Systems of differential equations which are competitive or cooperative: III. Competing species

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Systems of differential equations which are competitive or cooperative: III. Competing species

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Abstract. Persistent trajectories of the n-dimensional system $\dot{x}^i = x^i N^i(x^1, \ldots, x^n)$, $x^i \geq 0$, are studied under the assumptions that the system is competitive and dissipative with irreducible community matrices $[\partial N^i/\partial x^j]$. The main result is that there is a canonically defined countable (generically finite) family of disjoint invariant open $(n-1)$ cells which attract all non-convergent persistent trajectories. These cells are Lipschitz submanifolds and are transverse to positive rays. In dimension 3 this implies that an ω limit set of a persistent orbit is either an equilibrium, a cycle bounding an invariant disc, or a one-dimensional continuum having a non-trivial first Čech cohomology group and containing an equilibrium. Thus the existence of a persistent trajectory in the three-dimensional case implies the existence of a positive equilibrium. In any dimension it is shown that if the community matrices are strictly negative then there is a closed invariant $(n-1)$ cell which attracts every persistent trajectory. This shows that a seemingly special construction by Smale of certain competitive systems is in fact close to the general case.

1. Introduction

Consider n competing species represented by a system of differential equations:

$$\dot{x}^i = x^i N^i(x^1, \ldots, x^n) \equiv F^i(x^i, \ldots, x^n) \qquad (i = 1, \ldots, n) \tag{1}$$

where the vector $x = (x^1, \ldots, x^n)$ lies in the closed non-negative cone $\boldsymbol{C} = R^n_+$. The *per capita* growth rates N^i are taken to be C^1 functions satisfying the competition condition $\partial N^i/\partial x^j \leq 0$ for $i \neq j$. The C^1 vector field F generates a flow $\psi = \{\psi_t\}_{t \in \boldsymbol{R}}$ in $\boldsymbol{C}$.

When the N^i are affine, equations (1) form the classical Gause–Lotka–Volterra system. Even for this special case little is known about the general dynamics of such systems, except that it can be complex in dimensions $n > 2$. In dimension 3 there can be periodic orbits (Coste *et al* 1979, Gilpin 1975) and non-periodic oscillations (May and Leonard 1975, Schuster *et al* 1979, Phillipson *et al* 1985); in higher dimensions there can be numerically chaotic dynamics (Arnedo *et al* 1982). See also the papers by Coste *et al* (1978), Kerner (1961) and Levin (1970).

For a survey of competitive and related types of systems see the book by Freedman (1980). Recent papers include Hale and Somolinos (1983), Smith and Waltman (1988), Smith (1986a, c), Othmer (1976), Tyson and Othmer (1978), Freedman and Waltman (1985), Holtz (1987), Hirsch (1982a, 1984, 1985, 1987), and those referred to above.

Only rather special competitive systems have the desirable property that every trajectory converges to equilibrium as $t \to \infty$. These include the classical planar Gause–Lotka–Volterra systems, and even planar systems with nonlinear N^i (Albrecht *et al* 1974); systems with affine N^i and symmetric community matrices $DN(x)$ (MacArthur 1969); systems where $\boldsymbol{N}$ has a special algebraic form (Grossberg 1978, Cohen and Grossberg 1983, Chenciner 1977, Coste *et al* 1978); and C^{n-1} systems in $\boldsymbol{R}^n$ such that $\partial N^i/\partial x^j < 0$ for $|i-j|=1$ and $\partial N^i/\partial x^j = 0$ for $|i-j|>1$ (Smillie 1984).

Smale (1976) showed that an arbitrary smooth flow in the simplex $\Delta^{n-1} \subset \boldsymbol{R}^n$ spanned by the unit coordinate vectors can be embedded as an attractor in a system of type (1). This result has been interpreted as meaning that the competition condition is too weak to have interesting dynamical consequences in higher dimensions.

From the point of view of abstract dynamic complexity of individual orbits this interpretation is correct. But from a more global and geometrical perspective it is unduly pessimistic. Hirsch (1982a) showed that limit sets of competitive systems are subject to severe topological restrictions regarding their embedding in $\boldsymbol{R}^n$: they are nowhere dense, unknotted and unlinked, and project homeomorphically into hyperplanes orthogonal to vectors in $\boldsymbol{C}\backslash 0$.

