Non-periodicity of chemostats: a multi-dimensional negative Bendixson Dulac criterion

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1 Introduction and result

The chemostat plays a well-established role as a model open system in ecology the comprehensive monograph see [HSm95]. Basically, the chemostat consists of a nutrient input pumped at a constant rate into a well-mixed culture vessel. Volume is kept constant by pumping the mixed contents out at the same rate. We assume all nutrients needed for growth, except one, to be present in abundance. In addition to being a piece of laboratory apparatus for continuous culturing of bacteria, the chemostat is also a model for a very simple lake where exploitative competition is easily studied. Let $S(t)$ denote the nutrient concentration at time t and $x_i(t)$ the concentration of the i-th competing species, $i = 1, 2 \ldots N$. The model with possibly different removal rates d_i is then given by

$$\begin{aligned} \dot{S}(t) &= (S^0 - S)D - \sum_{i=1}^{N} p_i(S)x_i, \\ \dot{x}_i(t) &= (c_i p_i(S) - d_i)x_i, \end{aligned} \tag{1.1}$$

with initial conditions $S(0) > 0,\ x_i(0) > 0,\ i = 1, 2 \ldots N$. Here c_i is the conversion constant for the i-th species and the uptake rate $p_i(S)$ satisfies $p_i(0) = 0,\ p_i(S) > 0$ and $p_i'(S) > 0$ for $0 < S < S^{(0)}$. The input concentration $S^{(0)}$ and the washout rate D are assumed constant and are under the control of the experimenter.

Under the scaling $S \mapsto S/S^{(0)},\ t \mapsto Dt,\ p_i(S) \mapsto \dfrac{c_i}{d_i} p_i(S),\ x_i \mapsto \dfrac{d_i}{c_i} x_i,\ d_i = \dfrac{d_i}{D}$, the above simple chemostat equations take the form

$$\begin{aligned} \dot{S} &= 1 - S - \textstyle\sum_{j=1}^{N} p_j(S)x_j \\ \dot{x}_i &= \alpha_i(p_i(S) - 1)x_i \end{aligned} \tag{1.2}$$

with $S(0) > 0,\ x_i(0) > 0,\ i = 1, \ldots, N$.

One fundamental question on the chemostat model (1.2) is persistence of the species x_i. Looking for positive equilibria we have to solve

$$p_i(S) = 1, \tag{1.3}$$

simultaneously for all $i = 1, \ldots, N$. For $N \geq 2$ these conditions on S will contradict each other, in general. Therefore equilibria require extinction of all but one species.

In the present paper we address the next best option: *does the chemostat model* (1.2) *support persistence of all species in the form of a positive nonstationary periodic solution?*

Over the last decades many attempts have been made to negatively answer this periodicity question. To our knowledge, these attempts have exclusivley been based on Lyapunov functions. Indeed the existence of a Lyapunov function $V = V(S, x_1, \ldots, x_N)$ which deccreases strictly along nonstationary solutions precludes nonstationary periodicity. We survey and discuss some of these results in section 6.

Instead of aiming for yet another Lyapunov function, we try to develop and apply a higher-dimensional version of the planar negative Bendixson Dulac criterion: *planar vector fields of negative divergence do not possess nonstationary periodic orbits.* Indeed the resulting area contraction of the associated flow precludes invariance of the nonempty interior of the periodic orbit in the plane, or in any simply connected domain. The case $N = 1$ of a single species is a trivial illustration. Passing to $y_0 := S,\ y_1 = \log x_1$ we obtain

$$
\begin{aligned}
\dot{y_0} &= 1 - y_0 - p_1(y_0)e^{y_1} \\
\dot{y_1} &= \alpha_1(p_1(y_0) - 1)
\end{aligned}
\tag{1.4}
$$

with resulting divergence

$$
\text{div } = -1 - p_1'(y_0)e^{y_1} + 0 < 0. \tag{1.5}
$$

This is the simplistic paradigm which we plan to follow in the present paper. Standard prejudice, however, would immediately discard such an attempt because the area argument is essentially planar: curves delimit area, in $\mathbb{R}^2$, but do no delimit volume, in $\mathbb{R}^{N+1}$, for $N \geq 2$. But the area argument is based on integration of divergence over the interior, and on the Gauss theorem, to reach a contradiction. We will therefore invoke the Stokes theorem, with some difficulty, to derive a sufficient condition for non-periodicity in the chemostat.

In fact we are not able to utilize the double appearance of the per capita consumption rates as $p_j(S)$ and $p_i(S)$ in the original chemostat model (1.2). We will therefore address the slightly more general model

$$
\begin{aligned}
\dot{x_0} &= f_0 := 1 - x_0 - \textstyle\sum_{j=1}^{N} p_j(x_0)x_j, \\
\dot{x_i} &= f_i(x_0)x_i.
\end{aligned}
\tag{1.6}
$$

Here $x_0 := S$ denotes the substrate, and functions p_j and f_i, $\ 1 \leq i,j \leq N$, are given.

Theorem 1.1 *Let the C^1-functions p_j and f_i satisfy the following three conditions, for suitable $\lambda_i > 0$ and all $1 \leq i,j \leq N,\ 0 < x_j,\ 0 < x_0 < 1,\ j \neq i$:*

$$
p_j > 0; \tag{1.7}
$$

$$
f_i(x_0) \cdot (x_0 - \lambda_i) > 0, \quad \text{for} \quad x_0 \neq \lambda_i; \tag{1.8}
$$

$$
f_i(x_0) < 1 + (f_j(x_0) + (1 - x_0)p_j'(x_0)/p_j(x_0). \tag{1.9}
$$

Then (1.6) *does not possess positive nonstationary periodic orbits.*

The zero $x_0 = \lambda_i$ of f_i denotes the *break-even concentration* of the substrate x_0 where growth of x_i is balanced by death and dilution. For the standard chemostat, condition (1.8) reads $(p_i(x_0) - 1)(x_0 - \lambda_i) > 0$ and follows from monotonicity $p_i' > 0$. Condition (1.9) can in fact accomodate slightly negative p_i' but then becomes more restrictive on f_i. Condition (1.9) is trivially satsified in the single species case $N = 1$ which is also amenable to the standard negative Bendixson Dulac criterion.

The remaining sections are organized as follows. In section 2 we given an outline of the proof of theorem 1.1. We reduce the indirect proof to a string of several lemmas given in sections 3–5. Section 3 sets up the Stokes theorem and chooses an appropriate differential form. Based on the negative winding of projected trajectories $(x_i, x_0),\ 1 \leq i \leq N$, as discussed in section 4 we establish a contradiction in section 5 which is reminiscent of the planar proof via the Gauss theorem. The expert reader may also jump to (2.8) for a technical summary. In section 6 we summarize some earlier results based on Lyapunov functions and we compare these results with our Stokes based Bendixson approach.

