\mu}_{i^*} < 0$ for negative arguments, and then $\tilde{f}(t, s_{in}) \leq 0$ for any $t \geq 0$. The set $[0, s_{in}]$
 257 is thus forwardly invariant. Clearly, x_{i^*} is the solution of (4.1) for the initial value
 258 $y(0) = x_{i^*}(0)$ (which belongs to $[0, s_{in}]$).

259 According to Proposition 3.4, the functions ρ_{ii^*} for $i \in I^*$ are T -periodic and
 260 variables x_i for $i \notin I^*$ converge asymptotically to 0. We then consider the limiting
 261 function

$$262 \quad \tilde{f}_i(t, y) := \tilde{\mu}_{i^*} \left(s_{in} - \sum_{i \in I^*} \rho_{ii^*}(t) \alpha_i y^{\frac{\alpha_i}{\alpha_{i^*}}} \right)$$

7

263 which is T -periodic and verifies

$$264 \quad \lim_{t \rightarrow +\infty} |\tilde{f}(t, y)y - \tilde{f}_i(t, y)y| = 0 \text{ uniformly for } y \in [0, s_{in}].$$

265 Consequently, by Proposition 3.2 in [19], the non-autonomous semi-flow of (4.1) in
266 $[0, s_{in}]$ is asymptotically periodic with limit periodic semi-flow of

$$267 \quad (4.2) \quad \dot{y} = (\tilde{f}_i(t, y) - u(t))y$$

268 (for which $[0, s_{in}]$ is also forwardly invariant).

269 We follow now the approach exposed in [15] for one dimensional periodic dynam-
270 ics, but adapted here to our context. Let us consider the Poincaré map P associated
271 to the periodic dynamics (4.2)

$$272 \quad P : y_0 \in [0, s_{in}] \mapsto y(T, y_0) \in [0, s_{in}]$$

273 where $y(\cdot, y_0)$ denotes the solution of (4.2) with $y(0) = y_0$. One has clearly $P(0) = 0$,
274 and from the Theorem of continuous dependency of the solution of ordinary differential
275 equation with respect to the initial condition, P is continuously differentiable with
276 $P'(y_0) = z(T)$, where $z(\cdot)$ is solution of

$$277 \quad \dot{z} = \left(\partial_y \tilde{f}_i(t, y(t, y_0))y(t, y_0) + \tilde{f}_i(t, y(t, y_0)) - u(t) \right) z, \quad z(0) = 1$$

278 that is

$$279 \quad z(T) = \exp \left(\int_0^T \partial_y \tilde{f}_i(t, y(t, y_0))y(t, y_0) + \tilde{f}_i(t, y(t, y_0)) - u(t) dt \right) > 0.$$

280 The map P is thus increasing and one has $P'(0) = \exp(T(\mu_{i^*}(s_{in}) - \bar{u})) > 1$ (by
281 Assumption 3.5). So 0 is a repulsive fixed point of the map P , and for any $y_0 > 0$, the
282 sequence $\{P^k y_0\}_{k \in \mathbb{N}}$ is strictly monotonic and bounded, thus converging to a positive
283 fixed point y^* of P . Moreover, as $y(\cdot, y^*)$ is periodic, one has

$$284 \quad \int_0^T \tilde{f}_i(t, y(t, y^*)) - u(t) dt = 0$$

285 and thus

$$286 \quad P'(\bar{y}) = \exp \left(\int_0^T \partial_y \tilde{f}_i(t, y^*)y(t, y^*) dt \right).$$

287 As the functions $\tilde{\mu}_i$ are assumed to be increasing, one has $\tilde{\mu}'_{i^*} > 0$ which implies
288 $\partial_y \tilde{f}_i < 0$, and thus $P'(\bar{y}) < 1$. Therefore the map $y \mapsto P(y) - y$ is decreasing at each
289 root, which implies that it cannot have more than one root. We conclude that the
290 (positive) fixed point y^* is unique.

291 As P admits a finite number of fixed points (indeed only one), one can apply the
292 results about asymptotically autonomous discrete dynamical systems (Theorem 2.4
293 in [19]), from which one gets

$$294 \quad \lim_{k \rightarrow +\infty} x_{i^*}(t + kT) = y(t, y^*), \quad t \in [0, T].$$

295 and we conclude that the solution $x(\cdot)$ converges asymptotically to a periodic solution
 296 of (2.3) in Δ , for which all species in I^* are present, the other species being excluded:

$$297 \quad \lim_{k \rightarrow +\infty} |x(t + kT) - x^p(t)| = 0, \quad t \in [0, T]$$

298 where $x^p(\cdot)$ is the periodic solution given by

$$299 \quad x_i^p(t) = \begin{cases} \rho_{ii^*}(t)^{\alpha_i} y(t, y^*)^{\frac{\alpha_i}{\alpha_{i^*}}} > 0, & i \in I^*, \\ 0, & i \notin I^*, \end{cases}$$

300 for $t \in [0, T]$.

301 Consider now another positive initial condition in Δ but with the same initial
 302 ratios $\rho_{ii^*}(0)$ for $i \in I^*$. According to (3.4), the functions ρ_{ii^*} ($i \in I^*$) are identical and
 303 consequently the limiting periodic dynamics (4.2) is also identical. As this later one
 304 admits a unique periodic solution, we conclude that the solution of (2.3) converges
 305 asymptotically to the same periodic solution $x^p(\cdot)$.

306 We now show how to construct an infinity of distinct periodic solutions, when I^*
 307 is not reduced to a singleton. Consider a sequence $\{\rho_0^k\}_{k \in \mathbb{N}}$ of positive vectors in \mathbb{R}^n
 308 such that

$$309 \quad (4.3) \quad \max_{i \in I^* \setminus \{i^*\}} (\rho_0^{k+1})_i > \max_{t \in [0, T]} \max_{i \in I^* \setminus \{i^*\}} \rho_{ii^*}^k(t), \quad k \in \mathbb{N}$$

