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AN INDEX THEOREM FOR DISSIPATIVE SEMIFLOWS

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Dedicated to the memory of Geoffrey J. Butler

1. Introduction. Deterministic modelling in the biological sciences often leads to ordinary differential equations defined on the state space $\mathbf{R}_+^n$, each coordinate representing the population density of a component or "species" of the system. If only the relative population frequencies are of interest, or some conservation of total mass holds, then the state space reduces to the probability simplex $S_n = \{\mathbf{x} \in \mathbf{R}_+^n : \sum x_i = 1\}$. Often the boundary and hence the interior of the state space $\mathbf{R}_+^n$ or S_n is invariant under the flow as in ecological models, meaning that a species absent at time 0 will not appear at any future time. This leads to *ecological differential equations*

$$\dot{x}_i = x_i f_i(\mathbf{x}). \tag{1}$$

This is not true, however, for more general models, as in population genetics (selection models including mutation, recombination, or differential fertilities), epidemiology, ecological models with migration, or chemical reaction kinetics. Here $\mathbf{R}_+^n$ (as well as its interior) is only forward invariant, i.e., if $x_i(0) \geq 0$ (respectively > 0) for all i, then $x_i(t) \geq 0$ (respectively > 0) for all $t \geq 0$. Then $\operatorname{bd} \mathbf{R}_+^n$ is not invariant but "semipermeable." If the state space is strictly forward invariant (the flow being transverse to the boundary) then *Brouwer's degree theory* implies that the sum of the indices over all (interior) fixed points equals $+1$. Quite often, however, part of the boundary is invariant. Then some of the boundary fixed points have to be included in this index theorem.

We first single out these special boundary fixed points, which we call *saturated fixed points*. In §2 we describe some elementary properties and state the index theorem under the assumption that all of them are regular. The proofs are given in §3. In §4 a generalization to isolated fixed points is indicated, using the concept of the *boundary index*. This also allows an extension of the *Poincaré-Hopf theorem* to semiflows on manifolds with boundary, with singularities allowed on the boundary. We conclude with some applications to mathematical ecology, to game theory, and to mathematical programming.

2. Saturated fixed points. Consider a semiflow on the nonnegative orthant $\mathbf{R}_+^n$ which is given by a C^1 vector field

$$\dot{\mathbf{x}} = F(\mathbf{x}). \tag{2}$$

We make two assumptions.

(A1) $\mathbf{R}_+^n$ is *forward invariant*. By a well-known invariance principle (see Amann [**1**, p. 240]), this holds if and only if

$$x_i = 0 \Longrightarrow F_i(\mathbf{x}) \geq 0 \tag{3}$$

holds for all $i = 1, \dots, n$.

(A2) The semiflow generated by (2) is *dissipative* (see Hale [**8**]), i.e., there exists a compact set $K \subseteq \mathbf{R}_+^n$ such that, for all $\mathbf{x} \in \mathbf{R}_+^n$, there is some time $t(\mathbf{x})$ such that $\mathbf{x}(t) \in K$ holds for all $t \geq t(\mathbf{x})$. The set $K^+ = \cup_{t\geq 0} K(t)$ is then compact, forward invariant, and absorbing for the semiflow on $\mathbf{R}_+^n$. An equivalent statement is that the solutions of (2) are *eventually uniformly bounded*: there exists a constant $k > 0$ such that

$$\limsup_{t\to+\infty} x_i(t) \leq k$$

holds for all $\mathbf{x}(0) \in \mathbf{R}_+^n$. This assumption also guarantees the existence of the solutions $\mathbf{x}(t)$ for all positive times $t \geq 0$ so that (2) actually defines a (global) semiflow.

Let now $\overline{\mathbf{x}}$ be a fixed point of (2). Let $I = \{i : \overline{x}_i = 0\}$ and J be its complement, the support of $\overline{\mathbf{x}}$. We compute now the Jacobian $DF(\overline{\mathbf{x}})$ of (2) at $\overline{\mathbf{x}}$. Since, for $i \in I$ and $j \in J$, (3) implies $F_i(\overline{\mathbf{x}} + t\mathbf{e}_j) \geq 0$ for t in a neighborhood of 0 (here $\mathbf{e}_j$ is the jth unit vector in $\mathbf{R}^n$), we obtain

$$\frac{\partial F_i}{\partial x_j}(\overline{\mathbf{x}}) = 0, \quad i \in I, j \in J. \tag{4}$$