We shall show that under mild additional restrictions, competitive systems have a special overall structure regarding persistent trajectories, i.e. trajectories whose ω limit sets are in the interior $\boldsymbol{C}^0$ of the positive cone. In many applications only persistent trajectories are meaningful. Several authors have studied systems where every trajectory in $\boldsymbol{C}^0$ is persistent (Butler *et al* 1986, Hutson and Law 1985, Freedman and Waltman 1985, Hallam *et al* 1979). Coste (1985) looked at persistence probabilistically.

The main result of this paper is the following crude but universal description of the persistent dynamics of the flow ψ of system (1) under three conditions given below. There is a countable disjoint family $\mathscr{F}$ of invariant open $(n-1)$ cells which attract all non-convergent persistent trajectories. These cells have nice geometrical properties and are canonically determined by the system in a way to be described shortly. When all equilibria are simple, $\mathscr{F}$ is finite. In theorem 1.1 below we give a detailed statement, followed by discussion and applications.

Roughly speaking, this result means that the system is essentially $(n-1)$ dimensional. It also means that Smale's construction is not as special as it seems: the attracting cells in $\mathscr{F}$ play the role of his attracting simplex Δ^{n-1}. Thus a system (1) for which all trajectories in $\boldsymbol{C}^0$ are persistent is essentially composed of a family of disjoint systems, each similar to Smale's construction.

Smale's construction has the additional properties that $\partial N^i/\partial x^j < 0$ for all i, j and the origin is a source. Theorem 1.7 shows that these conditions essentially characterise his examples: they imply the existence of a closed $(n-1)$ cell which attracts all trajectories in $\boldsymbol{C}^0\backslash 0$, and which is homeomorphic to Δ^{n-1} under radial projection.

We assume the following three conditions hold for the system (1).

Dissipation. There is a compact invariant set Γ, called the *fundamental attractor,* which uniformly attracts each compact set of initial values.

Irreducibility. The community matrix $DN = [\partial N^i/\partial x^j]$ is irreducible at every point in the interior $\boldsymbol{C}^0$ of $\boldsymbol{C}$.

Competition. $\partial N^i/\partial x^j \leqslant 0$ for $i \neq j$.

Dissipation, or 'a source at ∞', is usually satisfied in applications; it means there is a ball B with the property that for every compact set K there exists $T > 0$ such that $\psi_t K \subset B$ for all $t > T$. Irreducibility means that for any $p \in \boldsymbol{C}^0$ and distinct $i, j \in \{1, \ldots, n\}$ there is a finite sequence $i = k_1, \ldots, k_m = j$ such that $\partial N^{k_r}/\partial x^{k_{r+1}}(p) \neq 0$ for $r = 1, \ldots, m-1$. The interpretation of this is that each species influences every other species, directly or indirectly. It is a mild non-degeneracy hypothesis, but without it the main results are not true. Competition is the motivation of this paper. It rarely occurs in physics, but is satisfied in many models of biological, chemical and economic systems.

Objects in $\boldsymbol{C}^0$ are called positive. A point x (or its orbit, trajectory, or omega limit set) is called persistent if its omega limit set $\omega(x)$ is positive.

The following notation will be used. For vectors $x, y \in \boldsymbol{R}^n$ we write $x \geqslant y$ if $x^i \geqslant y^i$ for all i, and $x > y$ if $x^i > y^i$ for all i. If $x \geqslant y$ but $x \neq y$ we write $x \blacktriangleright y$. The closed non-negative cone is the set $\boldsymbol{C} = \{x \in \boldsymbol{R}^n : x \geqslant 0\}$. The interior of $\boldsymbol{C}$ is the open cone $\boldsymbol{C}^0 = \{x \in \boldsymbol{R}^n : x > 0\}$. For sets A, B we write $A < B$ if $a < b$ for all $a \in A$, $b \in B$. Related notations such as $y \leqslant x$, $B > A$, etc, have the natural meanings.