310 where $\rho_{ii^*}^k(\cdot)$ are the periodic solutions of (3.4) with $\rho_{ii^*}^k(0) = (\rho_0^k)_i$ for $i \in I^* \setminus \{i^*\}$.
 311 Condition (4.3) imposes that for each $i \in I^* \setminus \{i^*\}$, the orbits $\gamma^+(\rho_{ii^*}^k) = \{\rho_{ii^*}^k(t), t \in$
 312 $[0, T]\}$ of (3.4) are all disjoint for $k \in \mathbb{N}$. Moreover, for each k , there exists a unique
 313 periodic solution $x^{pk}(\cdot)$ of (2.3) in Δ for which all species in I^* are present with
 314 ratios given by the functions $\rho_{ii^*}^k$. This implies that the periodic orbits $\gamma^+(x^{pk}) =$
 315 $\{x^{pk}(t), t \in [0, T]\}$, $k \in \mathbb{N}$, of (2.3) are all disjoint. Indeed, if $\gamma^+(x^{pk}) = \gamma^+(x^{pl})$ for
 316 some $k \neq l$, there should exist $\tau \geq 0$ such that $x^{pk}(t) = x^{pl}(t + \tau)$ for any $t \geq 0$. In
 317 particular, one should have $x_i^{pk}(t) = x_i^{pl}(t + \tau)$ for $i \neq i^*$ in I^* and any $t \geq 0$, but
 318 as the orbits $\gamma^+(\rho_{ii^*}^k)$, $\gamma^+(\rho_{ii^*}^l)$ are disjoint, one should have $\rho_{ii^*}^k(t + \tau) \neq \rho_{ii^*}^l(t)$ for
 319 some t , that is $x_i^{pk}(t) \neq x_i^{pl}(t + \tau)$ and thus a contradiction with the fact that
 320 the orbits are non distinct. \square

321 The results of Proposition 4.1 are twofold. First, they complete those of Proposi-
 322 tion 3.4, since we now have the persistence of the species of I^* , while the less fit species
 323 of $I \setminus I^*$ are washed-out. This stronger form of the competitive exclusion principle
 324 comes from Assumption 3.5 and the fact that there is no species outside the taxon
 325 I . This result allows coexistence in the periodic setting under the non-generic as-
 326 sumption that the surviving species belong to I^* . It generalizes known similar results
 327 in the non-autonomous setting [5]. Then, the second aspect of this result concerns
 328 the number of distinct periodic coexistence solutions of the system (2.3), which are
 329 a continuum of neutrally stable periodic solutions. Proposition 4.1 shows that if the
 330 growth functions are *close enough* to each other, in the sense that the corresponding
 331 species belong to I^* , then there are infinitely many periodic coexistence solutions. We
 332 may expect that eventual sufficient conditions for uniqueness forbid growth functions
 333 to be too close in a sense close to ours.

334 **5. Multiplicity of periodic solutions with more than one taxon.** In this
335 section, we show that it is possible to have coexistence of two taxa in competition, each
336 of them preserving the proportions of species having the same break-even concentra-
337 tions, leading to an infinite number of periodic orbits. Roughly speaking, the idea of
338 the proof of Proposition 5.2 below is to consider a non-autonomous planar system that
339 is asymptotically periodic, and to revisit the results about periodic planar dynamics
340 in this framework, with the help of the theory of asymptotic periodic semi-flows. For
341 technicalities, we need in this section the following additional hypothesis.

342 *Assumption 5.1.* The functions μ_i , $i \in \{1, \dots, n\}$, are analytic at any $s > \underline{s}$, and
343 u is an analytic function of t .

344 For convenience, we shall denote for any integrable scalar function $\zeta(\cdot)$ the average
345 quantity by

$$346 \quad \langle \zeta \rangle_T := \frac{1}{T} \int_0^T \zeta(t) dt.$$

347 **PROPOSITION 5.2.** *Assume that one has $\{1, \dots, n\} = I_a \sqcup I_b$, where species in*
348 *I_a , resp. I_b , belong to a same taxon. For any fixed positive initial condition in Δ ,*
349 *let $(s_a^p(\cdot), x_a^p(\cdot))$, resp. $(s_b^p(\cdot), x_b^p(\cdot))$ be the asymptotic periodic solution of (2.1) when*
350 *only species in I_a , resp. I_b , are initially present. If the conditions*

$$351 \quad (5.1) \quad \lambda_{ba} := \langle \mu_i(s_b^p) \rangle_T - \bar{u} > 0, \quad i \in I_a^*,$$

$$352 \quad (5.2) \quad \lambda_{ab} := \langle \mu_i(s_a^p) \rangle_T - \bar{u} > 0, \quad i \in I_b^*,$$

354 *are fulfilled, then the solution of (2.3) converges asymptotically to a periodic solution*
355 *for which all species in I_a^* and I_b^* are present, the other species being washed out.*
356 *Moreover, when there exists at least one positive initial condition satisfying the above*
357 *conditions, and at least one of the subsets I_a^* , I_b^* is not reduced to a singleton, there*
358 *exists an infinity of distinct periodic orbits of (2.3) for which all the species in $I_a^* \sqcup I_b^*$*
359 *are present.*

360 *Proof.* The taxa are characterized by generating functions φ_a , φ_b and numbers
361 $\alpha_i > 0$, $\beta_i \geq 0$ such that

$$362 \quad \mu_i(s) = \alpha_i \varphi_a(s) + \beta_i, \quad i \in I_a, \quad \mu_i(s) = \alpha_i \varphi_b(s) + \beta_i, \quad i \in I_b.$$

363 Take $i_a^* \in I_a^*$ and $i_b^* \in I_b^*$. Let $x(\cdot)$ be a positive solution of (2.3) in Δ and define the
364 functions, for $i \in I_a^* \sqcup I_b^*$

$$365 \quad (5.3) \quad r_i(t) = \begin{cases} \rho_{ii_a^*}(t), & i \in I_a^*, \\ \rho_{ii_b^*}(t), & i \in I_b^*, \end{cases} \quad t \geq 0.$$

366 Then, variables $x_{i_a^*}$, $x_{i_b^*}$ are solutions of the non-autonomous planar dynamics

$$367 \quad \begin{aligned} \dot{y}_a &= (f_a(t, y_a, y_b) - u(t))y_a, \\ \dot{y}_b &= (f_b(t, y_a, y_b) - u(t))y_b, \end{aligned}$$

368 with

$$369 \quad f_a(t, y_a, y_b) := \mu_{i_a^*}(s(t, y_a, y_b)), \quad f_b(t, y_a, y_b) := \mu_{i_b^*}(s(t, y_a, y_b)),$$

370 where

$$371 \quad s(t, y_a, y_b) = s_{in} - \sum_{i \in I_a^*} r_i(t)^{\alpha_i} y_a^{\frac{\alpha_i}{\alpha_{i_a}^*}} - \sum_{i \in I_b^*} r_i(t)^{\alpha_i} y_b^{\frac{\alpha_i}{\alpha_{i_b}^*}} - \sum_{i \notin I_a^* \sqcup I_b^*} x_i(t).$$