Moreover,

$$\frac{\partial F_i}{\partial x_j}(\overline{\mathbf{x}}) \geq 0, \quad i, j \in I, i \neq j, \tag{5}$$

since $F_i(\mathbf{x} + t\mathbf{e}_j) \geq 0$ for $t \geq 0$. Hence, after a rearrangement of the indices and taking $I = \{1, 2, \dots, k\}$, the Jacobian matrix at $\overline{\mathbf{x}}$ reduces to the block triangular form

$$DF(\overline{\mathbf{x}}) = \begin{pmatrix} \mathbf{A} & O \\ \mathbf{B} & \mathbf{C} \end{pmatrix}, \tag{6}$$

where the $k \times k$ matrix $\mathbf{A}$ is *quasimonotone*, i.e., its off-diagonal terms $a_{ij}, i \neq j$, are nonnegative. We call $\mathbf{A}$ the *external* part, and $\mathbf{C}$, the restriction to components present at $\overline{\mathbf{x}}$, the *internal* part of the Jacobian matrix (6). In the case of ecological equations (1), $\mathbf{A}$ is a diagonal matrix, $\mathbf{A} = \operatorname{diag}(f_i(\overline{\mathbf{x}}))$. Since $\mathbf{A}$ can be written as $\mathbf{A} = \mathbf{A}' - c\mathbf{1}$, with $\mathbf{A}'$ a nonnegative matrix, $c \in \mathbf{R}$ and $\mathbf{1}$ the identity matrix, the Perron-Frobenius theory applies. In particular, the *stability modulus* $s(\mathbf{A}) = \max\{\operatorname{Re}\lambda : \lambda \text{ an eigenvalue of } \mathbf{A}\}$ is itself an eigenvalue of $\mathbf{A}$ and there is a nonnegative eigenvector associated with it.

Definition. $\overline{\mathbf{x}}$ is said to be a (*strictly*) *saturated* fixed point of (2) if all eigenvalues of the external part $\mathbf{A} = \left(\partial F_i/\partial x_j\right)_{i,j \in I}$ of the Jacobian at $\overline{\mathbf{x}}$ have nonpositive (respectively negative) real part, i.e., $s(\mathbf{A}) \leq 0$ (respectively $s(\mathbf{A}) < 0$).

The term "saturated" reflects the intuition that, since all external eigenvalues are stable, none of the missing species $i \in I$ can invade the system at $\overline{\mathbf{x}}$. In order to decide whether a fixed point $\overline{\mathbf{x}}$ is saturated, the following results from the theory of M-matrices are useful (see [**3**]).

Lemma 1. *For a quasimonotone $k \times k$ matrix $\mathbf{A}$, the following conditions are equivalent*:

(a) $\mathbf{A}$ *is stable, i.e., $s(\mathbf{A}) < 0$.*

(b) *The leading principal minor of $\mathbf{A}$ of order i has sign $(-1)^i$, for $i = 1, 2, \dots, k$.*

(c) *The inverse matrix* $\mathbf{A}^{-1}$ *exists and has nonpositive entries only.*

(d) *There is a positive vector* $\mathbf{p} > 0$ *such that* $\mathbf{Ap} < 0$.

If $\mathbf{A}$ *is also irreducible, then the following are equivalent*:

(a′) $\mathbf{A}$ *is semistable, i.e.,* $s(\mathbf{A}) \leq 0$.

(b′) *The leading principal minor of* $\mathbf{A}$ *of order* i *has sign* $(-1)^i$ *or* 0, *for* $i = 1, \ldots, k$.

Therefore, an efficient way of checking whether a fixed point $\overline{\mathbf{x}}$ is saturated is the following. One splits the external part $\mathbf{A}$ into its irreducible blocks and computes the sign of their leading principal minors. For an ecological equation (1), these irreducible blocks reduce to the diagonal entries $f_i(\overline{\mathbf{x}})$. In this case $\overline{\mathbf{x}}$ is saturated if and only if $f_i(\overline{\mathbf{x}}) \leq 0$ holds for all $i \in I$. If $\overline{\mathbf{x}} > \mathbf{0}$ is a fixed point in $\operatorname{int} \mathbf{R}^n_+$, then $I = \varnothing$ and there is no external part. Such a fixed point is always saturated.

The importance of saturated fixed points is summarized in the following two theorems which will be proven in the next section.

THEOREM 1. *If a solution* $\mathbf{x}(t) \in \operatorname{int} \mathbf{R}^n_+$ *of the semiflow* (2) *converges to a point* $\overline{\mathbf{x}}$ *as* $t \to +\infty$, *then* $\overline{\mathbf{x}}$ *is a saturated fixed point. Conversely, if* $\overline{\mathbf{x}}$ *is strictly saturated, then there exists at least one solution* $\mathbf{x}(t) \in \operatorname{int} \mathbf{R}^n_+$ *such that* $\lim_{t\to+\infty} \mathbf{x}(t) = \overline{\mathbf{x}}$.

THEOREM 2. ("Index theorem"). *Every dissipative semiflow on* $\mathbf{R}^n_+$ (*i.e., an equation* (2) *satisfying both* (A1) *and* (A2)) *admits at least one saturated fixed point. Moreover, if all saturated fixed points are regular, the sum of their indices equals* $+1$.