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2 Outline of the proof of theorem 1.1

We outline the indirect proof o theorem 1.1, reducing the proof to a string of lemmas. The details are filled in in sections 3–5.
Section 3 specifies our choice of the differential 1-form

$$\alpha = g_0 dx_0 + g_1 dx_1 + \cdots + g_N dx_N \tag{2.1}$$

to enter the Stokes theorem. See [....] for a general background on the Cartan calculus of exterior forms and the Stokes theorem. Assuming, indirectly, that a positive nonstationary periodic orbit $\Gamma \subseteq \mathbb{R}^{N+1}$ exists, we choose an oriented immersed closed disk $\Omega \subseteq \mathbb{R}^{N+1}$

with (time) oriented boundary Γ, see lemma 4.1. In section 3 we choose the coefficients $g_0(x), \ldots, g_N(x),\ x = (x_0, \ldots, x_N)$ such that the Stokes theorem implies

$$0 = \int\limits_{\Gamma=\partial\Omega} \alpha = \int\limits_{\Omega} d\alpha; \tag{2.2}$$

see lemma 3.1. In lemma 3.2 we calculate the exterior derivative $d\alpha$ to be of the special form

$$d\alpha = dx_0 \wedge dH, \tag{2.3}$$

and we derive the explicit form of the scalar function $H = H(x)$. To prepare for a contradiction we evaluate the right-hand side of (2.2), again via Stokes:

$$\begin{aligned} \int\limits_{\Omega} d\alpha &= \int\limits_{\Omega} dx_0 \wedge dH = -\int\limits_{\Omega} d(H dx_0) = \\ &= -\int\limits_{\Gamma=\partial\Omega} H dx_0. \end{aligned} \tag{2.4}$$

In lemma 4.2 we show that

$$-\int\limits_{\Gamma} H dx_0 = \int\limits_{\underline{x}_0}^{\overline{x}_0} \sum_{k=1}^{k(x_0)} (-H(\xi^{+k}) + H(\xi^{-k})) dx_0. \tag{2.5}$$

Here the integral on the right extends from the minimum $\underline{x}_0$ to the maximum $\overline{x}_0$ of $x_0(t)$ on the periodic orbit Γ. Integration is with respect to increasing x_0 and not with respect to the differential form dx_0 along the orientation of Γ. For convenience we work with $\xi = (\xi_1, \ldots, \xi_N),\ \xi_i := p_i(x_0)x_i$, instead of x_i here and in the following lemmas. The points $(x_0, \xi^{\pm k}) \in \Gamma \cap (\{x_0\} \times \mathbb{R}^N),\ k = 1, \ldots, k(x_0)$, are enumerated such that the signs of the superscripts $\pm k$ indicate points on Γ where $\pm\dot{x}_0 > 0$. In particular we address finiteness of k in lemma 4.2. In lemma 4.3 we propose marriages based on the relative position of the components $\xi_j^{\pm k}$, for any fixed $1 \leq j \leq N$. Marriages are based on the fact that the projections of Γ onto each (x_j, x_0)-plane are negatively winding. More precisely we state that for each fixed $1 \leq j \leq N$ and almost all x_0 there exists a "marriage" numbering $x^{\pm k}$, which depends on j and x_0, such that

$$\xi_j^{+k} > \xi_j^{-k} \tag{2.6}$$

holds for all $1 \leq k \leq k(x_0)$.

In section 5 we reach a contradiction to our indirect assumption that a nonstationary periodic orbit Γ exists. In fact we use the marriage result of (2.6) to conclude that

$$\sum_{k=1}^{k(x_0)} H(\xi^{+k}) - \sum_{k=1}^{k(x_0)} H(\xi^{-k}) > 0, \tag{2.7}$$

at almost all levels of x_0. See lemma 5.2.

To reach a contradiction which completes the proof of theorem 1.1 we only have to read (2.2), (2.4), (2.5), and (2.7) sequentially:

$$\begin{aligned} 0 &= \int_\Gamma \alpha = \int_\Omega d\alpha = \int_\Omega dx_0 \wedge dH = -\int_\Gamma H dx_0 = \\ &= \int_{\underline{x}_0}^{\overline{x}_0} \Big(\sum_{k=1}^{k(x_0)} (-H(\xi^{+k}) + H(\xi^{-k})) \Big) dx_0 < 0. \end{aligned} \tag{2.8}$$

This reduces the proof of theorem 1.1 to lemmas 3.1, 3.2, 4.1-4.3, and 5.2 below.

3 Choice of differential forms

In the outline of our proof of theorem 1.1 we have required the construction of a differential 1-form

$$\alpha = g_0 dx_0 + g_1 dx_1 + \cdots + g_N dx_N \tag{3.1}$$

such that two properties hold:

$$\int_\Gamma \alpha = 0 \tag{3.2}$$

along the hypothetical nonstationary periodic orbit Γ of the generalized chemostat system (1.6), and

$$d\alpha = dx_0 \wedge dH \tag{3.3}$$

for an explicit scalar function $H = H(x_0, x_1, \ldots, x_N)$. See (2.2), (2.3).

Although we could simply confront our reader with our choices of $g_0, \dots, g_N$ we prefer to motivate these choices for the sake of transparency, and let our reader participate in the quest. By standard Cartan calculus of exterior forms (3.1) and (3.3) imply, respectively,

$$
\begin{aligned}
d\alpha &= \sum_{i=1}^{N} (-\partial_i g_0 + \partial_0 g_i) dx_0 \wedge dx_i + \\
&\quad + \sum_{1 \le i < j \le N} (-\partial_j g_i + \partial_i g_j) dx_i \wedge dx_j,
\end{aligned}
\tag{3.4}
$$

$$
d\alpha = \sum_{i=1}^{N} \partial_i H dx_0 \wedge dx_i. \tag{3.5}
$$

Here $\partial_i = \frac{\partial}{\partial x_i}$ indicate partial derivatives. Comparing coefficients, we observe two things:

$$
\partial_i g_j = \partial_j g_i, \tag{3.6}
$$

$$
\partial_0 g_i - \partial_i g_0 = \partial_i H; \tag{3.7}
$$

for all $1 \le i, j \le N$. Conversely, (3.6) and (3.7) imply (3.3) for the choice (3.1). In the positive orthant conditions (3.6) are equivalent to

$$
g_i = \partial_i G \tag{3.8}
$$

for $1 \le i \le N$ and a suitable scalar potential $G = G(x_0, x_1, \dots, x_N)$. Thus (3.7) reads $\partial_i(H + g_0 - \partial_0 G) = 0$, for all $1 \le i \le N$. Hence

$$
H + g_0 - \partial_0 G = c(x_0) \equiv 0 \tag{3.9}
$$

is a function of x_0 alone, which we choose to vanish without altering $d\alpha = dx_0 \wedge dH$.

