



**HAL**  
open science

# Multiplicity of periodic orbits with coexistence in the chemostat subject to periodic removal rate

Thomas Guilmeau, Alain Rapaport

► **To cite this version:**

Thomas Guilmeau, Alain Rapaport. Multiplicity of periodic orbits with coexistence in the chemostat subject to periodic removal rate. 2023. hal-03982233v2

**HAL Id: hal-03982233**

**<https://hal.inrae.fr/hal-03982233v2>**

Preprint submitted on 20 Oct 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

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-

---

\*CVN, Univ. Paris-Saclay, Inria, CentraleSupélec, Gif-sur-Yvette, France  
(thomas.guilmeau@inria.fr).

†MISTEA, Univ. Montpellier, INRAE, Institut Agro, Montpellier, France  
(alain.rapaport@inrae.fr).

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  $i = 1, \dots, n$ ,  $\mu_i$  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  $\Delta_0$  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  $\Delta_0$  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  $\Delta$  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  $\mu_i$  ( $i \in I$ ) 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  $\varphi$  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  $\varphi$  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  $\varphi$  is not unique but it  
 141 can typically represent a *canonical growth function* that verifies Assumption 2.1 so  
 142 that the growth functions  $\mu_i$  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  $\mu_i$  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  $\varphi$  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  $\varphi$  is increasing, a higher value  $\gamma_i$  corresponds to  
 167 a lower break-even concentration  $\lambda_i$ . 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  $\Delta$ , the dynamics of the ratios  $\rho_{ij}$  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  $\gamma_k$ ,  $k \in i, j$ , 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  $\rho_{ij}$  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  $\Delta$ , one has*

- 191 1. *For  $i, j$  in  $I^*$ ,  $\rho_{ij}$  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  $\rho_{ij}$  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  $\Delta$ , 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  $\Delta$  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  $\Delta$  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  $\mu_{i^*}$  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  $\mu_{i^*}$  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  $\rho_{ii^*}$  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  $\Delta$ , 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  $\Delta$  but with the same initial  
 302 ratios  $\rho_{ii^*}(0)$  for  $i \in I^*$ . According to (3.4), the functions  $\rho_{ii^*}$  ( $i \in I^*$ ) 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  $\Delta$  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  $\mu_i$ ,  $i \in \{1, \dots, n\}$ , 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  $\Delta$ ,*  
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  $\varphi_a$ ,  $\varphi_b$  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  $\Delta$  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  $\xi$ ,  $\zeta$

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

407 (remind from Proposition 3.4 that functions  $\rho_{ii^*}$  ( $i \in I_a$ ) or  $\rho_{ii^*}$  ( $i \in I_b$ ) 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  $\Gamma$  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  $\Gamma$  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  $\Gamma$  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  $\Delta$  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  $\rho_{ij}^\varepsilon$  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  $\alpha_i$  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  $\mu_{max}$ ,  $K$  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 ( $\varphi_b$ ) has a significantly  
 498 different shape. Graphs of the functions  $\varphi_a$ ,  $\varphi_b$ ,  $\varphi_c$  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  $\alpha_i$  and  $\beta_i$  following Equation (3.1). Since  $\alpha_i$   
 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  $\alpha_i$ ,

514 the higher is the maximal growth rate). Since  $\beta_i$  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  $\beta_i$ , 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  $\Delta$  with  $\underline{s} = 0.5$ . For the chosen value of  $\bar{u}$ , numbers  $\bar{s}$  and  $\gamma_i$  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
$\varphi$	$\varphi_a$			$\varphi_b$			$\varphi_c$		
$\alpha_i$	0.9	1.15	0.85	0.8	1.05	0.6	0.9	1.1	0.7
$\beta_i$	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
$\varphi$	$\varphi_a$			$\varphi_b$			$\varphi_c$		
$\bar{s}$	1.28			1.30			1.40		
$\gamma_i$	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  $\gamma_i$  (with  $\bar{u} = 0.8$ )