For any points x, y in $\boldsymbol{R}^n$ we define the open order interval $[[x, y]] = \{z \in \boldsymbol{R}^n : x < z < y\}$, and the closed order interval $[x, y] = \{z \in \boldsymbol{R}^n : x \leqslant z \leqslant y\}$. A set in $\boldsymbol{R}^n$ is order convex if it contains the closed order intervals defined by each pair of its elements.

An open k cell in a space X is a subset homeomorphic to $\boldsymbol{R}^k$. A closed k cell is a subset homeomorphic to the closed unit ball in $\boldsymbol{R}^k$.

The closure of a set $S \subset \boldsymbol{R}^n$ is denoted by $\bar{S}$ or $\operatorname{clos}(S)$. If $S \subset A \subset \boldsymbol{R}^n$ then the relative closure of S in A is $\bar{S} \cap A = \operatorname{clos}_A(S)$.

The solution to (1) with initial value $y \in \boldsymbol{C}$ is denoted by $\psi_t y$. The omega limit set of y is denoted by $\omega(y)$, or by $\omega(y, \psi)$ if more than one flow is under consideration. The alpha limit set is denoted by $\alpha(y)$. Notice that every limit set is compact owing to dissipation, and is therefore connected.

The set of equilibria is denoted by $\mathscr{E}$.

An equilibrium p is a weak source if in negative time it uniformly attracts some non-empty open set U: $\lim_{t\to\infty} |\psi_{-t}x - p| = 0$ uniformly in $x \in U$. The union of all such U is the basin of repulsion $R(p)$ of p. When $p \in R(p)$ then p is a source. By abuse of language we rephrase dissipation by calling ∞ a source, and we define $R(\infty)$ to be $\{x \in \boldsymbol{C} : \lim_{t\to-\infty} |\psi_t x| = \infty\}$. Thus a point belongs to $R(\infty)$ if its negative orbit is unbounded.

An equilibrium p is a weak sink if in positive time it uniformly attracts some non-empty open set.

A non-stationary periodic orbit is a cycle.

When we speak of the trajectory of x converging, or being attracted to a set, it is understood that this refers to the forward trajectory $\psi_t x$ for $t \geqslant 0$; convergence in this context refers to the limit as $t \to +\infty$. If $\psi_t x$ converges the limit is an equilibrium.

The following theorem, proved in §4, is the main result concerning system (1), which is always assumed to satisfy the conditions of competition, irreducibility and dissipation. Notice that no hyperbolicity assumptions are made.

Theorem 1.1. Let ψ be the flow in $\boldsymbol{C}$ of system (1). There is a countable disjoint family $\mathscr{F} = \{M_i\}$ of invariant open $(n-1)$ cells in $\boldsymbol{C}$ having the following properties.

(a) Every persistent non-convergent trajectory is asymptotic to a trajectory in an M_i. More precisely, suppose the trajectory of x is persistent and non-convergent, and $\omega(x) \subset M_i \cap \boldsymbol{C}^0$. If $x \notin M_i$ then there exists $y \in M_i$ such that $|\psi_t x - \psi_t y| \to 0$ as $t \to \infty$, and either $\psi_t x < \psi_t y$ for all $t \in \boldsymbol{R}$ or else $\psi_t x > \psi_t y$ for all $t \in \boldsymbol{R}$.

(b) Each M_i is a Lipschitz submanifold.

(c) For every M_i in $\mathscr{F}$, no two points of M_i are related by $<$, and no two points of $M_i \cap \boldsymbol{C}^0$ are related by $\blacktriangleleft$.

(d) The cardinality of $\mathscr{F}$ is at most 1 plus the number of weak sources in $\boldsymbol{C}^0$.

The family $\mathscr{F}$ of $(n-1)$ cells of theorem 1.1 is canonical. In order to describe it we make the following definitions.

The basin of lower repulsion of a weak source p is the set $R_-(p)$ of points x in the basin of repulsion $R(p)$ such that there exists $t_0 < 0$ with $\psi_t x < p$ for all $t < t_0$. The basin of upper repulsion $R_+(p)$ is analogously defined. The basin of lower repulsion of ∞ and the basin of repulsion of ∞ are other names for $R(\infty)$, denoted also by $R_-(\infty)$.