Recall that a fixed point $\overline{\mathbf{x}}$ is said to be *regular* if the Jacobian $DF(\overline{\mathbf{x}})$ is nonsingular. The *index* of $\overline{\mathbf{x}}$ is then defined as the sign of the determinant of $-DF(\overline{\mathbf{x}})$. Note that the minus sign is included here for convenience so that a stable fixed point gets index $+1$ in any dimension, in contrast to the classical definition in [**16**].

A simple consequence of these theorems is the following. *If the* *dissipative semiflow* (2) *has no interior fixed point, then there must be at least one saturated fixed point on the boundary. If, in addition, this point is strictly saturated* (which should be the "generic" case), *then at least one interior solution must converge to the boundary.*

This has obvious applications to the problem of persistence of species which will be briefly discussed together with other applications in the last section. A flow on $\mathbf{R}^3_+$ studied by Butler and Waltman [**5**] shows that the above result is in some sense the best possible: Their flow has no interior fixed point, yet an interior limit cycle attracts *all* orbits in $\operatorname{int}\mathbf{R}^3_+$, *up to just one* orbit which converges to a (strictly) saturated fixed point on the boundary.

However, as F. Zanolin pointed out to me, on can modify the examples by Wilson [**19**] to construct dissipative flows on $\mathbf{R}^n_+$ with no interior fixed point, where every interior orbit has its ω-limit in $\operatorname{int}\mathbf{R}^n_+$. One can give such examples even with a unique saturated (but not strictly saturated) fixed point on the boundary.

3. Proofs of Theorems 1 and 2. Let $\overline{\mathbf{x}}$ be a fixed point of (2) and I, J as defined above, and assume again $I = \{1, 2, \dots, k\}$. Then the first k equations of (2) may be rewritten as

$$\dot{x}_i = \sum_{j=1}^{k} a_{ij}(\mathbf{x})x_j + d_i(x_1, \dots 6, x_n). \tag{8}$$

Here

$$d_i(x_1, \dots, x_n) = F_i(0, \dots, 0, x_{k+1}, \dots, x_n)$$

and

$$a_{ij}(x_1, \dots, x_n) = \\ = \big(F_i(0, \dots, x_j, x_{j+1}, \dots, x_n) - F_i(0, \dots, x_{j+1}, \dots, x_n)\big)/x_j$$

inductively for $j = k, \dots, 1$. Since $F_i \in C^1(\mathbf{R}^n_+)$, the $a_{ij}(\mathbf{x})$ is still continuous on $\operatorname{bd}\mathbf{R}^n_+$ and C^1 in the interior of $\mathbf{R}^n_+$. With $x = (x_1, \dots, x_k)$ and $\mathbf{x} = (x_1, \dots, x_n)$ for short, we can rewrite (8) as

$$\dot{x} = \mathbf{A}(\mathbf{x})x + d(\mathbf{x}). \tag{9}$$

From (3) we see again that, for $i, j \in I, d_i(\mathbf{x}) \geq 0, d_i(\overline{\mathbf{x}}) = 0$, and $a_{ij}(\overline{\mathbf{x}}) \geq 0$ for $i \neq j$. Of course $\mathbf{A}(\overline{\mathbf{x}})$ equals the external part $\mathbf{A}$ of the Jacobian at $\overline{\mathbf{x}}$.

PROOF OF THEOREM 1. Suppose $\overline{\mathbf{x}}$ is not saturated. Then there exists a positive eigenvalue $\lambda > 0$ and a nonnegative left eigenvector (i.e., a row vector) $\mathbf{v} \geq 0$ of $\mathbf{A} = \mathbf{A}(\overline{\mathbf{x}}) : \mathbf{vA} = \lambda \mathbf{v}$. Rearranging indices, we may assume $v_i > 0$ for $i = 1, \dots, m$ and $v_i = 0$ for $i > m$. Here $m \leq k$. Then (8) implies, for $i = 1, \dots, m$,

$$\dot{x}_i = \sum_{j=1}^{m} a_{ij}(\mathbf{x})x_j + F_i(0, \dots, 0, x_{m+1}, \dots, x_n). \tag{10}$$

From (3) we get

$$\sum_{i=1}^{m} v_i \dot{x}_i \geq \sum_{i,j=1}^{m} v_i a_{ij}(\mathbf{x}) x_j > 0 \tag{11}$$

for $\mathbf{x} \in \operatorname{int} \mathbf{R}^n_+$ sufficiently close to $\overline{\mathbf{x}}$, since $\sum_i v_i a_{ij}(\mathbf{x}) > 0$ for each i.