This general derivation of H does not address condition (3.2) yet, which requires

$$
\begin{aligned}
0 &= \int_{\Gamma} \alpha = \int_0^T (g_0 \dot{x}_0 + g_1 \dot{x}_1 + \dots + g_N \dot{x}_N) dt \\
&= \int_0^T (f_0 g_0 + x_1 f_1 g_1 + \dots + x_N f_N g_N) dt
\end{aligned}
\tag{3.10}
$$

along the T-periodic orbit Γ. Here $f_0 = f_0(x) = 1 - x_0 - \sum p_j x_j$ depends on all variables, whereas $f_i = f_i(x_0)$ for $1 \le i \le N$. Without additional global information on the periodic orbit Γ we must require the integrand to vanish pointwise everywhere – as we would in the planar case. This motivates our Ansatz

$$g_i \;:=\; f_0 q_i, \quad \text{for} \quad 1 \le i \le N; \tag{3.11}$$

$$g_0 \;:=\; -\sum_{j=1}^{N} x_j f_j q_j \tag{3.12}$$

with functions q_j yet to be determined.

Lemma 3.1 *With the choice* (3.11), (3.12) *of* $g_0, g_1, \ldots, g_N$ *we have*

$$f_0 g_0 + \sum_{j=1}^{N} x_j f_j g_j \equiv 0. \tag{3.13}$$

In particular $\int\limits_{\Gamma} \alpha = 0$, *as required in* (2.2), (3.2).

Proof. Trivial by Ansatz (3.11), (3.12) and by (3.10). ⋈

To satisfy (3.6) alias (3.8) the functions q_i in (3.11) must solve

$$0 = \partial_i g_j - \partial_j g_i = -p_i q_j + p_j q_i + f_0(\partial_i q_j - \partial_j q_i), \tag{3.14}$$

for all $1 \le i, j \le N$. Here we have used $\partial_i f_0 = \partial_i \left(1 - x_0 - \sum_{j=1}^{N} p_j x_j\right) = -p_i$. To facilitate the solution of this complicated linear system of PDEs for the vector q we only consider the gradient case

$$q_i = \partial_i Q, \tag{3.15}$$

$1 \le i \le N$ with a scalar potential Q. Other choices are possible and cumbersome. Then (3.14) is equivalent to

$$-p_i \partial_j Q + p_j \partial_i Q = 0 \tag{3.16}$$

which possesses the general solution

$$Q = Q(x_0, \sigma) \tag{3.17}$$

with the abbreviations

$$\sigma := \xi_1 + \cdots + \xi_N, \qquad \xi_i := p_i x_i. \tag{3.18}$$

Here we have of course used that $p_i = p_i(x_0)$ are independent of x_j, $1 \le j \le N$. With the abbreviation Q_σ for $\frac{\partial}{\partial\sigma}Q$ this specifies

$$q_i = p_i Q_\sigma \tag{3.19}$$

by (3.15), and therefore the 1-form α, by (3.1), (3.11), (3.12). The choice of $Q = Q(x_0, \sigma)$ is still free.

Lemma 3.2 *Let $Q = Q(x_0, \sigma)$ be an arbitrary C^1-function. Let $D_0 Q$ denote the partial derivative of Q with respect to its first argument and let Q^σ denote a primitive function with respect to the second argument. Let G and H be defined via* (3.8), (3.11), (3.12), (3.19) *above. Then*

$$G = f_0 Q + Q^\sigma \tag{3.20}$$

up to an integration "constant" which depends on x_0, only. Similarly, the differential 1-form α from (3.1) *and lemma 3.1 satisfies $d\alpha = dx_0 \wedge dH$, as required in* (3.3)*, with H given explicitly by*

$$H = -Q + \big(\sum_{j=1}^{N} \xi_j (f_j + f_0 \pi_j')\big) Q_\sigma + f_0 D_0 Q + (D_0 Q)^\sigma, \tag{3.21}$$

again up to an integration "constant". Here we have substituted

$$\pi_j := \log p_j, \qquad \pi_j' = p_j'/p_j. \tag{3.22}$$

Proof. To determine G, first, we integrate $\partial_i G = g_i$ and suppress integration constants which depend on x_0 only. An elementary calculation yields

$$\begin{aligned} G &= \int^x \sum_{j=1}^{N} \partial_i G dx_i = \int^x \sum_{i=1}^{N} g_i dx_i = \int^x \sum_{i=1}^{N} f_0 q_i dx_i \\ &= \int^x \sum_{i=1}^{N} (1 - x_0 - \sigma)\partial_i Q dx_i = (1 - x_0 - \sigma) Q + \int^x \sum_{i=1}^{N} (\partial_i \sigma) Q dx_i \\ &= (1 - x_0 - \sigma) Q + \int^x \sum_{i=1}^{N} \partial_i Q^\sigma dx_i = f_0 Q + Q^\sigma. \end{aligned} \tag{3.23}$$

Here $\sigma = \xi_1 + \cdots + \xi_N = p_1 x_1 + \cdots + p_N x_N$, as in (3.18), so that $f_0 = 1 - x_0 - \sigma$. We have successively used (3.8), (3.11) (3.15), (3.18), integration by parts, and (3.17). This proves claim (3.20).

We can now determine H from (3.9), and (3.23), as follows:

$$H = \partial_0 G - g_0 = (\partial_0 f_0)Q + f_0 \partial_0 Q + \partial_0(Q^\sigma) - g_0. \tag{3.24}$$

In (3.17) we have noticed the restricted form $Q = Q(x_0, \sigma) = Q(x_0, p_1 x_1 + \cdots + p_N x_N)$ for our choice of the q-potential $Q = Q(x_0, x_1, \ldots, x_N)$. Here is a little trap concerning the treatment of $\partial_0 Q$ and $(\partial_0 Q)^\sigma$. Since σ depends on x_0 via $p_j = p_j(x_0)$, the partial differential operator $\partial_0 = \dfrac{\partial}{\partial x_0}$ in (3.24) becomes

$$\partial_0 = D_0 + \partial_0 \sigma \cdot \partial_\sigma \tag{3.25}$$

when applied to $Q = Q(x_0, \sigma)$. Here D_0 denotes the partial derivative with respect to the explicit first entry x_0 of $Q(x_0, \sigma)$, as in the statement of the lemma. Also note that $\pi'_j = p'_j / p_j$, from (3.22), implies

$$\partial_o \sigma = \sum_{j=1}^{N} \xi_j \pi'_j. \tag{3.26}$$

The preparations (3.25), (3.26) now enable us to insert

$$-g_0 = \sum_{j=1}^{N} x_j f_j \partial_j Q = \sum_{j=1}^{N} \xi_j f_j Q_\sigma \tag{3.27}$$

from (3.12), (3.15), (3.19) into (3.24) and group terms:

$$\begin{aligned} H &= \partial_0(1 - x_0 - \sigma) \cdot Q + f_0(D_0 Q + \partial_0 \sigma \cdot Q_\sigma) \\ &\quad + (D_0 Q)^\sigma + \partial_0 \sigma \cdot Q - g_0 \\ &= -Q + \Big(\sum_{j=1}^{N} \xi_j (f_j + f_0 \pi'_j) \Big) Q_\sigma + f_0 D_0 Q + (D_0 Q)^\sigma. \end{aligned} \tag{3.28}$$

This proves (3.21) and the lemma. ⋈

Corollary 3.3 *In lemma 3.2 choose*

$$Q(x_0, \sigma) := \log \sigma \tag{3.29}$$

to be independent of the first variable. Then lemma 3.2 holds with the simplified expression

$$H = \frac{1}{\sigma}\Big(\sum_{j=1}^{N} \xi_j (f_j + f_0 \pi'_j)\Big) - \log \sigma. \tag{3.30}$$

Since $\sigma = \xi_1 + \cdots + \xi_N$, the first term is a convex combination of the values $f_j + f_0\pi'_j$, $1 \leq j \leq N$, for any fixed x_0.