A point z is in the lower boundary $\partial_- S$ of a set $S \subset \boldsymbol{R}^n$ provided there is a sequence $\{s_i\}$ in S converging to z with $s_i > z$, but no sequence $\{x_i\}$ in S converging to z with $x_i < z$. The upper boundary $\partial_+ S$ is defined analogously.

Let Γ denote the fundamental attractor for the flow ψ of theorem 1.1. Since the theorem is vacuous unless Γ meets $\boldsymbol{C}^0$, from now on we assume $\Gamma \cap \boldsymbol{C}^0$ is non-empty.

We can now describe the $(n-1)$ cells making up the family $\mathscr{F}$: they are the lower boundaries of the basins of lower repulsion of the weak sources in $\boldsymbol{C}^0$, together with the lower boundary of the basin of repulsion of ∞: $\mathscr{F} = \{\partial_- R_-(p) : p \in (\mathscr{E} \cap \boldsymbol{C}^0) \cup \{\infty\}\}$. The fact that these are open $(n-1)$ cells is proved in §4.

We now discuss some applications of theorem 1.1. We always assume that system (1) satisfies dissipation, irreducibility and competition.

Roughly speaking, theorem 1.1 means that the interesting dynamics of ψ comes from the dynamics in some invariant Euclidean space of one dimension lower. To the extent that systems in $\boldsymbol{R}^{n-1}$ have simpler dynamics than systems in $\boldsymbol{R}^n$, we may conclude that competitive systems have simpler dynamics than arbitrary systems. In particular, their positive limit sets are restricted in their intrinsic topology and dynamics and their position in $\boldsymbol{R}^n$. Results of this type were obtained in Hirsch (1982a, 1985) (in a somewhat different setting); they imply that the flow in any limit set of system (1) is conjugate to the flow in some invariant set of a Lipschitz vector field in $\boldsymbol{R}^{n-1}$. The following consequence of theorem 1.1 sharpens this for positive limit sets.

Theorem 1.2. Every positive limit set lies in an invariant open $(n-1)$ cell, in which the flow is conjugate to the flow of a Lipschitz vector field in an open $(n-1)$ cell in $\boldsymbol{R}^{n-1}$.

A different way to exploit theorem 1.1 is to apply Brouwer's fixed-point theorem to certain negatively invariant closed $(n-1)$ cells to obtain positive equilibria. In this way we shall prove the following theorem in §5.

Theorem 1.3. Let p be an equilibrium satisfying one of the following conditions:

(a) $p > 0$ and p is a source;

(b) $p > 0$ and some compact invariant set is $>p$;

(c) $p = 0$ and p is asymptotically stable.

Then there is an equilibrium greater than p.

Much of the literature on competitive systems has focused on dimensions 2 and 3. In dimension 2 the main result is that every trajectory converges (see Albrecht *et al* 1974). In his dissertation Holtz (1987) completely classifies two-dimensional competitive systems. For results on three-dimensional systems see the papers by Coste *et al* (1978, 1979), Freedman and Waltman (1985), Hallam *et al* (1979), May and Leonard (1975), Rescigno (1968), Schuster *et al* (1979), Smith (1986d), and Smith and Waltman (1988).

Theorem 1.1 is very powerful for analysing three-dimensional competitive flows since it effectively reduces them to planar flows, which have very simple dynamics. We obtain the following general result.

Theorem 1.4. Let $n = 3$ and let $K \subset \boldsymbol{C}^0$ be a positive limit set. Then one of the following holds:

(a) K is an equilibrium;

(b) K is a one-dimensional set containing an equilibrium, and if K does not consist entirely of equilibria then the Čech cohomology group $\check{H}^1(K)$ is non-trivial;

(c) K is a cycle which bounds a positive invariant disc, and this disc contains an equilibrium.

Corollary 1.5. If $n = 3$ and there exists a positive limit set then there exists a positive equilibrium.

The following result is a global stability theorem for persistent orbits.

Theorem 1.6. Suppose $n = 3$. Assume there is a unique positive equilibrium p and p is hyperbolic, and there are no positive cycles. Then every persistent trajectory converges to p.