372 Let $\tilde{\mu}_{i_a^*}, \tilde{\mu}_{i_b^*}$ be C^1 increasing extensions of the functions $\mu_{i_a^*}, \mu_{i_b^*}$ for negative argu-
373 ments, and consider the dynamics

$$374 \quad (5.4) \quad \begin{aligned} \dot{y}_a &= (\tilde{f}_a(t, y_a, y_b) - u(t))y_a, \\ \dot{y}_b &= (\tilde{f}_b(t, y_a, y_b) - u(t))y_b, \end{aligned}$$

375 in the plane, where the functions \tilde{f}_a, \tilde{f}_b are defined with the expressions of f_a, f_b
376 replacing the functions $\mu_{i_a^*}, \mu_{i_b^*}$ by their extensions $\tilde{\mu}_{i_a^*}, \tilde{\mu}_{i_b^*}$. As one has $\alpha_i/\alpha_{i_a^*} \geq 1$
377 for $i \in I_a^*$, and $\alpha_i/\alpha_{i_b^*} \geq 1$ for $i \in I_b^*$, this dynamics is Lipschitz in (y_a, y_b) . Moreover
378 the set

$$379 \quad \mathcal{S} := [0, s_{in}] \times [0, s_{in}]$$

380 is forwardly invariant as one has $f_a(t, s_{in}, y_b) < 0, f_b(t, y_a, s_{in}) < 0$ for any $(y_a, y_b) \in \mathcal{S}$
381 and $t \geq 0$. Solutions of (5.4) are thus well defined in \mathcal{S} and unique. The pair
382 $(x_{i_a^*}(\cdot), x_{i_b^*}(\cdot))$ is such a solution for $(y_a(0), y_b(0)) = (x_{i_a^*}(0), x_{i_b^*}(0))$.

383 With Proposition 3.4, we know that the functions r_i with $i \in I_a^* \sqcup I_b^*$ are T -
384 periodic, and variables x_i with $i \notin I_a^* \sqcup I_b^*$ converge asymptotically to 0. We thus
385 consider the limiting dynamics

$$386 \quad (5.5) \quad \begin{aligned} \dot{y}_a &= (\tilde{f}_a^l(t, y_a, y_b) - u(t))y_a, \\ \dot{y}_b &= (\tilde{f}_b^l(t, y_a, y_b) - u(t))y_b, \end{aligned}$$

387 where

$$388 \quad \tilde{f}_a^l(t, y_a, y_b) := \tilde{\mu}_{i_a^*}(s^l(t, y_a, y_b)), \quad \tilde{f}_b^l(t, y_a, y_b) := \tilde{\mu}_{i_b^*}(s^l(t, y_a, y_b))$$

389 with

$$390 \quad s^l(t, y_a, y_b) := s_{in} - \sum_{i \in I_a^*} r_i(t)^{\alpha_i} y_a^{\frac{\alpha_i}{\alpha_{i_a^*}}} - \sum_{i \in I_b^*} r_i(t)^{\alpha_i} y_b^{\frac{\alpha_i}{\alpha_{i_b^*}}},$$

391 which are time periodic functions. One has also

$$392 \quad \lim_{t \rightarrow +\infty} |(\tilde{f}_a(t, y_a, y_b) - \tilde{f}_a^l(t, y_a, y_b))y_a| = \lim_{t \rightarrow +\infty} |(\tilde{f}_b(t, y_a, y_b) - \tilde{f}_b^l(t, y_a, y_b))y_b| = 0$$

393 uniformly for $(y_a, y_b) \in \mathcal{S}$. Therefore, the non-autonomous semi-flow of (5.4) in \mathcal{S} is
394 asymptotically periodic with limit periodic semi-flow of (5.5) (see Proposition 3.2 in
395 [19]). The system (5.5) is competitive and we can apply the results of the literature
396 about periodic competitive planar systems, which states that any bounded solution
397 converges to a periodic solution $(y_a^p(\cdot), y_b^p(\cdot))$ (see for instance Theorem 4.2 in [15]).
398 Let P be the Poincaré map associated to this dynamics

$$399 \quad P : Y_0 \in \mathcal{S} \mapsto Y(T, Y_0) \in \mathcal{S}$$

400 where $Y(\cdot, Y_0)$ denotes the solution $(y_a(\cdot), y_b(\cdot))$ of (5.5) with $(y_a(0), y_b(0)) = Y_0$.
401 On the axis $y_a = 0$ or $y_b = 0$, the dynamics is with a single taxon. One can then
402 reproduce the arguments of the proof of Proposition 4.1 to show that there are unique
403 fixed points $Y_a^* = (y_a^*, 0), Y_b^* = (0, y_b^*)$ of P in \mathcal{S} with $y_a^* > 0, y_b^* > 0$. Moreover,

404 one has $y_a^* = (x_a^p)_{i_a^*}(0)$, $y_b^* = (x_b^p)_{i_b^*}(0)$, where $x_a^p(\cdot)$, $x_b^p(\cdot)$ are the asymptotic periodic
 405 solutions of (2.3) for the initial conditions ξ , ζ

$$406 \quad \xi_i = \begin{cases} x_i(0), & i \in I_a, \\ 0, & i \in I_b, \end{cases} \quad \zeta_i = \begin{cases} 0, & i \in I_a, \\ x_i(0), & i \in I_b \end{cases}$$

407 (remind from Proposition 3.4 that functions ρ_{ii^*} ($i \in I_a$) or ρ_{ii^*} ($i \in I_b$) remain the
 408 same).

409 The linearized dynamics $\dot{Y} = M(t)Y$ of (5.5) is given by the matrix

$$410 \quad M(t) = \begin{bmatrix} a(t) & b(t) \\ c(t) & d(t) \end{bmatrix}$$

411 with

$$412 \quad a(t) = \tilde{f}_a^l(t, y_a(t), y_b(t)) - u(t) + \partial_{y_a} \tilde{f}_a^l(y_t, y_a(t), y_b(t))y_a(t),$$

$$413 \quad b(t) = \partial_{y_b} \tilde{f}_a^l(t, y_a(t), y_b(t))y_a(t),$$

$$414 \quad c(t) = \partial_{y_a} \tilde{f}_b^l(t, y_a(t), y_b(t))y_b(t),$$

$$415 \quad d(t) = \tilde{f}_b^l(t, y_a(t), y_b(t)) - u(t) + \partial_{y_b} \tilde{f}_b^l(t, y_a(t), y_b(t))y_b(t).$$

417 Along the periodic solution $(x_a^p(\cdot), 0)$, one has

$$418 \quad M(t) = \begin{bmatrix} \star & \star \\ 0 & f_b^l(t, ((x_a^p)_{i_a^*}(t), 0) - u(t) \end{bmatrix}$$

419 for which the characteristics multiplier $\exp \int_0^T f_b^l(t, ((x_a^p)_{i_a^*}(t), 0) - u(t) dt$ is equal to
 420 $\exp(T\lambda_{ba})$ and larger than 1 under condition (5.1). The fixed point Y_a^* is thus hy-
 421 perbolic repulsive. In a similar way, Y_b^* is an hyperbolic repulsive fixed point under
 422 condition (5.2). This implies that Y_a^* and Y_b^* are isolated fixed points of P .