Proof. Insert $Q = \log \sigma$ in (3.21). ⋈

4 Orientation, winding, and marriage

We construct the oriented immersed closed disk Ω spanned by the hypothetical nonstationary periodic orbit $\Gamma = \partial\Omega$; see lemma 4.1. In lemma 4.2 we use integration by parts to show

$$\int_\Gamma H dx_0 = \int_{\underline{x}_0}^{\bar{x}_0} \sum_{k=1}^{k(x_0)} (H(\xi^{+k}) - H(\xi^{-k}))dx_0, \tag{4.1}$$

as was claimed in (2.5). Here we recall that $\xi_j^k = p_j(x_0)x_{k_j}$ and $\xi^{\pm k} \in \Gamma$ enumerate the points of Γ at level x_0 where $\pm\dot{x}_0 > 0$. See fig. 4.1. The integral on the left follows the orientation of the periodic orbit Γ. The integral on the right, on the other hand, follows the orientation of x_0 on $\mathbb{R}$ between the extrema $\underline{x}_0$ and $\bar{x}_0$ of x_0 on Γ. In lemma 4.3 we conclude from the specific form of the generalized chemostat (1.6) that there exist j-marriages favorable to the positivity of (4.1). See fig. 4.1 again.

Lemma 4.1 *Let Γ be a closed embedded C^k-curve in $\mathbb{R}^{N+1}, N \geq 1, k > 1$. Then there exists a closed disk Ω which is C^k immersed up to the boundary Γ.*

Proof. For $N = 1$ choose Ω to be the closure of the interior of Γ in the plane.
For $N \geq 2$ observe that the two-dimensional union of (affine) tangent lines to Γ does not fill $\mathbb{R}^{N+1}$. Choose any point $\mathbf{O}$ outside that union such that Γ lies to one side of a hyperplane through $\mathbf{O}$ without intersecting its normal through $\mathbf{O}$ itself. For minimal period T of the regular parametrization $\mathbf{x}(t) \in \Gamma$ and $r\exp(i\varphi)$ in the complex unit disk define the mapping.

$$I : (r, \varphi) \mapsto \mathbf{O} + r(\mathbf{x}(\varphi T/2\pi) - \mathbf{O}). \tag{4.2}$$

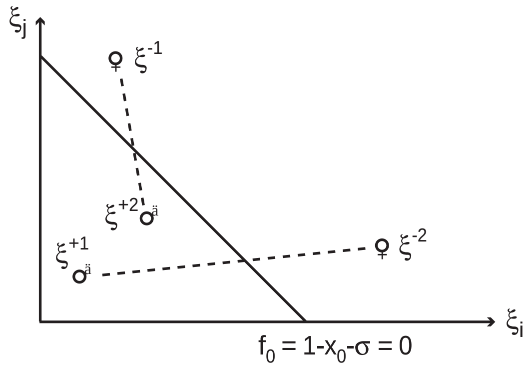

Figure 4.1: At fixed level x_0, "male" points ξ^{+k} with $\dot{x}_0 > 0$ and "female" points ξ^{-k} with $\dot{x}_0 < 0$ are in a j-marriage configuration indicated by dashed lines between couples. Note how partners change when i-marriage is required: $\pi_j = (12)$ whereas $\pi_i = id$.

By definition of $\mathbf{O}$ this is an immersion except possibly at $\mathbf{O}$ itself. Now Γ is on one side of a hyperplane through $\mathbf{O}$ and Γ does not intersect the normal to the hyperplane at $\mathbf{O}$. Therefore we may easily smooth any resulting corner at $\mathbf{O}$ by local normal projection onto the hyperplane.

This proves the lemma. For analytic Γ minimal surfaces of disk type provide an alternative construction of an immersion up to the boundary. $\bowtie$

Lemma 4.2 *Let Γ be a C^1-curve and let H be C^0 on Γ. Then (4.1) holds. In particular $k(x_0)$ is finite for almost all x_0.*

Proof. The only difference between the two integrals in (4.1) lies in the orientation of dx_0. Let $\mathbf{x}(t) \in \Gamma$ parametrize the oriented C^1-curve Γ, alias the periodic orbit. Then $dx_0 = \dot{x}_0(t)dt$, on the left, whereas $dx_0 = |\dot{x}_0(t)|dt$ on the right. The summation on the right takes care of this discrepancy, if the summation $k = 1, \ldots, k(x_0)$ is finite.

We claim that $k(x_0)$ is finite at regular values of the coordinate function $t \mapsto x_0(t)$ on the periodic orbit Γ, i.e. at values $\eta \in \mathbb{R}$ such that $x_0(t) = \eta$ implies $\dot{x}_0(t) \neq O$. By Sard's theorem Lebesgue almost all values η are regular, and therefore it is sufficient to consider the regular value case in the integrals of (4.1).

To prove finiteness of $k(x_0)$ at regular values $x_0 = \eta$ assume the contrary. Then the "males" $\mathbf{x} = (\eta, x_1^{+k}, \ldots, x_N^{+k}) \in \Gamma$ possess an accumulation point $\mathbf{x}^* = (\eta, x_1^*, \ldots, x_N^*)$ being confined by positivity and by $p_i x_i^{+k} = \xi_i^{+k} \leq \sum_{j=1}^{N} \xi_j^{+k} = \sigma < 1 - x_0$. Indeed "males" have

$O < \dot{x}_0 = f_0 = 1 - x_0 - \sigma$. Since the periodic orbit possesses finite length we must have $f_0(\mathbf{x}^*) = 0$ at the accumulation point. Indeed Γ cannot traverse a finite distance from the "males" in $\{f_0 < 0\}$ infinitely often. Therefore $\dot{x}_0 = f_0(\eta, x_1^*, \ldots, x_N^*) = 0$ at $\mathbf{x}^* \in \Gamma$ and $x_0 = \eta$ is not a regular value. This contradiction proves finiteness of $k(x_0)$ in (4.1), not claiming uniform boundedness, and proves the lemma. $\bowtie$

We call points ξ^{+k} of the sum in (2.5), (4.1), where $\dot{x}_0 > 0$ "male", and points ξ^{-k} with $\dot{x}_0 < 0$ "female". This terminology arises as follows. In lemma 5.2 below we establish positivity of pair differences $H(\xi^{+k}) - H(\xi^{-k})$ in (4.1) for suitable pairings which we call married couples. Feasible mass marriages, for this purpose, are prepared by the following marriage lemma.