526



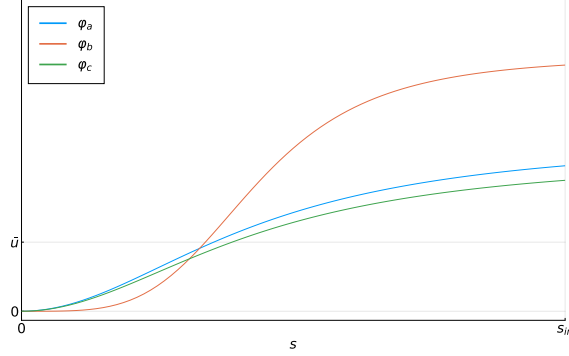


Fig. 6.1: Graphs of the generating growth functions:  $\varphi_a$  and  $\varphi_c$  are close to each other with  $\varphi_a$  slightly above  $\varphi_c$ , while  $\varphi_b$  has a different shape.

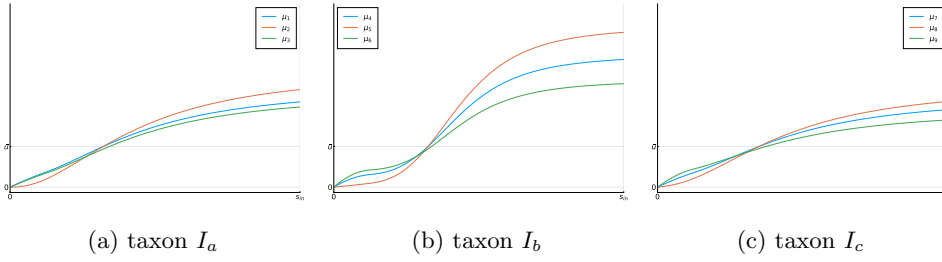


Fig. 6.2: Graphs of the growth functions within each taxon. The orange and blue growth functions reach the value  $\bar{u}$  for lower values of  $s$  than the green one, implying that the species associated with the latter is expected to be washed-out by the two other ones.

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  $\gamma_i$  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  $\alpha_i$  (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.

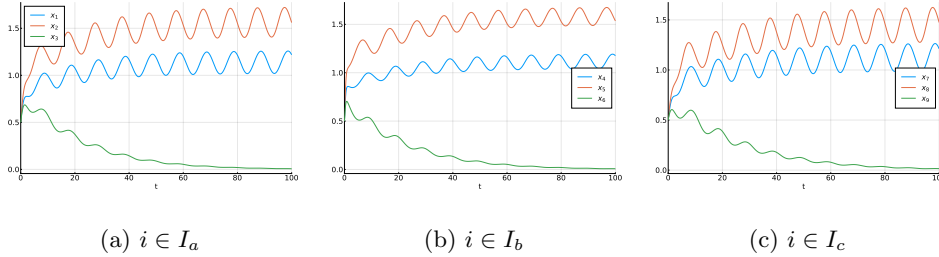


Fig. 6.3: Simulations with species of the same taxon, with  $x_i(0) = 0.5$  for each  $i$ . One species is washed-out by the two others. The curves for taxa  $a$  and  $c$  look alike, related to the similarity between  $\varphi_a$  and  $\varphi_c$ .

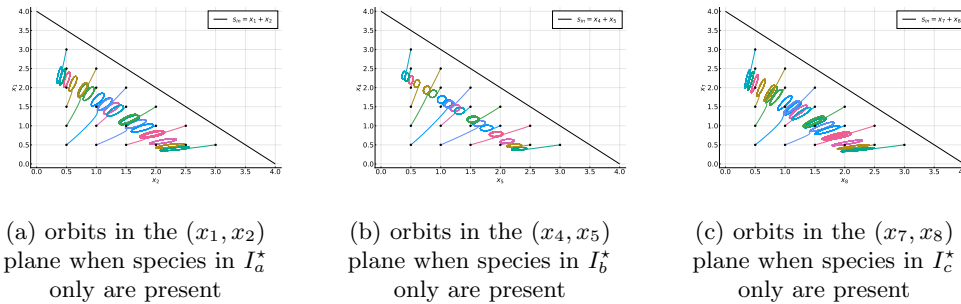


Fig. 6.4: Multiplicity of periodic orbits among a single taxon. The shape of the periodic solutions varies according to the taxon.