423 For $Y_0 = 0$, the solution of (5.5) is identically null and one has

$$424 \quad M(t) = \begin{bmatrix} \mu_{i_a^*}(s_{in}) - u(t) & 0 \\ 0 & \mu_{i_b^*}(s_{in}) - u(t) \end{bmatrix}.$$

425 The characteristics multipliers are thus $\exp \int_0^T \mu_{i_a^*}(s_{in}) - y(t) dt$, $\exp \int_0^T \mu_{i_b^*}(s_{in}) -$
 426 $y(t) dt$ which are larger than one under Assumption 3.5. The zero solution is thus
 427 repulsive.

428 Along any positive solution $y_a(\cdot)$, $y_b(\cdot)$, note that one has $b(t) < 0$ and $c(t) < 0$
 429 at any $t \in [0, T]$. Then, one has $\dot{Y}_1 > 0$ for $Y_1 = 0$ and $\dot{Y}_2 < 0$, and $\dot{Y}_2 < 0$ for $Y_1 > 0$
 430 and $Y_2 = 0$. Therefore, the second and fourth quadrant are invariant by the linear
 431 dynamics $\dot{Y} = M(t)Y$, which implies that the matrix $P'(Y_0)$ has strictly positive
 432 diagonal elements and strictly negative off-diagonal elements for a positive $Y_0 \in \mathcal{S}$.
 433 Let $\mathcal{S}' = \{Y \in \mathcal{S}; s^l(0, Y) \in (\underline{s}, s_{in}]\}$. By Lemma 2.3, \mathcal{S}' is invariant by P and any
 434 fixed point of P belongs to \mathcal{S}' , including Y_a^* and Y_b^* . Following the arguments given in
 435 [2], the positive fixed points of P lie on a continuous curve Γ in \mathcal{S}' , which connects the
 436 fixed points Y_a^* , Y_b^* . Under Assumption 5.1, $x(\cdot)$ is analytic and the functions $r_i(\cdot)$ as
 437 well. Therefore, the map P is analytic on \mathcal{S}' . Then, the curve Γ is also analytic (see
 438 [2, 4]). If there were an infinite number of fixed points of P in \mathcal{S} then all the points
 439 of the curve Γ will be fixed points by analyticity, which contradicts the fact that Y_a^*
 440 and Y_b^* are isolated fixed points.

441 Finally, as P has a finite number of fixed points on \mathcal{S} , we can apply the results
 442 about asymptotically autonomous discrete dynamical systems (Theorem 2.4 in [19]),
 443 from which one gets

$$444 \quad \lim_{k \rightarrow +\infty} (x_{i_a^*}(t + kT), x_{i_b^*}(t + kT)) = Y(T, Y^*), \quad t \in [0, T].$$

445 where Y^* is a fixed point of P in \mathcal{S} . As the fixed points on the axes 0 , Y_a^* and Y_b^* are
 446 all repulsive, we conclude that Y^* is positive, and that $x(\cdot)$ converges asymptotically
 447 to the periodic solution $x^P(\cdot)$ given by

$$448 \quad x_i^P(t) = \begin{cases} r_i(t)^{\alpha_i} y_a(t, Y^*)^{\frac{\alpha_i}{\alpha_{i_a^*}}} > 0, & i \in I_a^*, \\ r_i(t)^{\alpha_i} y_b(t, Y^*)^{\frac{\alpha_i}{\alpha_{i_b^*}}} > 0, & i \in I_b^*, \\ 0, & i \notin I_a^* \sqcup I_b^*, \end{cases}$$

449 for $t \in [0, T]$.

450 When I_a^* is not reduced to a singleton, take $i_a^\dagger \neq i_a^*$ in I_a^* and consider perturba-
 451 tions $x^\varepsilon(\cdot)$ of the solution $x(\cdot)$, as solutions of (2.3) for the initial condition

$$452 \quad (5.6) \quad x_i^\varepsilon(0) = \begin{cases} x_i(0), & i \neq i_a^\dagger, \\ (r_{i_a^\dagger}(0) + \varepsilon)^{\alpha_{i_a^\dagger}} x_{i_a^*}(0)^{\frac{\alpha_i}{\alpha_{i_a^*}}}, & i = i_a^\dagger, \end{cases}$$

453 with $\varepsilon > 0$. By continuity of solutions of (2.1) with respect to the initial condition,
 454 there exists $\bar{\varepsilon} > 0$ such that for any $\varepsilon \in (0, \bar{\varepsilon})$ $x^\varepsilon(0)$ belongs to Δ and conditions
 455 (5.1), (5.2) are fulfilled for this new initial condition. As before, we deduce that $x^\varepsilon(\cdot)$
 456 converges asymptotically to a periodic solution $x^{\varepsilon, P}(\cdot)$ for which all species in I_a^* and
 457 I_b^* are present.

458 Let ρ_{ij}^ε be the ratio functions for the initial condition $x_i^\varepsilon(0)$. Note from (5.6) that
 459 one has $\rho_{i_a^\dagger i_a^*}^\varepsilon(0) = \rho_{i_a^\dagger i_a^*}(0) + \varepsilon$. One gets from (3.4)

$$460 \quad \begin{aligned} \rho_{i_a^\dagger i_a^*}^\varepsilon(t) &= \rho_{i_a^\dagger i_a^*}^\varepsilon(0) \exp \int_0^t (\bar{u} - u(\tau)) (\alpha_{i_a^\dagger}^{-1} - \alpha_{i_a^*}^{-1}) d\tau \\ &= \rho_{i_a^\dagger i_a^*}(t) + \varepsilon \exp \int_0^t (\bar{u} - u(\tau)) (\alpha_{i_a^\dagger}^{-1} - \alpha_{i_a^*}^{-1}) d\tau, \quad t \geq 0. \end{aligned}$$

461 Therefore, the orbits $\gamma^+(\rho_{i_a^\dagger i_a^*}^\varepsilon)$ for $\varepsilon \in (0, \bar{\varepsilon})$ are all distinct and we deduce, as in
 462 the proof of Proposition 4.1 that the orbits of the periodic solutions $\gamma^+(x^{\varepsilon, P})$ are all
 463 distinct. \square