In higher dimensions it is more difficult to draw general dynamical conclusions from theorem 1.1 owing to our lack of knowledge about the dynamical differences between systems in $\boldsymbol{R}^n$ and systems in $\boldsymbol{R}^{n-1}$. Moreover Smale (1976) has shown that any C^1 system in an $(n-1)$ cell can be embedded as an attracting invariant set in a system in $\boldsymbol{R}^n$ of type (1), with the $(n-1)$ cell corresponding to the simplex Δ^{n-1} spanned by the unit coordinate vectors.

In Smale's construction the origin is a source and $\partial N^i/\partial x^j < 0$ for all i, j. Since these conditions imply that the only weak source in $\boldsymbol{C}$ is the origin, therefore by theorem 1.1(c) and the description of $\mathscr{F}$ the only cell in $\mathscr{F}$ is $\partial_- R(\infty)$. In this case it turns out that the closure of $\partial_- R(\infty) \cap \boldsymbol{C}^0$ is a closed $(n-1)$ cell Σ which attracts all forward orbits. We obtain the following result; observe that its hypotheses are inherited by the restriction of the system to every face of $\boldsymbol{C}$.

Theorem 1.7. In system (1) assume additionally that the origin is a source for the flow in $\boldsymbol{C}$, and that at every equilibrium in $\boldsymbol{C}\backslash 0$ we have $\partial N^i/\partial x^j < 0$ for all i, j. Then every trajectory in $\boldsymbol{C}\backslash 0$ is asymptotic to one in Σ; and Σ is homeomorphic to Δ^{n-1} by radial projection.

This result shows that Smale's construction, seemingly very special, is in fact typical of the subclass of systems (1) which are totally competitive in the sense that all partial derivatives of the N^i are negative.

The attracting cell Σ can be thought of as a generalisation of the carrying capacity K of the one-variable logistic equation $\mathrm{d}x/\mathrm{d}t = rx(1-x/K)$ with positive constants r and K.

The proof of theorem 1.1 is based on the theorem of Müller (1926) and Kamke (1932), which implies that if ψ is the flow of a competitive system then the reversed time flow $\varphi = \{\varphi_t\}_{t\in\boldsymbol{R}}$, defined by $\varphi_t = \psi_{-t}$, is monotone, together with the analysis of monotone flows given in Hirsch (1982a, 1985).

Properties of φ are developed in §§2 and 3; the proof of theorem 1.1 is given in §4; proofs of other results are given in §5.

2. Invariant cells in strongly monotone flows

Let ψ be the solution flow in $\boldsymbol{C}$ to system (1) of the introduction subject to the assumptions of dissipation, irreducibility and competition. In this section we consider a dynamical system $(\boldsymbol{C}, \varphi)$, where $\varphi = \{\varphi_t\}_{t\in\boldsymbol{R}}$ is the reversed time flow obtained from ψ, defined by $\varphi_t = \psi_{-t}$. The fundamental attractor Γ of ψ is now the fundamental repellor of φ. In terms of φ, Γ is characterised as the set of points with bounded orbits, while $x \in \boldsymbol{C}\backslash\Gamma$ if and only if $\lim_{t\to-\infty} |\varphi_t x| = \infty$.

The interior of Γ is denoted by Γ^0.

It follows from dissipation that for each $x \in \boldsymbol{C}$ the trajectory of x is defined for all t in an open interval of the form $(-\infty, T_x)$, $0 < T_x \leqslant \infty$. Notice that $T_x = \infty$ for all $x \in \Gamma$ because Γ is compact and invariant. Each map φ_t is a diffeomorphism between non-empty relatively open sets in $\boldsymbol{C}: \varphi_t: D_t \to R_t$. Observe that $\Gamma \subset D_t$ for all $t \geqslant 0$.