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  $\lambda_{ba}$ ,  $\lambda_{ab}$  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.

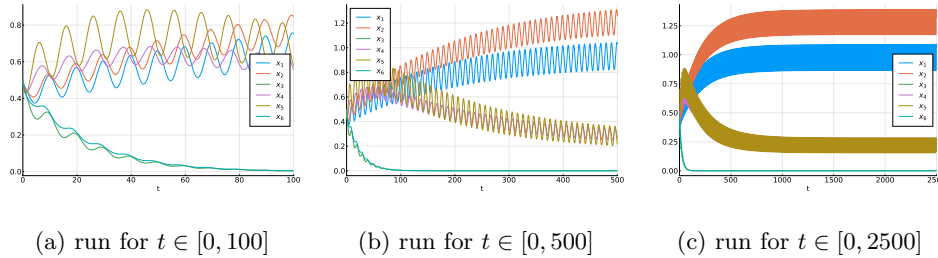


Fig. 6.5: Simulations with  $x_i(0) = 0.5$ , for  $i \in I_a \cup I_b$ . Species 5 and 6 are washed-out while the others (which do not belong to the same taxon) are able to coexist together.

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  $\lambda_{ca}$  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  $\lambda_{ba}$  and  $\lambda_{cc}$  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).

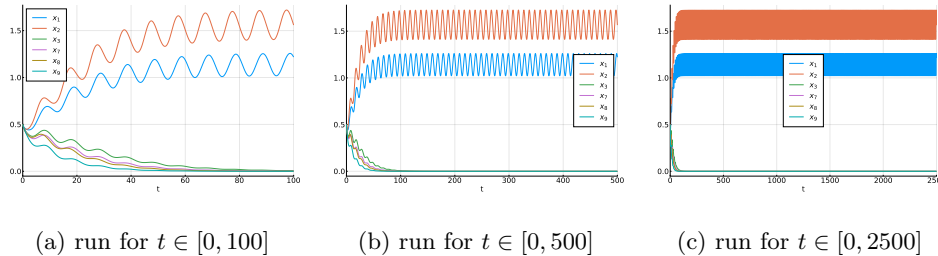


Fig. 6.6: Simulations with  $x_i(0) = 0.5$ , for  $i \in I_a \cup I_c$ . Species 1 and 2 from the taxon  $a$  coexist but wash-out all the other species.

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  $\gamma_i$ , 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  $\mu_2$  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  $\eta$  is a smooth function null at 0  
 588 with  $\eta(\lambda_2(\bar{u})) > 0$  that is not proportionate to  $\varphi_a$ , and  $\varepsilon$  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 
$$\dot{\rho}_{12'} = (\varepsilon + (\bar{u} - u(t))(\alpha_1^{-1} - \alpha_2^{-1})) \rho_{12'}.$$

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

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  $\mu_2$  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.

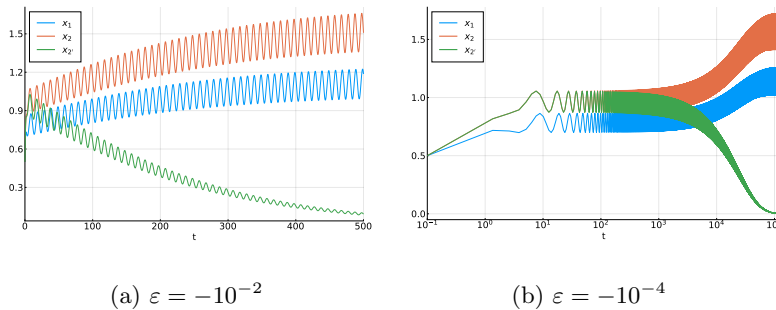


Fig. 6.7: Simulations with species 1, 2,  $2'$  together when  $\varepsilon < 0$ . Species  $2'$  is washed-out after a transient regime whose length depend on  $\varepsilon$ .