Suppose now that an interior orbit $\mathbf{x}(t)$ converges to $\overline{\mathbf{x}}$ as $t \to +\infty$. Then, for large t, (11) will hold along the orbit, meaning that $v(x) = \sum v_i x_i$ increases finally. This is a contradiction, as $x_i(t) \to 0$ for all $i \in I$.

Conversely, if $\overline{\mathbf{x}}$ is strictly saturated, then the external part $\mathbf{A}$ is stable. The stable invariant subspace of the linearized vector field at $\overline{\mathbf{x}}$ is then an (at least k-dimensional) linear subspace transverse to the subspace $\{\mathbf{x} \in \mathbf{R}^n : x_i = 0 \text{ for } i \in I\}$ in $\mathbf{R}^n$. Hence the stable manifold of $\overline{\mathbf{x}}$, being tangent to that linear subspace, meets $\operatorname{int} \mathbf{R}^n_+$. □

For the proof of Theorem 2 we need the following Lemma.

LEMMA 2. *A vector field $\dot{\mathbf{x}} = f(\mathbf{x})$ on $\mathbf{R}^n$ which gives rise to a dissipative semiflow has degree $+1$ with respect to any bounded open set containing all its fixed points.*

Here the degree is the classical Brouwer degree of a function $f : U \subseteq \mathbf{R}^n \to \mathbf{R}^n$, that is,

$$\deg(f, U) = \sum \{ \operatorname{ind}(\overline{\mathbf{x}}) : \overline{\mathbf{x}} \in U, f(\overline{\mathbf{x}}) = 0\},$$

if 0 is a regular value of f (see [**1, 16**]), up to our different normalization (see the remark after Theorem 2).

Proof. Let K be a compact set which contains all ω-limits of the orbits in $\mathbf{R}^n$ in its interior. Define $\tau(\mathbf{x})$ as the time of the first entrance into K:

$$\tau(\mathbf{x}) = \inf\{t \geq 0 : \mathbf{x}(t) \in \operatorname{int} K\}. \tag{12}$$

The function $\tau(\mathbf{x})$ is defined for all $\mathbf{x} \in \mathbf{R}^n$, and the continuity of $t \mapsto \mathbf{x}(t)$ implies that τ is upper semicontinuous and therefore locally bounded. Let

$$T = \max\{\tau(\mathbf{x}) : \mathbf{x} \in K\}$$

be the maximum time for orbits leaving K to return to K. Then the set

$$K^+ = \{\mathbf{x}(t) : \mathbf{x}(0) \in K, 0 \leq t \leq T\} = \{\mathbf{x}(t) : \mathbf{x}(0) \in K, t \geq 0\}$$

is compact and forward invariant.

Consider now a ball $B \supseteq K^+$. The entrance time τ will again attain an upper bound T_1 on B. We consider now the homotopy

$$h(\mathbf{x}, t) = \begin{cases} f(\mathbf{x}), & t = 0 \\ \frac{\mathbf{x}(t) - \mathbf{x}(0)}{t}, & t > 0. \end{cases} \tag{13}$$

Clearly $h(\mathbf{x}, t) \neq 0$ for all $\mathbf{x} \in \operatorname{bd} B$ and $t \in \mathbf{R}$ since there are neither fixed points nor periodic points on $\operatorname{bd} B$. Therefore the degree of the vector field $\mathbf{x} \mapsto h(\mathbf{x}, t)$ with respect to B is defined for all $t \geq 0$ and is independent of t. For $t \geq T_1, h(\mathbf{x}, t)$ points inwards on $\operatorname{bd} B$ and so its degree is $+1$. Hence the degree of the vector field $\dot{\mathbf{x}} = f(\mathbf{x})$ with respect to B (or any other open bounded set which contains K or at least all fixed points) equals $+1$. □

Proof Of Theorem 2. We consider a small perturbation of (2) by adding a small inward flow,

$$\dot{x}_i = F_i(\mathbf{x}) + \varepsilon_i \rho(\mathbf{x}). \tag{14-ε}$$

Here, either $\varepsilon = (\varepsilon_1, \ldots, \varepsilon_n)$ is an n-vector of positive numbers or $\varepsilon = \varepsilon_1 = \cdots = \varepsilon_n > 0$ for simplicity. The function $\rho(\mathbf{x})$ will be chosen as follows to retain the dissipativity for (14-ε). Let $K \subseteq \mathbf{R}^n_+$ be a compact forward invariant set for (2) which contains the ω-limits of all orbits $\mathbf{x}(t) \geq \mathbf{0}$ in its interior (relative to $\mathbf{R}^n_+$). Denote $K(t) = \{\mathbf{x}(t) : \mathbf{x}(0) \in K\}$, and let