For each equilibrium p we define the following sets in $\boldsymbol{C}$.

$$\begin{aligned} A(p) &= \text{the basin of attraction (or stable manifold)} \\ &= \{x \in \boldsymbol{C} : \lim_{t\to\infty} \varphi_t x = p\} \\ A_-(p) &= \text{the basin of lower attraction} \\ &= \{x \in A(p) : \varphi_t x < p \text{ for all sufficiently large } t > 0\} \\ A_+(p) &= \text{the basin of upper attraction} \\ &= \{x \in A(p) : \varphi_t x > p \text{ for all sufficiently large } t > 0\} \\ V_-(p) &= \text{the lower attraction boundary} = \partial_- A_-(p) \\ V_+(p) &= \text{the upper attraction boundary} = \partial_+ A_+(p). \end{aligned}$$

We also assign analogous sets to the fictional equilibrium ∞:

$$\begin{aligned} A(\infty) &= \text{the basin of attraction of } \infty \\ &= \boldsymbol{C} \backslash \Gamma \\ A_-(\infty) &= A(\infty) \\ A_+(\infty) &= \varnothing \\ V_-(\infty) &= \text{the lower attraction boundary of } \infty \\ &= \partial_- A(\infty) \\ V_+(\infty) &= \varnothing. \end{aligned}$$

It follows from theorem 2.1(c) that $A_-(p)$ and $A_+(p)$ are open. Therefore if either is non-empty then p is a weak sink.

The next theorem is the main result of this section.

Theorem 2.1. Let p, q denote elements of $\mathscr{E} \cup \{\infty\}$. Then

(a) the sets $A(p)$, $A_-(p)$, $A_+(p)$, $V_-(p)$ and $V_+(p)$ are invariant;

(b) $A(p)$, $A_-(p)$ and $A_+(p)$ are order convex; $A_-(p)$ and $A_+(p)$ are relatively open in $\boldsymbol{C}$;

(c) $A_-(p) \cap A_-(q)$ and $V_-(p) \cap V_-(q)$ are empty if $p \neq q$;

(d) $V_-(p)$ is unordered with respect to $<$, and $V_-(p) \cap \Gamma^0$ is unordered with respect to $\blacktriangleleft$;

(e) let $P_E: \boldsymbol{R}^n \to E$ be an orthogonal projection onto a hyperplane E orthogonal to a vector >0. Then $P_E \mid V_-(p)$ is a homeomorphism $g_E: V_-(p) \to U$ onto an open subset $U \subset E$; g_E and $(g_E)^{-1}$ are Lipschitz;

(f) if $A_-(p)$ is non-empty then $A_-(p)$ is an open n cell and $V_-(p)$ is an open $(n-1)$ cell;

(g) if $x \in \operatorname{clos} V_-(p)$ and $x \blacktriangleleft p$ then $x \in V_-(p)$;

(h) results analogous to (c), (d), (e) and (f) hold for $V_+(p)$ and $A_+(p)$.

Before giving the proof we develop some properties of the flow φ.

Recall that a map f between subsets of $\boldsymbol{R}^n$ is monotone if $x \leqslant y$ implies $f(x) \leqslant f(y)$, and strongly monotone if $x \blacktriangleleft y$ implies $f(x) < f(y)$. A flow $\{f_t\}$ is (strongly) monotone if for all $t > 0$ the map f_t is (strongly) monotone.

Proposition 2.2. φ is monotone and the restriction of φ to $\boldsymbol{C}^0$ is strongly monotone. Moreover $\varphi_t x < \varphi_t y$ provided $t > 0$, $x \blacktriangleleft y$, and $y \in \boldsymbol{C}^0$.

Proof. The first statement follows from competition, irreducibility and the Müller–Kamke theorem; see Hirsch (1985, theorem 1.5). The second sentence is proved as follows. Choose $v \in \boldsymbol{C}^0$, $x \blacktriangleleft v \blacktriangleleft y$. Fix $t > 0$ so that $x, v, y \in D_t$. Then $\varphi_t x \leqslant \varphi_t v \blacktriangleleft \varphi_t y$ by the first part, whence $\varphi_t x < \varphi_t y$.

In view of this result we can apply to φ the results on monotone flows proved in Hirsch (1982a, 1985; hereafter referred to as I and II). Although these theorems were stated for flows in open sets, the proofs are readily adapted to current hypotheses. (See also Hirsch (1987) for a more general setting.) In particular the following proposition is valid.

Proposition 2.3. (*a*) Suppose $x \in \Gamma$ has the property that $\varphi_t x > x$ (respectively, $\varphi_t x < x$) for some $t > 0$. Then $\omega(x)$ is an equilibrium $p > x$ (respectively, $p < x$).