464 *Remark 5.3.* Conditions (5.1), (5.2) are independent of the choice of $i \in I_a^*$, I_b^* .
 465 Indeed, let $\bar{s}_a = \lambda_i(\bar{u})$ which is identical for any $i \in I_a^*$, and one has

$$466 \quad \begin{aligned} \langle \mu_i(s_b^P) \rangle_T - \bar{u} &= \alpha_i \langle \varphi_a(s_b^P) \rangle_T + \beta_i - \bar{u} \\ &= \alpha_i \langle \varphi_a(s_b^P) - \varphi_a(\bar{s}_a) \rangle_T + \alpha_i \varphi_a(\bar{s}_a) + \beta_i - \bar{u} \\ &= \alpha_i \langle \varphi_a(s_b^P) - \varphi_a(\bar{s}_a) \rangle_T \end{aligned}$$

467 (using the property $\bar{u} = \mu_i(\bar{s}_a) = \alpha_i \varphi_a(\bar{s}_a) + \beta_i$ for $i \in I_a^*$). The sign of $\langle \mu_i(s_b^P) \rangle_T - \bar{u}$ is
 468 thus independent of $i \in I_a^*$, the numbers α_i being positive. One obtains symmetrically
 469 the same property for the sign of $\langle \mu_i(s_a^P) \rangle_T - \bar{u}$ with $i \in I_b^*$.

470 Similarly to Proposition 4.1, Proposition 5.2 generalizes known results providing
 471 a continuum of neutrally stable periodic solutions of system (2.3). Indeed, when each
 472 taxon contains only one species, we recover exactly the results in [15]. However, thanks
 473 to our taxonomic assumptions, we are able to extend it from two species to two taxa,
 474 under very similar conditions. Then, we are also able to establish the existence of an
 475 infinite number of periodic coexistence solutions, generalizing the result of Proposition
 476 4.1 from one to two taxa.

477 **6. Numerical illustrations.** In this section, we illustrate numerically our re-
 478 sults with the class of Hill functions [8]

$$479 \quad \mu(s) = \frac{\mu_{max} s^p}{K^p + s^p}$$

480 that are parameterized by the three positive numbers μ_{max} , K and p . This class of
 481 increasing growth functions is quite popular in microbiology, pharmacology or bio-
 482 chemistry for its flexibility and effectiveness in fitting experimental data, and also
 483 because it enlarges the well known class of Monod functions

$$484 \quad \mu(s) = \frac{\mu_{max} s}{K + s}$$

485 as the particular case of p equal to 1. The parameter p measures in some way a
 486 distance from the Monod model. Quite often, practitioners conduct experiments first
 487 with large values of s to estimate the maximal growth rate $\mu_{max} = \lim_{s \rightarrow +\infty} \mu(s)$ and
 488 then look for the value of s for which the growth rate is equal to $\mu_{max}/2$. One can
 489 straightforwardly check that this value is equal to the affinity constant K (sometimes
 490 also called the half-saturation constant), whatever is p . This is enough to identify the
 491 Monod growth function, but without additional data, different candidates of growth
 492 functions in the class of Hill functions could also suit, depending on the parameter p .

493 To obtain a variety of different situations, we have considered three generating
 494 functions with p equal to 2 or 4

$$495 \quad (6.1) \quad \varphi_a(s) = \frac{m_a s^2}{K_a^2 + s^2}, \quad \varphi_b(s) = \frac{m_b s^4}{K_b^4 + s^4}, \quad \varphi_c(s) = \frac{m_c s^2}{K_c^2 + s^2}.$$

497 with parameters given in Table 6.1, so that one of them (φ_b) has a significantly
 498 different shape. Graphs of the functions φ_a , φ_b , φ_c are depicted on Figure 6.1. For
 499 $p > 1$, the graphs of these functions are convex up to K and then concave for larger
 500 values. The larger is p , the more the convexity/concavity is pronounced, as one can
 501 see on Figure 6.1. Mixing species from taxa a and b or from taxa a and c allows
 502 then to generate contrasted situations. Imposing the same constant K is a way to
 503 consider species having similar affinity for the resource and to focus on the impact of
 504 the different shapes of the growth functions away from this point. We have generated
 505 nine growth functions within these three taxa with characteristic numbers given in
 506 Table 6.2 and $\underline{s} = 0.5$. Let us denote the sets of indices of species belonging to a
 507 same taxon $I_a = \{1, 2, 3\}$, $I_b = \{4, 5, 6\}$, $I_c = \{7, 8, 9\}$. The graphs of these functions
 508 are depicted in Figure 6.2, where we have considered for each of these nine growth
 509 functions a C^1 extension for $s \leq \underline{s}$ as a polynomial increasing on $[0, \underline{s}]$ and null at
 510 0. Clearly, Assumptions 2.1, 2.2, 3.5, 5.1 are satisfied. Within a taxon, each species
 511 i is characterized by the parameters α_i and β_i following Equation (3.1). Since α_i
 512 multiplies the generating growth function, it affects more the behavior of the species
 513 for large values of the growth rates, hence for larger values of s (the larger is α_i ,

514 the higher is the maximal growth rate). Since β_i is added to the generating growth
 515 function, its impact is greater for smaller values of the growth rates hence at small
 516 values of s (the lower is β_i , the smaller is the growth function). These effects can be
 517 seen on Table 6.2 and Figure 6.2.

518 The operating conditions have been chosen as follows

519
$$s_{in} = 4, \quad \bar{u} = 0.8, \quad T = 10$$

520 where the periodic removal rate is

521 (6.2)
$$u(t) = \bar{u} + 0.2 \sin\left(\frac{2\pi t}{T}\right)$$

522 For these values, we have checked in all our simulations that the solutions remain in
 523 the set Δ with $\underline{s} = 0.5$. For the chosen value of \bar{u} , numbers \bar{s} and γ_i defined in (3.2)
 524 and (3.3) are given in Table 6.3 for each taxon. Note that we do not impose the value
 525 \bar{s} to be the same for each taxon. Accordingly to Remark 3.2, the fittest species within
 each taxon are given by the subsets of indices $I_a^* = \{1, 2\}$, $I_b^* = \{4, 5\}$, $I_c^* = \{8, 9\}$.

i	a	b	c
m_i	2	2.95	1.8
K_i	$\sqrt{3}$	$\sqrt{3}$	$\sqrt{3}$

Table 6.1: Parameters defining the generating functions $\varphi_a, \varphi_b, \varphi_c$

i	1	2	3	4	5	6	7	8	9
φ	φ_a			φ_b			φ_c		
α_i	0.9	1.15	0.85	0.8	1.05	0.6	0.9	1.1	0.7
β_i	0.161	-0.0165	0.1455	0.232	0.0545	0.326	0.161	0.019	0.261