Lemma 4.3 *Let $\mathbf{x}^{\pm k} \in \Gamma, k = 1, \ldots, k(x_0)$, enumerate the intersection points of the periodic orbit with any fixed regular value $x_0(t) = \eta$ and fix any component $1 \le j \le N$. Let $f_j(x_0)$ possess only one sign change, as required in (1.8).*
Then there exists a j-marriage permutation π_j of the superscripts $k = 1, \ldots, k(x_0)$ such that females exceed males in j-value in each couple:

$$(4.3) \qquad \begin{aligned} x_j^{\pi_j(k)} &< x_j^{-k}, \\ \xi_j^{\pi_j(k)} &< \xi_j^{-k}, \end{aligned}$$

for all $k = 1, \ldots, k(x_0)$.

Proof. Consider the j-th component of the chemostat, i.e.

$$(4.4) \qquad \dot{x}_j = f_j(x_0) x_j.$$

By assumption (1.8) the sign of $\dot{x}_j$ changes only at $x_0 = \lambda_j > 0$, for positive x_j. In particular the projection $(x_j(t), x_0(t))$ of $\mathbf{x}(t) \in \Gamma$ to the (x_j, x_0)-plane is a negatively (right, clockwise) winding curve, possibly with self-intersections. Indeed $\dot{x}_j \gtrless 0$ for $x_0 \gtrless \lambda_j$; see fig. 4.2.

For regular levels $x_0 = \eta \ge \lambda_j$ we propose the following j-marriage. Consider the arches of $\mathbf{x}(t) \in \Gamma$ above η, in the (x_j, x_0)-plane. Since $\dot{x}_j > 0$ along these arches, these are graphs $x_0 = x_0(x_j)$ over x_j. Each arch k terminates at a "female" point $\mathbf{x}^{-k} = (\eta, x_1^{-k}, \ldots, x_N^{-k})$ and emanates from some "male" point $\mathbf{x}^{+\pi_j(k)}$. Conversely, each $\mathbf{x}^{\pm k}$ is on some arch. Therefore the arches define a marriage permutation $\pi_j(k)$ assigning a "male" $+\pi(k)$ to each "female" $-k$. Moreover the "male" has lower j-value than the "female", $x_j^{\pi_j(k)} < x_j^{-k}$, for each couple. Indeed $\dot{x}_j > 0$ along each arch, and the arch emanates from the male. By $p_j > 0$ this implies $\xi_j^{\pi_j(k)} < \xi_j^{-k}$ and proves the lemma in case $x_0 = \eta \ge \lambda_j$.

For $x_0 = \eta < \lambda_j$ we repeat the above argument using the arches of Γ below the level $x_0 = \eta$ where $\dot{x}_j < 0$. Note that the arches which j-marry $\mathbf{x}^{-k}$ to $\mathbf{x}^{+\pi_j(k)}$ emanate from

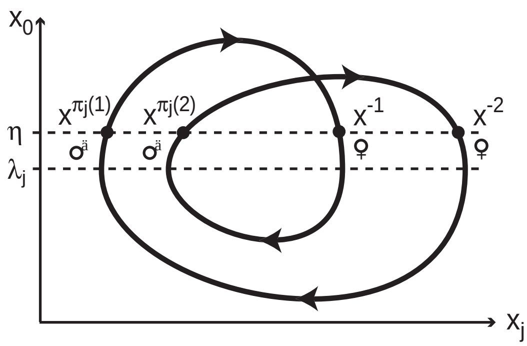

Figure 4.2: Periodic orbit Γ projected into the (x_j, x_0)-plane. Couples $(\mathbf{x}^{\pi_j(k)}, \mathbf{x}^{-k})$ at level $x_0(t) = \eta \geq \lambda_j$ of x_0. Ascending "males" $\mathbf{x}^{\pi_j(k)}$ and descending "females" $\mathbf{x}^{-k}$ are married by permutation π_j via arches of the periodic orbit Γ above η. Note how marriages change at levels $x_0 = \eta < \lambda_j$ where arches of Γ below η are used.

the "females", this time, which still exceed their "male" partners in j-value. Also note how marriages may switch at $x_0 = \eta = \lambda_j$. This proves the j-marriage lemma. $\bowtie$

5 Marriage and positivity

In this section we complete the proof of theorem 1.1. In sections 2–4 we have constructed a function

$$H = \frac{1}{\sigma}\Big(\sum_{j=1}^{N} \xi_j (f_j + f_0 \pi_j')\Big) - \log \sigma, \tag{5.1}$$

see (3.30) such that

$$0 = \int_\Gamma \alpha = -\int_{\mathbf{x}_0}^{\bar{x}_0} \mathcal{H}(x_0) dx_0 \tag{5.2}$$

where $\mathcal{H}(x_0)$ abbreviates the sum

$$\mathcal{H}(x_0) := \sum_{k=1}^{k(x_0)} (H(\xi^{+k}) - H(\xi^{-k})). \tag{5.3}$$

We have seen in lemma 4.2 how this sum is finite for all regular values $x_0(t) = \eta$ along the nonstationary periodic orbit Γ, i.e for Lebesgue almost all values. To reach a contradiction to the assumed existence of Γ we show positivity, $\mathcal{H} > 0$, in lemma 5.2, based on marriage lemma 4.3. To prepare for the wedding we collect some monotonicity facts on H in lemma 5.1. This is the only place where we use assumption (1.9), which equivalently reads

$$f_i \; < \; 1 + \min_{j \neq i}(f_j + (1 - x_0)\pi'_j) \tag{5.4}$$

with $\pi_j := \log p_j$ and for all $1 \leq i \leq N$.

Lemma 5.1 *Fix any $1 \leq i \leq N$ and positive x_0 and ξ_j, for $j \neq i$. Let $\sigma_0 := \sum_{j \neq i} \xi_j$. Define ξ_i^* such that*

$$\sigma_* := \xi_i^* + \sigma_0 = 1 - x_0 \tag{5.5}$$

makes $f_0 = 1 - x_0 - \sigma$ vanish: $f_0 = 0$. Let $H_+ := H(\xi)$ with $\xi_i = \xi_i^*$. Then assumption (1.9)*, alias* (5.4)*, implies*

$$H(\xi) \; > \; H_* \;\; \text{for} \;\; 0 \leq \xi_i < \xi_i^*; \tag{5.6}$$

$$H(\xi) \; < \; H_* \;\; \text{for} \;\; \xi_i > \xi_i^*. \tag{5.7}$$

Note that ξ_i^* can be negative, in the latter case.