$$\Omega = \bigcap_{t \geq 0} K(t) \subseteq \operatorname{int} K \tag{15}$$

be the global attractor of the semiflow. Now choose ρ as a nonnegative C^1-function on $\mathbf{R}^n_+$ such that $\rho(\mathbf{x}) > 0$ for $\mathbf{x} \in \Omega$ and $\rho(\mathbf{x}) = 0$ for $\mathbf{x} \notin K$. Then the solutions $\mathbf{x}^\varepsilon(t)$ of (14-ε) coincide with those of (2) as long as they are outside K. Hence K is absorbing and forward invariant for (14-ε) as well. The attracting sets Ω_ε for the semiflows (14-ε) are then contained in $K \cap \operatorname{int} \mathbf{R}^n_+$. Let $B = \{x \in \mathbf{R}^n_+ : x_i \leq b\}$ be a box which contains K. Then for every $\varepsilon > 0$, the degree of the vector field (14-ε) with respect to $\operatorname{int} B$ is 1, as Lemma 2 shows. (The semiflow there is defined on $\mathbf{R}^n$, and (14-ε) a priori only on $\mathbf{R}^n_+$, but it can be extended to an open neighborhood of $\mathbf{R}^n_+$ which is homeomorphic to $\mathbf{R}^n$). Therefore (14-ε) has at least one fixed point $\overline{\mathbf{x}}(\varepsilon) \in \operatorname{int} B \subseteq \operatorname{int} \mathbf{R}^n_+$, and if all fixed points of (14-ε) are regular then the sum of their indices is 1. In order to complete the proof of Theorem 2 it remains to show the following two assertions.

(A) *A limit point $\overline{\mathbf{x}}$ of fixed points $\overline{\mathbf{x}}(\varepsilon)$ of* (14-ε), *as $\varepsilon \to 0$, is a saturated fixed point of* (2).

(B) *If $\overline{\mathbf{x}}$ is a regular, saturated fixed point of* (2), *then its unique continuation $\overline{\mathbf{x}}(\varepsilon)$ to a C^1 family of fixed points of* (14-ε) *yields fixed points $\overline{\mathbf{x}}(\varepsilon) \in \operatorname{int} \mathbf{R}^n_+$ for $\varepsilon > 0$.*

Proof Of (A). Suppose the fixed points $\overline{\mathbf{x}}(\varepsilon)$ of (14-ε) accumulate at $\overline{\mathbf{x}}$ as $\varepsilon \to 0$. If $\overline{\mathbf{x}}$ is not saturated we proceed as in the proof of Theorem 1. Take $\mathbf{v} \geq \mathbf{0}$ with $v_i > 0, i = 1, 2, \ldots, m$, and $\mathbf{vA} = \lambda \mathbf{v}$,

$\lambda > 0$. (14-ε) can be written as

$$\dot{x}_i = \sum_{j=1}^{m} a_{ij}(\mathbf{x})x_j + F_i(0,\dots,0,x_{m+1},\dots,x_n) + \varepsilon\rho(\mathbf{x}). \tag{16}$$

And (11) shows that

$$\sum_{i,j=1}^{m} v_i a_{ij}(\mathbf{x})x_j > 0 \tag{17}$$

holds for $\mathbf{x}$ in a neighborhood of $\overline{\mathbf{x}}$. On the other hand, at $\mathbf{x} = \overline{\mathbf{x}}(\varepsilon)$, (16) implies

$$\sum_{j=1}^{m} a_{ij}(\mathbf{x})x_j = -F_i(\mathbf{x}) - \varepsilon\rho(\mathbf{x}) < 0$$

for $i = 1, 2, \dots, m$, which contradicts (17). Hence $\overline{\mathbf{x}}$ is saturated. □

Proof of (B). If $\overline{\mathbf{x}}$ is a regular fixed point of (2) in $\mathbf{R}^n_+$, there exists a unique C^1 family $\overline{\mathbf{x}}(\varepsilon)$ of fixed points of (14-ε), in a neighborhood of $\mathbf{R}^n_+$, by the implicit function theorem. In the notation of (9), $\overline{\mathbf{x}}(\varepsilon)$ is then a solution of the system of k nonlinear equations

$$\mathbf{A}(\mathbf{x})\mathbf{x} + d(\mathbf{x}) + \varepsilon\rho(\mathbf{x}) = 0. \tag{18}$$