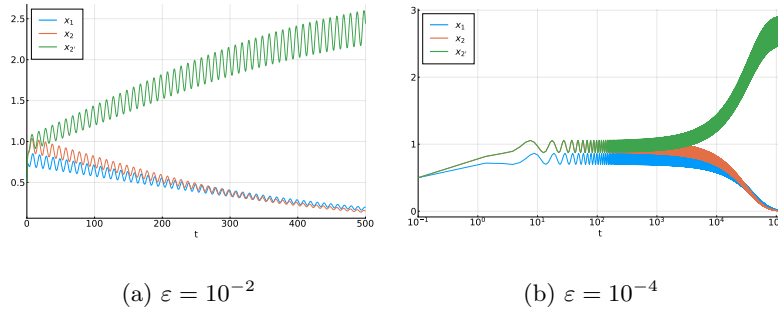


Fig. 6.8: Simulations with species 1, 2, 2' together when  $\varepsilon > 0$ . Species 1 and 2 are both washed-out after a transient regime whose length depend on  $\varepsilon$ .

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  $\varepsilon$ , 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  $\varepsilon$  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.

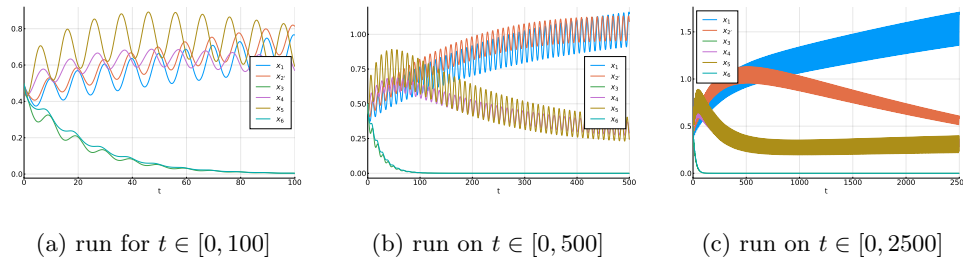


Fig. 6.9: Simulations with species 1, 2', 3, 4, 5, 6 together when  $\varepsilon = -10^{-3}$ . Species 2' does not belong to  $I_a^*$  and is washed-out after a long transient regime.

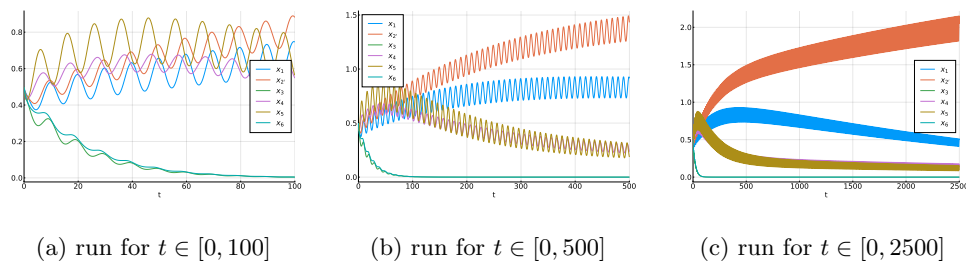


Fig. 6.10: Simulations with species 1, 2', 3, 4, 5, 6 together when  $\varepsilon = 10^{-3}$ . Now  $I_a^*$  is reduced to species 2', which is the only species of taxon  $a$  to persist.

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.