Proof. To prove claims (5.6), (5.7) on the partial map $\xi_i \mapsto H(\xi)$ we first calculate the partial derivative:

$$\sigma^2 \partial_i H = (-1 + f_i + f_0 \pi'_i)\sigma - \sum_{j=1}^{N} \xi_j (f_j + f_0 \pi'_j)$$

The right-hand side is affine linear in ξ_i with coefficient -1. Therefore the lemma is proved provided we show

$$H_0 := H\Big|_{\xi_i = 0} > H_*. \tag{5.8}$$

To show (5.8) we write out H_0 and H_* from (5.1), replacing f_0 in H_0 by $\xi_i^* = \sigma_* - \sigma_0$ to get

$$\begin{aligned} H_0 &= -\log \sigma_0 + \frac{1}{\sigma_0} \sum_{j \neq i} \xi_j (f_j + \frac{\sigma_* - \sigma_0}{\sigma_*} \sigma_* \pi'_j); \\ H_* &= -\log \sigma_* + \frac{1}{\sigma_*}(\sigma_* - \sigma_0) f_i + \frac{\sigma_0}{\sigma_*} \cdot \frac{1}{\sigma_0} \sum_{k \neq i} \xi_j f_j. \end{aligned} \tag{5.9}$$

Taking differences, using concavity of the logarithm and noting that the sums $\frac{1}{\sigma_0}\sum$ over $j \neq i$ with coefficients ξ_j amount to convex combinations we obtain

$$
\begin{aligned}
(5.10) \qquad \frac{\sigma_*}{\sigma_* - \sigma_0}(H_0 - H_*) &= \sigma_* \frac{\log \sigma_* - \log \sigma_0}{\sigma_* - \sigma_0} - f_i + \frac{1}{\sigma_0} \sum_{j \neq i} \xi_j (f_j + \sigma_* \pi'_j) \\
&\geq 1 - f_i + \min_{j \neq i}(f_j + (1 - x_0)\pi'_j) > 0.
\end{aligned}
$$

Here we have used assumption (1.9), alias (5.4) in the last step to complete the proof of claim (5.8) and of the lemma.

Lemma 5.2 *Under the assumptions of theorem* (1.2)*, the integrand* $\mathcal{H}(x_0)$ *defined in* (5.2), (5.3) *is strictly positive for Lebesgue almost every* x_0*.*

Proof. For the regular level $x_0 = \eta$ let $1 \leq i \leq N$ denote the index with maximal f_i. We prove the lemma in two steps. First we project the ξ_i-component, both of the "males" ξ^{+k} and of the "females" ξ^{-k} to the diagonal

$$(5.11) \qquad f_0 = 1 - x_0 - \sigma = 0,$$

i.e. to $\sigma = \sigma_* = 1 - x_0$, leaving all other components $\xi_j^{\pm k}$ with $j \neq i$ fixed. Then we apply the j-marriage lemma 4.3, separately for each $j \neq i$, to conclude positivity of $\mathcal{H}$.

To perform the diagonal projection let $\xi^{*\pm k}$ denote $\xi^{\pm k}$ with ξ_i replaced by $\xi_i^* := \sigma_* - \sigma + \xi_i$. For "females" we have $0 > \dot{x}_0 = f_0 = 1 - x_0 - \sigma = \sigma_* - \sigma$ so that $\xi_i^* < \xi_i$. For "males" we have the opposite inequalities, $0 < \xi_i < \xi_i^*$; because $0 > \dot{x}_0$. Abbreviating $H^{\pm k} := H(\xi^{\pm k})$ and $H_*^{\pm k} := H(\xi^{*\pm k})$, lemma 5.1 imples $H^{+k} > H_*^{+k}$ for the "males" by (5.6), and $H^{-k} < H_*^{-k}$ for the "females" by (5.7). Summing up over k this shows

$$(5.12) \qquad \mathcal{H} = \sum_{k=1}^{k(x_0)} (H^{+k} - H^{-k}) > \sum^{k(x_0)} (H_*^{+k} - H_*^{-k}) =: \mathcal{H}^*$$

This completes the diagonal projection step.

In our second step we use j-marriage lemma 4.3, for every $j \neq i$, to conclude $\mathcal{H}^* \geq 0$ is nonnegative. Explicitly

$$(5.13) \qquad \xi_i^* + \sum_{j \neq i} \xi_j = \sigma_* = 1 - x_0$$

for all $\xi^{*\pm k}$. We use (5.13) to replace ξ_i^* in $H_*^{\pm k} = H(\xi^{*\pm k})$ and obtain

$$(5.14) \qquad H_*^{\pm k} = \frac{1}{\sigma_*}\Big(\sum_{j \neq i} \xi_j^{\pm k}(f_j - f_i) \Big) f_i - \log \sigma_*,$$

from (5.1), because $f_0 = 0$ at $\xi^{*\pm k}$. Note that the components $\xi_j^{\pm k}$ with $j \neq i$ have not been touched by the diagonal i-projection. Moreover our choice of i to provide the maximal f_i ensures $f_j - f_i \geq 0$ for all coefficients of $\xi_j^{\pm k}$ in (5.14). Summing up and rearranging by the permutations π_j of j-marriage lemma 4.3 we finally obtain

$$
\begin{aligned}
\sigma_* \mathcal{H}^* &= \sum_{k=1}^{k(x_0)} \sigma_* (H_*^{+k} - H_*^{-k}) \\
&= \sum_{k=1}^{k(x_0)} \sum_{j \neq i} (\xi_j^{+k} - \xi_j^{-k})(f_j - f_i) \\
&= \sum_{k=1}^{k(x_0)} \sum_{j \neq i} (\xi_j^{\pi_j(k)} - \xi_j^{-k})(f_j - f_i) \geq 0.
\end{aligned}
\tag{5.15}
$$

Indeed (4.3) prevents any of the summands to be negative. Because $\sigma_* = 1 - x_0 > 0$ on the hypothesized nonstationary periodic orbit Γ we conclude strict positivity of $\mathcal{H}(x_0)$ from (5.12), (5.15). This completes the proof of the final lemma and, in view of section 2, of theorem 1.1. ⋈

6 Discussion

We survey some previous results on competitive exclusion and absence of periodic orbits in the chemostat, which are based on Lyapunov functions. We recall here that competitive exclusion means global convergence to equilibria where all but one species go extinct. We also comment on some previous results of negative Bendixson Dulac type for other types of equations.