Since the external part of the Jacobian of (2) at the strictly saturated fixed point $\overline{\mathbf{x}}, \mathbf{A}(\overline{\mathbf{x}})$, is a stable quasimonotone matrix we have, by Lemma 1(c), $-\mathbf{A}^{-1} \geq \mathbf{0}$. Hence, the vector

$$x^* = -\mathbf{A}^{-1}(d(\overline{\mathbf{x}}) + \varepsilon\rho(\overline{\mathbf{x}}))$$

in $\mathbf{R}^k$ has all entries positive as $d(\overline{\mathbf{x}}) = 0$ and $\rho(\overline{\mathbf{x}}) > 0$. By continuity, the fixed point $\mathbf{x} = \overline{\mathbf{x}}(\varepsilon)$ which satisfies (18) and hence

$$x = -\mathbf{A}(\mathbf{x})^{-1}(d(\mathbf{x}) + \varepsilon\rho(\mathbf{x}))$$

is still positive for small $\varepsilon > 0$. □

4. The boundary index. Theorem 2 assumes that the saturated fixed points are all regular. In an attempt to relax this condition we consider now an isolated fixed point $\overline{\mathbf{x}} \in \mathbf{R}^n_+$. Let U be an isolating neighborhood of $\overline{\mathbf{x}}$ and $U_+ = U \cap \mathbf{R}^n_+$. Then, for small perturbations $\varepsilon_i(\mathbf{x}) > 0$, the vector field $\dot{x}_i = F_i(\mathbf{x}) + \varepsilon_i(\mathbf{x})$ will not have fixed points on $\operatorname{bd} U_+$, so that its degree is well-defined and depends neither on the perturbation (because they are all homotopic) nor on the isolating neighborhood. We call this the *boundary index* of $\overline{\mathbf{x}}$ for the given vector field (2):

$$\text{bd–ind}\,(\overline{\mathbf{x}}) = \deg(F(\mathbf{x}) + \varepsilon(\mathbf{x}), U_+). \tag{19}$$

If $\overline{\mathbf{x}}$ is not saturated then $\text{bd–ind}\,(\overline{\mathbf{x}}) = 0$, since, by assertion (A) of §3, the perturbed field has no fixed point near $\overline{\mathbf{x}}$ in $\mathbf{R}^n_+$. Assertion (B), on the other hand, shows that, for a *regular saturated* fixed point $\overline{\mathbf{x}}$, $\text{bd–ind}\,(\overline{\mathbf{x}}) = \text{ind}\,(\overline{\mathbf{x}}) = +1$ or -1. For saturated fixed points which are not regular, the boundary index generally differs from the index, however. A simple example is the vector field $\dot{x}_i = -x_i^2$ on $\mathbf{R}^n_+$ for which the origin $\mathbf{0}$ has boundary index $+1$ but index 0.

It is obvious that, with the boundary index, Theorem 2 extends to the case that all saturated fixed points are isolated. The theorem also easily extends to dissipative semiflows on differentiable manifolds M with corners, as treated in Michor [**15**]. Such manifolds are, by definition, locally diffeomorphic to open subsets of $\mathbf{R}^n_+$. Hence the concepts of a saturated fixed point and the boundary index extend via charts to this situation. The sum of the indices then equals the Euler characteristic $\chi(M)$ of the manifold M (which must be finite if such a dissipative flow exists on M).

5. Applications. We conclude by indicating several applications of the index theorem. The first three concern the special case where $\operatorname{bd} \mathbf{R}^n_+$ is actually invariant, so that the vector field is of the form (1), where the proofs of Theorems 1 and 2 simplify considerably (see [**13**, Chapter 19]).

5.1. *Persistence of ecological systems.* An ecological system modelled by a dissipative equation (1) or (2) has been called *weakly persistent*, respectively *persistent* [**7**], if, for all interior orbits $\mathbf{x} \in \operatorname{int} \mathbf{R}^n_+$,

$$\limsup_{t \to +\infty} x_i(t) > 0, \tag{20}$$

respectively

$$\liminf_{t\to+\infty} x_i(t) > 0, \tag{21}$$

holds for all $i = 1, 2, \ldots, n$. Furthermore, *uniform persistence* [**4**] or *permanence* [**12, 13**] means the existence of a constant $c > 0$ such that

$$\liminf_{t\to+\infty} x_i(t) > c \tag{22}$$

holds for all $\mathbf{x}(0) > \mathbf{0}$. It has been observed several times that uniform persistence implies the existence of an interior fixed point. Actually, the easiest way to prove this seems to be to apply Lemma 2 above, after mapping $\operatorname{int}\mathbf{R}^n_+$ diffeomorphically onto $\mathbf{R}^n$, e.g., with $(x_i) \mapsto (\log x_i)$. The results of §2 allow us to extend this result to *robustly weakly persistent* systems. These are systems of the form (1) or (2) which remain weakly persistent after a small C^1 perturbation of the vector field (within the class described by assumption (A1)). Without the robustness assumption this need not be true, however, as was pointed out at the end of §2.