Table 6.2: Characteristic numbers of the nine growth functions with respect to their taxon

species	1	2	3	4	5	6	7	8	9
φ	φ_a			φ_b			φ_c		
\bar{s}	1.28			1.30			1.40		
γ_i	0.09	0.09	0.03	0.09	0.09	0.01	0.09	0.09	0.03

Table 6.3: For each taxon, numbers \bar{s} and γ_i (with $\bar{u} = 0.8$)

526

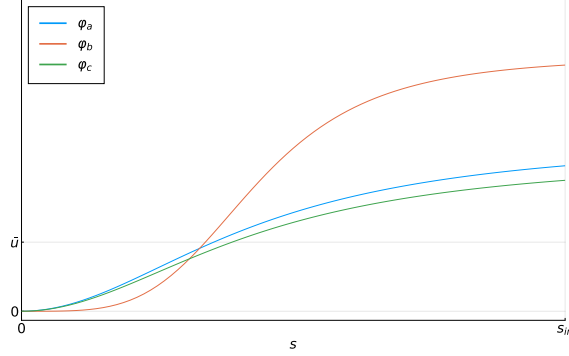


Fig. 6.1: Graphs of the generating growth functions: φ_a and φ_c are close to each other with φ_a slightly above φ_c , while φ_b has a different shape.

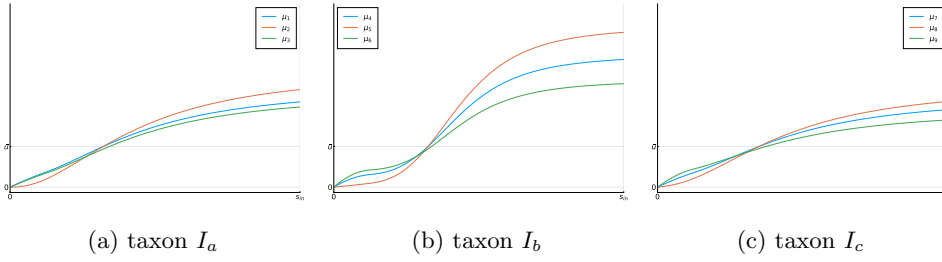


Fig. 6.2: Graphs of the growth functions within each taxon. The orange and blue growth functions reach the value \bar{u} for lower values of s than the green one, implying that the species associated with the latter is expected to be washed-out by the two other ones.

527 **6.1. Simulations with species of a single taxon.** To illustrate Proposition
528 4.1, we have run simulations with all the three species in each taxon. For various
529 initial conditions, we found the same asymptotic orbits with the same initial ratios
530 of species, as expected. We observed that species that are not the fittest within their
531 taxon i.e. that do not belong to I_a^* , I_b^* or I_c^* are washed-out in presence of all the
532 species in I_a , I_b or I_c respectively. On the opposite, species with the largest values of
533 γ_i coexist, that are 1 and 2 for taxon a , 4 and 5 for taxon b , and 7, 8 for taxon c (see
534 Table 6.3). To illustrate trajectories over time, we have chosen for simplicity uniform
535 initial distribution between species. Figure 6.3 shows how the green species 3, 6 or 9
536 are washed-out within their taxon, while trajectories of the orange and blue species
537 which coexist are more or less close to each other depending on the taxon. This is
538 related to the distance of their graphs (see Figure 6.2) or how close are the values
539 of α_i (see Table 6.2). Additionally, Figure 6.4 represents the solutions in the phase
540 portrait for different initial distributions. It shows the multiplicity of periodic orbits
541 with coexistence of two species, which is the main result of the present work. For
542 different initial distributions, we obtained qualitatively the same behaviors but with

543 orbits that are more or less elongated. This is explained by the fact that proportions
 544 are periodically conserved since initial time (but not the total biomass). One can also
 545 observe on Figure 6.4 that the size of the orbits depends on the taxon. This is related
 546 to the amplitude of the periodic solutions: the more similar the species are (i.e. the
 547 closer their graphs are), the largest amplitudes are. This is why orbits with taxon b
 548 are smaller than for the two other taxa.

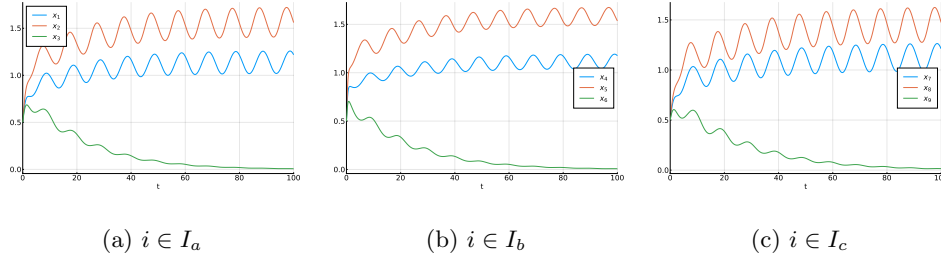


Fig. 6.3: Simulations with species of the same taxon, with $x_i(0) = 0.5$ for each i . One species is washed-out by the two others. The curves for taxa a and c look alike, related to the similarity between φ_a and φ_c .

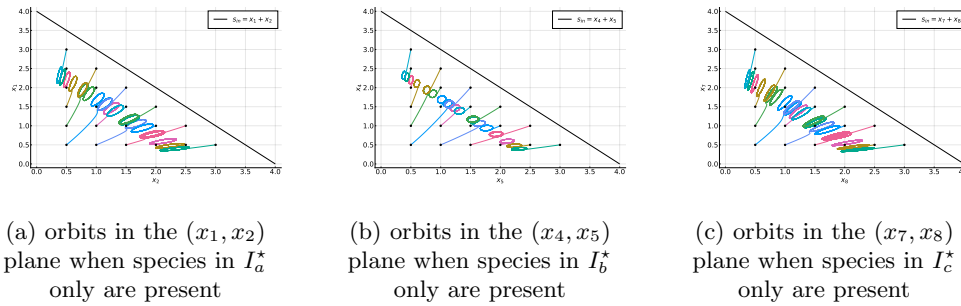


Fig. 6.4: Multiplicity of periodic orbits among a single taxon. The shape of the periodic solutions varies according to the taxon.