We first consider the simple chemostat

$$
\begin{aligned}
\dot{x}_0 &= 1 - x_0 - \sum_{j=1}^{N} p_j(x_0) x_j \\
\dot{x}_i &= f_i(x_0) x_i
\end{aligned}
\tag{6.1}
$$

of (1.2) with equal normalized dilution rates $d_i = D = 1$ and net growth rates q_i proportional to the uptake rates p_i,

$$
f_i(x_0) = q_i(x_0) - d_i;
\tag{6.2}
$$

$$q_i(x_o) = b_i p_i(x_0). \tag{6.3}$$

In this setting [HHW77]have established competitive exclusion for uptakes p_i of Michaelis-Menten type

$$p_i(x_0) = m_i \frac{x_0}{a_i + x_0}. \tag{6.4}$$

Their methods are "elementary" and neither use a Lyapunov function nor a negative Bedixson type theorem. They show that the species with smallest break-even concentration λ_i wins the competition , and all other species go extinct. [Hsu78] constructed a Lyapunov function of the form

$$V(S, x_1 \dots x_N) = \int_{\lambda_1}^{S} \frac{\xi - \lambda_1}{\xi} d\xi + c_1 \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{N} c_i x_i \tag{6.5}$$

with suitable constants $c_i > 0$. He proves that the equilibrium $E_1 = (\lambda_1, x_1^*, 0 \dots 0)$ is globally asymptotically stable for the case of different removal rates $d_i \neq D$ and for Michaelis-Menten uptake p_i. Wolkowicz and Lu [WL92] used a different Lyapunov function of the type

$$V(S, x_1 \dots x_n) = \int_{\lambda_1}^{x_0} Q(\xi) d\xi + c_1 \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{N} c_i x_i \tag{6.6}$$

to prove global stability of E_1 for more general uptakes p_i including Holling type III

$$p_i(x_0) = m_i x_0^2 / (a_i + x_0^2). \tag{6.7}$$

B. Li [Li98] also constructs a Lyapunov function for some non-monotone uptakes p_i. Armstrong and McGehee [AM80] proved competitive exclusion for general monotone uptake rates $p_i(x_0) > 0$. They used two Lyapunov functions to complete the proof.

Our system (1.6) is more general than the simple chemostat equation (6.1), (6.3). We do not require $f_i(x_0)$, the net growth rate, to be proportional to the uptake rate $p_i(x_0)$. The construction of Lyapunov functions in [Hsu78], [AM80], [WL92], [Li98] strictly depends on the proportionality $f_i = c_i p_i - d_i$ required in (6.2), (6.3). Moreover, our growth rates $f_i(x_0)$ are allowed to be non-monotone as long as the break-even concentrations stay unique; see the sign condition (1.8).

To discuss our crucial and most restrictive condition, (1.9), consider the case $N = 1$ of a single species first. Then (1.9) holds trivially and there is no periodic orbit for system (6.1). Similarly, (1.9) holds for N identical species: $f_i(x_0) = f_j(x_0)$ for all $1 \leq i, j \leq N$.

It has long been known that the yield is not a fixed constant in the chemostat model. Droop [D] introduced a *variable yield* model, also called *internal storage model*, to replace the classical fixed yield chemostat model. In the present paper we allow that the uptake rate $p_i(x_0)$ and the net growth rate $q_i(x_0)$ are not proportional. Assume $f_i(x_0) = f_i(x_0) - d_i$ as in (6.2). Consider the case $N = 2$ and $d_1 = d_2$. If $f_1(x_0) < f_2(x_0)$ for $0 < x_0 < 1$, then it is easy to verify that $x_1(t) \leq C x_2(t) e^{-\delta t}$ for some $\delta > 0, C > 0$. In particular x_1 dies out: $\lim_{t\to\infty} x_1(t) = 0$. Thus we assume for some x_0^*, $0 < x_0^* < 1$

$$
\begin{aligned}
&q_2(x_0) > q_1(x_0), \quad 0 < x_0 < x_0^*, \\
&q_2(x_0) > q_1(x_0), \quad x_0^* < x_0 \leq 1.
\end{aligned} \tag{6.8}
$$

Then (1.9) is equivalent to

$$
\begin{aligned}
q_1(x_0) - q_2(x_0) &< 1 + (1 - x_0)\frac{p_2'(x_0)}{p_2(x_0)}, \quad 0 < x_0 < x_0^* \\
q_2(x_0) - q_1(x_0) &< 1 + (1 - x_0)\frac{p_1'(x_0)}{p_1(x_0)}, \quad x_0^* < x_0 \leq 1
\end{aligned} \tag{6.9}
$$

Similarly consider N species, $N \geq 2$, with equal dilution rates $d_1 = \ldots = d_N = D$ and net growth rates

$$
q_i(x_0) = \frac{M_i x_0}{K_i + x_0}, \tag{6.10}
$$

all of Michaelis-Menten type. Assume positivity of all p_i and p_i'. Then it is easy to verify that assumptions (1.7)–(1.9) of theorem 1.1 all hold provided that

$$
M_i < K_i + 1 \tag{6.11}
$$

for all $1 \leq i \leq N$. The same conditions are also sufficient for Holling type III net growth rates, replacing (6.10), or in fact for any positive uptake rates $q_i(x_0)$ such that

$$
q_i'(x_0) > 0, \quad q_i(1) < 1 \tag{6.12}
$$

for all $0 < x_0 \leq 1$ and all $1 \leq i \leq N$.

In the literature there are several alternative approaches to periodic orbit exclusion which do not make use of Lyapunov functions. We have mentioned the classical planar negative Bendixson, or Dulac, divergence criterion in the introduction; see (1.4), (1.5). Before we comment on its direct generalization to higher dimensions we discuss approaches based on higher-dimensional generalizations of the likewise classical planar Poincaré-Bendixson theorem.

For planar C^1 vector fields the classical Poincaré-Bendixson theorem establishes the following property of ω-limit sets $\omega(\mathbf{x}^0)$ of bounded forward trajectories $\mathbf{x}(t)$ with initial condition $\mathbf{x}(0) = \mathbf{x}^0$. Either $\omega(\mathbf{x}^0)$ is a single periodic orbit, or else $\omega(\mathbf{y}^0)$ and the α-limit set $\alpha(\mathbf{y}^0)$ consist entirely of equilibria for any initial condition $\mathbf{y}^0$ in the original invariant ω-limit set $\omega(\mathbf{x}^0)$. Exclusion of periodic orbits, in this context, implies the presence of equilibria in $\omega(\mathbf{x}^0)$.

One type of higher-dimensional Poincaré-Bendixson theorems originates with work by Russel Smith [RSm81], [RSm86]. He imposes conditions which basically imply contraction of area functionals under the linearized flow, and absence of periodic orbits. Moreover the Hausdorff dimension of compact invariant sets is less than two. For some further generalizations in this spirit see [Mul90]. An application to the Lorenz system was given in [LM93]. For refined dimension estimates see also [BLR05].