THEOREM 3. *If a system* (1) *or* (2) *is robustly weakly persistent, then it has an interior fixed point. Moreover,* $\deg(F(x), U) = 1$ *for every open set* U *with* $\overline{U} \subseteq \operatorname{int}\mathbf{R}^n_+$ *which contains all interior fixed points.*

PROOF. We note first that there is no saturated fixed point on $\operatorname{bd}\mathbf{R}^n_+$. Indeed, if $\mathbf{x}$ were such a rest point with $s(\mathbf{A}(\mathbf{x})) \leq 0$ then, by a suitable perturbation, $\mathbf{x}$ would become strictly saturated, i.e., $s(\mathbf{A}(\mathbf{x})) < 0$ (replacing just those $F_i(\mathbf{x})$ with $i \in I$ by $F_i(\mathbf{x}) - \varepsilon x_i$, with $\varepsilon > 0$ small, will do). Together with Theorem 1 this contradicts the weak persistence of the perturbed system.

Therefore, the set S of saturated fixed points of (2) is a compact subset of $\operatorname{int}\mathbf{R}^n_+$. Let U be any open neighborhood of S with $\overline{U} \subseteq \operatorname{int}\mathbf{R}^n_+$. Then assertion (A) above implies that, for $\varepsilon > 0$ small enough, (14-ε) has no fixed point in $\mathbf{R}^n_+ - U$, so that, by homotopy,

$$\deg(F(\mathbf{x}), U) = \deg(F(\mathbf{x}) + \varepsilon\rho(\mathbf{x}), U) = \deg(F(\mathbf{x}) + \varepsilon\rho(\mathbf{x}), \operatorname{int}\mathbf{R}^n_+) = 1$$

This implies also the existence of an interior fixed point. □

In the case of Lotka-Volterra equations, i.e., $f_i(\mathbf{x}) = r_i - (\mathbf{Ax})_i$ in (1), a variation of Theorem 3 leads to explicit characterizations of permanence and robust weak persistence in low dimensions $n = 3, 4$ (see [**10, 13**]).

5.2. *Game theory.* A classical situation in game theory, see Owen [**17**], is that each of the two players has a set of available tactics $E_1, \dots, E_n$, respectively $F_1, \dots, F_m$, which he is allowed to play with certain probabilities $x_1, \dots, x_n$, respectively $y_1, \dots, y_m$. In a contest of E_i versus F_j, the payoff for the first player is a_{ij} and for the second b_{ji}. If mixed strategies $\mathbf{x} \in S_n, \mathbf{y} \in S_m$ are played, the respective payoffs are $\mathbf{x} \cdot \mathbf{Ay} = \sum x_i a_{ij} y_j$ and $\mathbf{y} \cdot \mathbf{Bx} = \sum y_j b_{ji} x_i$.

A pair of strategies $(\mathbf{p}, \mathbf{q}) \in S_n \times S_m$ is said to be a *Nash equilibrium* for the *bimatrix game* $(\mathbf{A}, \mathbf{B})$ if

$$\forall (\mathbf{x}, \mathbf{y}) \in S_n \times S_m, \quad \mathbf{p} \cdot \mathbf{Aq} \geq \mathbf{x} \cdot \mathbf{Aq} \quad \text{and} \quad \mathbf{q} \cdot \mathbf{Bp} \geq \mathbf{y} \cdot \mathbf{Bp}; \tag{23}$$

this means that $\mathbf{p}$ is a best reply to $\mathbf{q}$ and $\mathbf{q}$ is a best reply to $\mathbf{p}$.

THEOREM 4. *Every bimatrix game has a Nash equilibrium. For generic payoff matrices* $(\mathbf{A}, \mathbf{B})$ *the number of Nash equilibria is odd.*

This classical and well-known theorem, which, in game theory, is usually proven by constructive algorithms, is a simple corollary of our index theorem. The key is to associate to the game $(\mathbf{A}, \mathbf{B})$ a certain differential equation on $S_n \times S_m$, namely, its standard evolutionary dynamics [**13**, Chapter 27]:

$$\dot{x}_i = x_i((\mathbf{Ay})_i - \mathbf{x} \cdot \mathbf{Ay}), \quad \dot{y}_j = y_j((\mathbf{Bx})_j - \mathbf{y} \cdot \mathbf{Bx}). \tag{24}$$

This equation is a special case of (1), and it is easy to check that the saturated equilibria of (24) are precisely the Nash equilibria of $(\mathbf{A}, \mathbf{B})$.

5.3. *Complementarity problems.* Given a function $\mathbf{f} : \mathbf{R}^n_+ \to \mathbf{R}^n$, the *complementarity problem* is to find a solution of $\mathbf{x} \geq \mathbf{0}, \mathbf{f}(\mathbf{x}) \geq \mathbf{0}$ and $\sum x_i f_i(\mathbf{x}) = 0$. In our terminology solutions $\mathbf{x}$ of the complementarity problem are thus precisely the saturated fixed points of the ecological equation

$$\dot{x}_i = -x_i f_i(\mathbf{x}) \tag{25}$$

on $\mathbf{R}^n_+$. This complementarity problem was introduced in mathematical programming in order to unify different problems like computation of optimal solutions, game theoretic equilibria, or economic equilibrium theory. (See [**14**] for a survey.) Of particular interest is the linear complementarity problem, where $\mathbf{f}(\mathbf{x}) = M\mathbf{x} + \mathbf{q}$. It consists in finding the saturated equilibria in Lotka-Volterra equations. There, a rather complete answer is possible, see [**11**]. Here we concentrate on the nonlinear case and present one typical (though admittedly weak) existence result as a consequence of Theorem 2 above. Stronger results may also be obtained with degree methods, see [**18**].