549 **6.2. Simulations with species of two different taxa.** In this section, we
 550 have simulated species from two different pairs of taxa. As explained formerly, we
 551 have considered two contrasted situations: significantly different taxa (a and b) and
 552 taxa relatively close to each other (a and c). Initial conditions have been chosen with
 553 uniform distribution between the six species (three from each taxon), for simplicity.
 554 We have first computed numerically numbers λ_{ba} , λ_{ab} defined in (5.1), (5.2):

$$555 \quad \lambda_{ba} = 0.012576 > 0, \quad \lambda_{ab} = 0.006272 > 0$$

556 According to Proposition 5.2, inter-taxon coexistence is thus possible as these two
 557 numbers are positive for the periodic function (6.2). On Figure 6.5, one can see that
 558 species that were washed-out when together with species of the same taxon (species
 559 3 and 6, see Section 6.1) are also washed-out here, as expected. We have now four

560 species from $I_a^* \cup I_b^*$ that coexist. Additional information about the transients are
 561 revealed. One can observe that species from taxon b (4 and 5) are initially raising
 562 faster than those of taxon a (1 and 2). This is due to the fact that the initial level s of
 563 the resource is relatively large, which favors species from the taxon b as their growth
 564 functions take larger values (see Figure 6.2). One can also observe that the time to
 565 reach a quasi-periodic regime is much slower than in the previous simulations with a
 566 single taxon. Note that there are twice as many species that coexist than before, and
 567 that the transient dynamics is governed by a scalar dynamics (4.1) for the single taxon
 568 case while it is now ruled by a two dimensional one (5.4) for which the transients can
 569 be slower.

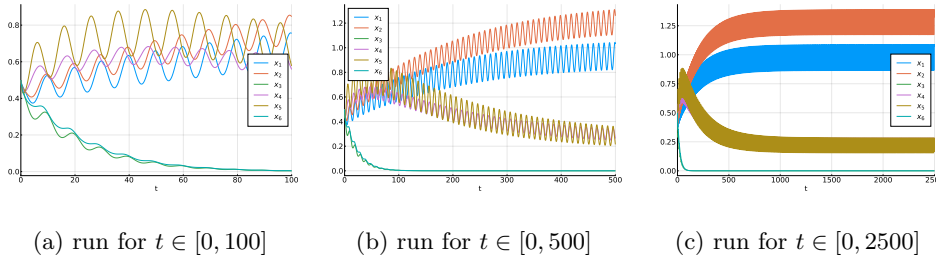


Fig. 6.5: Simulations with $x_i(0) = 0.5$, for $i \in I_a \cup I_b$. Species 5 and 6 are washed-out while the others (which do not belong to the same taxon) are able to coexist together.

570 We have then considered species of I_a in presence with those of I_c (Figure 6.6).
 571 In this case, we computed the numbers

$$572 \quad \lambda_{ca} = 0.071 > 0, \quad \lambda_{ac} = -0.0639 < 0.$$

573 According to Proposition 5.2, inter-taxa coexistence is now no longer guaranteed.
 574 However, as the number λ_{ca} is positive, we deduce that taxon a can settle. However,
 575 although taxon c seems closer from taxon a than b if one looks at their growth curves
 576 only (Figure 6.2), any species from taxon c loses the competition with taxon a . here,
 577 one needs to explicitly compute the sign of numbers λ_{ba} and λ_{cc} to predict the issue
 578 of the competition. Finally, only species 1 and 2 are asymptotically present, with a
 579 transient speed similar to the simulations with the single taxon a (cf Figure 6.3a).

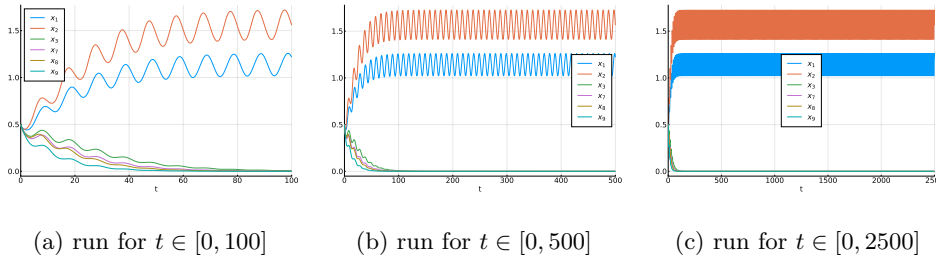


Fig. 6.6: Simulations with $x_i(0) = 0.5$, for $i \in I_a \cup I_c$. Species 1 and 2 from the taxon a coexist but wash-out all the other species.

580 **6.3. Simulations under approximate taxon condition.** The conditions for
 581 species to belong to a same taxon, and that some of them have identical numbers
 582 γ_i , are not generic among all increasing growth functions. In the spirit of former
 583 works [12, 3] for constant removal rate, we investigate here numerically cases where
 584 the condition (3.1) is only approximately satisfied.

585 For this purpose, we considered an additional species labeled $2'$ whose growth
 586 function $\mu_{2'}$ is closed to μ_2 but that does not belong to the taxon I_a . For the illus-
 587 tration, we have simply taken $\mu_{2'} = \mu_2 + \varepsilon\eta$, where η is a smooth function null at 0
 588 with $\eta(\lambda_2(\bar{u})) > 0$ that is not proportionate to φ_a , and ε is a small number.

589 *Remark 6.1.* In the particular case where the perturbation is such that $\mu_{2'}$ still
 590 satisfies the taxonomic assumption with $\alpha_{2'} = \alpha_2$ and $\gamma_{2'} = \gamma_2 - \varepsilon$ (recall that $\gamma_2 = \gamma_1$),
 591 it is possible to study how the perturbation propagates over time. Indeed, we have
 592 from Proposition 3.3 that

$$593 \quad \dot{\rho}_{12'} = (\varepsilon + (\bar{u} - u(t))(\alpha_1^{-1} - \alpha_2^{-1})) \rho_{12'}.$$

594 If $x_2(0) = x_{2'}(0)$ and the other initial conditions are the same, we can integrate this
 595 dynamics over $k \in \mathbb{N}$ periods from $t = 0$ and obtain the following comparison result:

$$596 \quad \rho_{12'}(kT) = \rho_{12}(kT)e^{k\varepsilon T}.$$

597 For the numerical illustration, we have taken $\eta(s) = \frac{s}{1+s}$ and first run simulations
 598 with species 1, 2 and $2'$. For $\varepsilon < 0$, the species $2'$ is asymptotically conducted to wash-
 599 out. However, as one can see on Figure 6.7, the transients can be very long when $\mu_{2'}$ is
 600 very close to μ_2 so that the three species coexist in an almost periodic manner during
 601 a long time horizon. On the opposite, for $\varepsilon > 0$, the species $2'$ is the final winner of
 602 the competition (Figure 6.8). However, it can take a long time for the other species
 603 to decline, so that here also the three species coexist in an almost periodic manner
 604 during a long time period.