Another type of generalizations is based on nodal sign-changing properties of Sturm type. Such properties refine monotonicity or comparison porperties, as reviewed by [HHSm05] and originate as early as 1836 with Sturm's seminal work [Stu1836] on the nodal properties of solutions to linear parabolic PDEs. Nonlinear variants have been successfully revived by Matano [Mat82] in a scalar, one-dimensional PDE setting. For a Poincaré-Bendixson theorem see [FMP89] and the references there. For related results in the ODE setting of cyclic monotone feedback systems see [MPHSm90]. Time delayed systems have been addressed by [MPS96]. In the PDE-setting $u = u(t, \xi)$ time periodic orbits can easily be excluded under separated boundary conditions because the projection

$$\begin{array}{rcl} \omega & \mapsto & \mathbb{R}^2 \\ u & \mapsto & (u(\xi_0), u_\xi(\xi_0)) \end{array} \tag{6.13}$$

is injective for any fixed ξ_0. Choosing ξ_0 on the domain boundary, the right-hand side becomes one-dimensional. For example Dirichlet conditions impose $u(\xi_0) = 0$ at boundary points ξ_0. Injectivity of (6.13) thus excludes periodic orbits.

A first application to ecological dynamics of the negative Bendixson Dulac criterion, based on the Stokes theorem, was given by [CHW98]. That paper addresses the asymmetric. May-Leonard model of three competing species. They proved the nonexistence of periodic solutions by contradiction. Assuming there exists a periodic orbit Γ, they constructed an explicit surface Ω with boundary Γ and a differential 1-form α such that the Stokes theorem provides a contradiction. The basic strategy of [CHW98] had been proposed in [BD93], including some applications to population dynamics under restrictive homogeneity assume.

In our present paper one may dispute whether or not we have actually used the Stokes theorem. Admittedly our summary (2.8) uses the Stokes theorem twice in the equalities

$$0 = \int_{\Gamma} \alpha = \int_{\Omega} d\alpha = \int_{\Omega} dx_0 \wedge dH = - \int_{\Gamma} H dx_0 < 0. \tag{6.14}$$

However, we may avoid the Stokes theorem altogether with the Ansatz

$$\alpha = dG - H dx_0. \tag{6.15}$$

As a consequence we then obtain

$$d\alpha = dx_0 \wedge dH, \tag{6.16}$$

as we have observed in (2.3). In (3.4)–(3.9) we have actually derived (6.15) as a consequence of (6.16). If we start from (6.15), conversely, we may abbreviate (6.14) and conclude

$$0 = \int_{\Gamma} \alpha = - \int_{\Gamma} H dx_0 < 0, \tag{6.17}$$

directly. Here we have only used the primeval form $\int_{\Gamma} dG = 0$ of the Stokes theorem. The planar negative Bendixson Dulac theorem, by the way, can be subsumed under this view point, in the notation of (1.4), (1.5), if we define $H := \int^{y_1} \mathrm{div} < 0$. Up to an integration "constant" $c(x_0)$ which depends on x_0 only, this choice coincides with our abstract choice in corollary 3.3, (3.30) when applied to the planar case $N = 1$. We may therefore argue our negative Bendixson Dulac theorem to circumvent the Stokes theorem and the required construction of explicit surfaces Ω with boundary Γ, altogether, just like the planar negative Bendixson Dulac criterion does.

References

[AM80] R.A. Armstrong, R. McGehee: *Competitive exclusion.* American Naturalist **115**, 151–157 (1980).

[BLR05] V.A. Boichenko, G.A. Leonv, V. Reitmann: *Dimension Theory for Ordinary Differential Equations.* Teubner, Wiesbaden (2005).

[BD93] S. Busenberg, P. Van Den Driessche: *A method for proving the non-existence of limit cycles.* J. Math. Analysis Appl. **172**, 463–479 (1993).

[CHW98] C.W. Chi, S.B. Hsu, L.I. Wu: *On the asymmetric May-Leonard model of three competing species.* SIAM J. Appl. Math. **58**, 211–226 (1998).

[FMP89] B. Fiedler, J. Mallet-Paret: *A Poincaré-Bendixson theorem for scalar reaction diffusion equations.* Arch. Ration. Mech. Analysis **107**, 325–345 (1989).

[HHSm05] M.W. Hirsch, H.L. Smith: *Monotone dynamical systems.* In: Handbook of Differential Equations, Ordinary Differential Equations. Vol. II. A. Canada et al. (eds.), Elsevier, Amsterdam, 239–357 (2005).

[Hsu78] S.B. Hsu: *Behavior of competing species.* SIAM J. Appl. Math. **344**, 760–763 (1978).

[HHW77] S.B. Hsu, S.P. Hubbell, P.E. Waltman: *A mathematical theory for single-nutrient competition in continuous culture of microorganisms.* SIAM J. Appl. Math. **32**, 366-382 (1977).

[Li98] B. Li: *Global asymptotic behavior of the chemostat: General response functions and different removal rates.* SIAM J. Appl. Math. **59**, 411-422 (1998).

[LM93] Y. Li, J.S. Muldowney: *On Bendixson's criterion.* J. Differential Eq. **106**, 27–39 (1993).

[MPS96] J. Mallet-Paret, G.R. Sell: *The Poincaré-Bendixson theorem for monotone cyclic feedback systems with delay.* J. Differential Eqs. **125**, 441–489 (1996).

[MPHSm90] J. Mallet-Paret, H.L. Smith: *The Poincaré-Bendixson theorem for monotone cyclic feedback systems.* J. Dyn. Differ. Equations **2**, 367–421 (1990).

[Mat82] H. Matano: *Nonincrease of the lap-number of a solution for a one-dimensional semilinear parabolic equation.* J. Fac. Sci., Univ. Tokyo, Sect. I A **29**, 401–441 (1982).

[Mul90] J.S. Muldowney: *Compound matrices and ordinary differential equations.* Rocky Mt. J. Math. **20**, 857–872 (1990).

[HSm95] H.L. Smith: *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems.* American Mathematical Society, Providence RI (1995).

[HSmW95] H.L. Smith, P. Waltman: *The Theory of the Chemostat. Dynamics of Microbial Competition.* Cambridge Univ. Press (1995).

[RSm81] R.A. Smith: *An index theorem and Bendixson's negative criterion for certain differential equations of higher dimension.* Proc. Roy. Soc. Edinburgh A **91**, 63–69 (1981).

[RSm86] R.A. Smith: *Some applications of Hausdorff dimension inequalities for ordinary differential equations.* Proc. Roy. Soc. Edinburgh A **104**, 235–259 (1986).

[Stu1836] C. Sturm: *Sur une classe d'équations à différences partielles.* J. Math. Pures Appl. **1**, 373–444 (1836).

[WL92] G.S. Wolkowicz, Z. Lu: *Global dynamics of a mathematical model of competition in the chemostat: General response function and different death rates.* SIAM J. Appl. Math. **52**, 222–233 (1992).