THEOREM 5. *Let* $\mathbf{f}$ *be* C^1*, and assume that* $\mathbf{x}\cdot\mathbf{f}(\mathbf{x}) > 0$ *holds for large* $\mathbf{x} \geq \mathbf{0}$*. Then the complementarity problem has at least one solution. If all solutions are regular, then their number is odd.*

PROOF. The assumption implies that $S(\mathbf{x}) = \sum x_i$ is a strictly decreasing Lyapunov function for large $\mathbf{x}$ for (25). This shows that (25) is dissipative and Theorem 2 applies. □

5.4. *Migration models.* One of the simplest models describing the dispersion of a single species among n patches is given by

$$\dot{x}_i = x_i \mathcal{G}_i(x_i) + \sum_{j \neq i} d_{ij} x_j - \Big(\sum_{j\neq i} d_{ji}\Big) x_i. \tag{26}$$

Here x_i is the density of the species in the i-th patch, $d_{ij} \geq 0$ is the migration rate from patch j to patch i, and $\mathcal{G}_i(x_i)$ is the growth rate in the i-th patch.

We assume that the dispersion matrix (d_{ij}) is irreducible, that the basic growth rates $r_i = \mathcal{G}_i(0) > 0$, and $\mathcal{G}_i(x_i) < 0$ for large x_i. The following theorem, which improves a result in [**2**], was also proved in Freedman and Takeuchi [**6**].

THEOREM 6. *Under the above assumptions,* (26) *has a positive equilibrium* $\overline{\mathbf{x}} \in \operatorname{int}\mathbf{R}^n_+$*. If, furthermore,* $\mathcal{G}_i'(x_i) < 0$ *for* $x_i > 0$*, for all* i*, then* $\overline{\mathbf{x}}$ *is unique and globally stable.*

PROOF. First observe that

$$\sum_{i=1}^{n} \dot{x}_i = \sum_{i=1}^{n} x_i \mathcal{G}_i(x_i).$$

This is negative for large x_i which shows that (26) is dissipative. For small $x_i \approx 0$, this is approximately $\sum x_i \mathcal{G}_i(0) > 0$, which shows that $\mathbf{0}$ is not saturated (e.g., by Theorem 1). Since, by irreducibility of the matrix $(d_{ij}), \mathbf{0}$ is the only fixed point on $\operatorname{bd} \mathbf{R}^n_+$, the index theorem implies the existence of a fixed point $\overline{\mathbf{x}} \in \operatorname{int} \mathbf{R}^n_+$. Now compute the Jacobian matrix $J(\overline{\mathbf{x}})$ at such a fixed point $\overline{\mathbf{x}}$:

$$J(\overline{\mathbf{x}})_{ij} = \Big(x_i \mathcal{G}_i'(x_i) + \mathcal{G}_i(x_i) - \Big(\sum_{k \neq i} d_{ki} \Big) \Big) \delta_{ij} + d_{ij}(1 - \delta_{ij}).$$

Then

$$\begin{aligned}(J(\overline{\mathbf{x}}) \cdot \overline{\mathbf{x}})_i &= \sum_{j=1}^{n} J(\overline{\mathbf{x}})_{ij} \overline{\mathbf{x}}_j \\ &= x_i^2 \mathcal{G}_i'(x_i) + x_i \mathcal{G}_i(x_i) + \sum_{j \neq i} d_{ij} x_j - \Big(\sum_{k \neq i} d_{ki} \Big) x_i \\ &= x_i^2 \mathcal{G}_i'(x_i) < 0.\end{aligned}$$

Hence, $J(\overline{\mathbf{x}}) \cdot \overline{\mathbf{x}} < \mathbf{0}$ and Lemma 1(d) shows that the quasimonotone matrix $J(\overline{\mathbf{x}})$ is stable. In particular, $\operatorname{ind}(\overline{\mathbf{x}}) = 1$ holds for any interior fixed point $\overline{\mathbf{x}}$ of (26). The index theorem then implies uniqueness of $\overline{\mathbf{x}}$. Since (26) is a cooperative system in the sense of Hirsch [**9**], uniqueness, local stability and dissipativity together give global stability of $\overline{\mathbf{x}}$. □

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