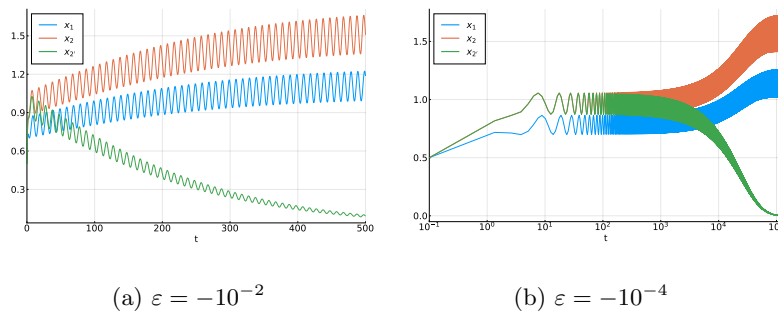


Fig. 6.7: Simulations with species 1, 2, $2'$ together when $\varepsilon < 0$. Species $2'$ is washed-out after a transient regime whose length depend on ε .

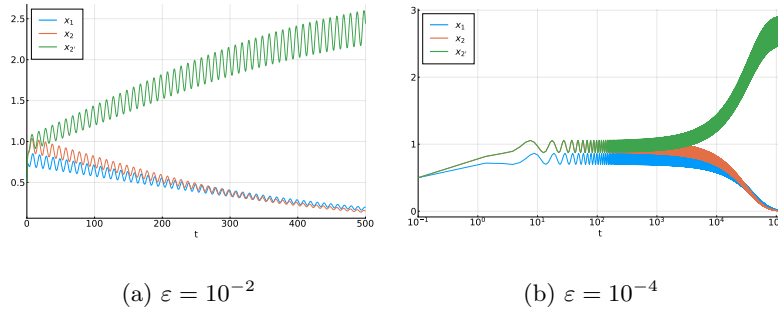


Fig. 6.8: Simulations with species 1, 2, 2' together when $\varepsilon > 0$. Species 1 and 2 are both washed-out after a transient regime whose length depend on ε .

605 Then, we have considered species of taxa I_a and I_b together, as before (Figure 6.5),
 606 but where species 2 is replaced by species 2'. Figures 6.9, 6.10 show that depending
 607 on the sign of ε , species 2' belongs to the the final composition of the ecosystem or
 608 not, and that the time necessary to distinguish this issue can be very long, even for
 609 values of ε not extremely small. Note that coexistence of several species is maintained
 610 in both cases. A message here is that the analysis of non generic situations, as we
 611 do here, could be of some interest when facing cases likely to be closed from the non-
 612 generic case, and we believe that this could be even more likely when considering a
 613 large number of species.

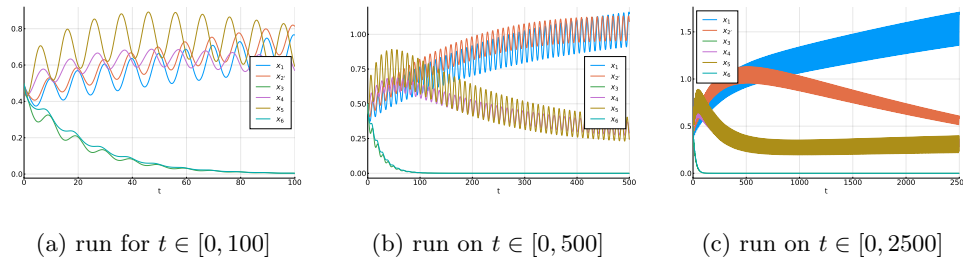


Fig. 6.9: Simulations with species 1, 2', 3, 4, 5, 6 together when $\varepsilon = -10^{-3}$. Species 2' does not belong to I_a^* and is washed-out after a long transient regime.

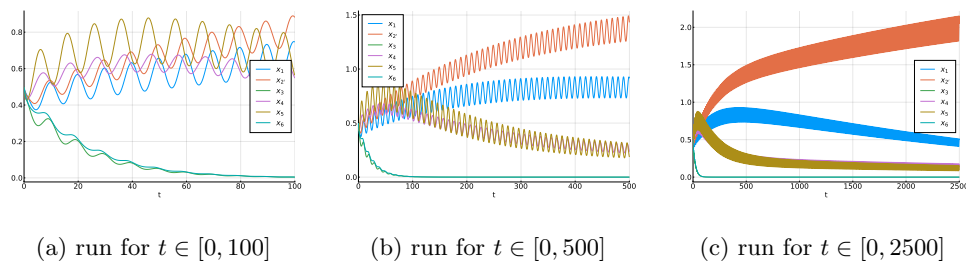


Fig. 6.10: Simulations with species 1, 2', 3, 4, 5, 6 together when $\varepsilon = 10^{-3}$. Now I_a^* is reduced to species 2', which is the only species of taxon a to persist.

614 **7. Conclusion.** In this work, we have proposed a taxonomic condition on growth
 615 functions, that allows the coexistence under periodic removal rate of two or more
 616 species with the same break-even concentrations within a single taxon. This gener-
 617 alizes the neutral condition of identical break-even concentrations in the chemostat
 618 with constant removal rate, which ensures coexistence at steady state.

619 Our condition is defined relatively to a generating growth function that charac-
 620 terizes a taxon, independently of the period and the shape of the periodic signal.
 621 This makes the coexistence result robust with this respect, as well as the extinction
 622 of species in the taxon with larger break-even concentrations. Relying on the theory
 623 of asymptotic periodic semi-flows, we have shown that when persistence of a taxon is
 624 guaranteed, then any solution converges to a periodic orbit, and moreover that there
 625 exists an infinite number of distinct periodic orbits depending on the initial propor-
 626 tions of the species (within the taxon). There exists then a continuum of neutrally
 627 stable periodic orbits. In addition, we have generalized the existing results about
 628 coexistence of two species in the periodic chemostat model to the case of two taxa in
 629 competition, leading to a double infinity of periodic orbits with species of both taxon.

630 The condition of belonging to a taxon is non-generic and gives non-hyperbolic
 631 periodic orbits, but we believe that it could guide future constructions of sufficient
 632 conditions for the uniqueness of hyperbolic periodic orbits in the chemostat model
 633 with periodic removal rate, an open problem for general classes of growth functions.

634 Finally, we have shown with the help of numerical simulations that when these
 635 non-generic conditions are just "almost" fulfilled, what is likely to happen among a
 636 huge number of species, then one can observe many almost periodic solutions with
 637 coexistence on a long time window, justifying a posteriori the present analysis of
 638 neutrally stable periodic solutions.

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