639

#### REFERENCES

- 640 [1] G.J. BUTLER, S.B. HSU AND P.E. WALTMAN, *A mathematical model of the chemostat with*  
 641 *periodic washout rate*, SIAM Journal of Applied Mathematics, 45, 435–449, 1985.  
 642 [2] P. DE MOTTONI AND A. SCHIAFFINO, *Competition systems with periodic coefficients: a geometric*  
 643 *approach*, Journal of Mathematical Biology, 11, 319–335, 1981.  
 644 [3] M. EL HAJJI AND A. RAPAPORT, *Practical coexistence of two species in the chemostat - a slow-*  
 645 *fast characterization -*, Mathematical Biosciences, 218(1), 33–39, 2009.  
 646 [4] J.K. HALE AND A.S. SOMOLINOS, *Competition for fluctuating nutrient*, Journal of Mathematical  
 647 Biology, 18, 255–280, 1983  
 648 [5] J. HARMAND, C. LOBRY, A. RAPAPORT, T. SARI, *The chemostat, mathematical theory of con-*  
 649 *tinuous culture of micro-organisms*, ISTE Press, London, 2017.

- 650 [6] S.B. HSU, *A Competition Model for a Seasonally Fluctuating Nutrient* Journal of Mathematical  
651 Biology, 9, 115–132, 1980.
- 652 [7] P. LENAS AND S. PAVLOU, *Coexistence of three competing microbial populations in a chemostat  
653 with periodically varying dilution rate*, Mathematical Biosciences 129, 111–142, 1995.
- 654 [8] H. MOSER, *The dynamics of bacterial populations maintained in the chemostat*, Carnegie Insti-  
655 tution of Washington Publication, 1958.
- 656 [9] S. NAKAOKA AND Y. TAKEUCHI, *How can three species coexist in a periodic chemostat? Mathe-  
657 matical and Numerical Study*, Proceedings of the 9th International Conference “Difference  
658 Equations and Discrete Dynamical Systems”, L. Allen, B. Aulbach, S. Elaydi, R. Sacker  
659 (Editors), Los-Angeles (USA), 2–7 Aug. 2004, World Scientific, 121–133, 2005.
- 660 [10] S. NOWACK AND I. KLAPPER, *Exclusion in a Temporally Varying Chemostat System: Dependence  
661 on Trade-Offs*, SIAM Journal on Applied Mathematics 78(5), 2819–2839, 2018.
- 662 [11] Q.-L. PENG AND H.I.FREEDMAN, *Global Attractivity in a Periodic Chemostat with General  
663 Uptake Functions*, Journal of Mathematical Analysis and Applications, 249(2), 300–323,  
664 2000.
- 665 [12] A. RAPAPORT, D. DOCHAIN AND J. HARMAND, *Long run coexistence in the chemostat with  
666 multiple species*, Journal of Theoretical Biology, 257(2), 252–259, 2009.
- 667 [13] P.L. SILVERSON, R.R. HUDGINS, *Periodic Operations of Bioreactors*, Elsevier, 2013.
- 668 [14] H. L. SMITH, *Competitive coexistence in an oscillating chemostat*, SIAM Journal on Applied  
669 Mathematics, 40, 498–522, 1981.
- 670 [15] H. SMITH, P. WALTMAN, *The theory of chemostat, dynamics of microbial competition*, Cam-  
671 bridge Studies in Mathematical Biology, Cambridge University Press, 1995.
- 672 [16] G. STEPHANOPOULOS, A. FREDERICKSON, R. ARIS, *The growth of competing microbial popula-  
673 tions in a cstr with periodically varying inputs*, AIChE Journal, 25(5), 863–872, 1979.
- 674 [17] F. WANG AND G. PANG, *Competition in a chemostat with Beddington DeAngelis growth rates  
675 and periodic pulsed nutrient*, Journal of Mathematical Chemistry, 44(3), 691–710, 2008.
- 676 [18] G. WOLKOWICZ AND X.-Q. ZHAO, *N-species competition in a periodic chemostat*, Differential  
677 Integral Equations 11, 465–491, 1998.
- 678 [19] X.-Q. ZHAO, *Asymptotic behavior for asymptotic periodic semiflows with applications*, Commu-  
679 nications on Applied Nonlinear Analysis, 3(4), 43–66, 1996.