(*b*) Suppose $x < y$ in Γ and $\omega(x)$ or $\omega(y)$ meets C^0. Then either $\omega(x) \cap C^0 < \omega(y) \cap C^0$ or else $\omega(x) \cap C^0 = \omega(y) \cap C^0 \subset \mathscr{E}$.

(*c*) The set $\{x \in \Gamma^0 : \omega(x) \cap C^0 \not\subset \mathscr{E}\}$ has Lebesgue measure 0. Therefore the set $\{x \in \Gamma^0 : \omega(x) \cap C^0 \subset \mathscr{E}\}$ is dense in $\Gamma \cap C^0$.

(*d*) If $x < y$ in Γ then every point of $\omega(x) \cap \omega(y)$ is a weak sink.

(*e*) If $K \subset \Gamma$ is an alpha or omega limit set then no points of K are related by $\blacktriangleleft$, and no points of $K \cap C^0$ are related by $<$.

Proof. (*a*) See I, theorem 2.1 or II, theorem 2.2.

(*b*) The proof of II, theorem 3.8 applies with minor modifications.

(*c*) The proof is essentially the same as that of II, theorem 4.1.

(*d*) See lemma 2.1 of II or lemma 6.7 of Hirsch (1987).

(*e*) Follows from (*a*), or alternatively from Hirsch (1987), lemma 6.1.

We proceed to prove theorem 2.1.

Proof. (*a*) Invariance of $A(p)$, $A_-(p)$ and $A_+(p)$ is obvious from the definition; invariance of $V_-(p)$ and $V_+(p)$ follows from monotonicity of φ_t for $t \geqslant 0$.

(*b*) To prove order convexity of $A(p)$ suppose $x \leqslant y \leqslant z$ and $x, z \in A(p)$ where p is finite (i.e. $p \in \mathscr{E}$). Then $y \in \Gamma$ because Γ is order convex. Fix any $\varepsilon > 0$ and choose $T > 0$ so large that $\varphi_t x$ and $\varphi_t z$ belong to the ε ball $B_\varepsilon(p)$ for all $t > T$. By monotonicity of φ_t and order covexity of ε balls, $\varphi_t y \in B_\varepsilon(p)$. Therefore $y \in A(p)$. Order convexity of $A_-(p)$ and $A_+(p)$ are similarly proved. To see that $A_-(p)$ is open fix $x \in A_-(p)$. We can successively choose positive numbers r, s, t such that $\varphi_r x < \varphi_s x < \varphi_t x < p$. By order convexity $A_-(p) \supset [\varphi_r x, \varphi_t x]$, and the latter set is a neighbourhood of $\varphi_s x$. Since $A_-(p)$ is invariant and φ_s is continuous, $\varphi_s^{-1}[\varphi_r x, \varphi_t x]$ is a neighbourhood of x in $A_-(p)$. Similarly for $A_+(p)$. The case of $p = \infty$ is similar.

(*c*) Suppose $p \neq q$; then $A(p)$ cannot meet $A(q)$, proving disjointness of $A_-(p)$ and $A_-(q)$. Disjointness of $V_-(p)$ and $V_-(q)$ follows from the following general fact.

Lemma 2.4. Let B and B' be disjoint order convex sets. Then $\partial_- B$ and $\partial_- B'$ are disjoint, as are $\partial_+ B$ and $\partial_+ B'$.

Proof. Let $w \in \partial_- B$ and $\{y_k\}$ a sequence in B converging to w such that $w < y_{k+1} < y_k$ for all k. By order convexity B contains the union of the open order intervals $[[y_k, y_1]]$, which is $[[w, y_1]]$. Therefore no point of B' can be in $[[w, y_1]]$. For any $z < w$. Then $[[z, y_1]]$ is a neighbourhood of w such that if $x \in [[z, y_1]]$ and $x > w$ then $x \in [[w, y_1]]$. Since such an x could not be in B' it follows that $w \notin \partial B'$.

Part (*d*) of theorem 2.1 follows from the following general result.

Lemma 2.5. Let V denote the lower or upper boundary of an order convex set B. Then V is unordered by $<$. Moreover if V is invariant under a map which is strongly monotone in C^0 then $V \cap C^0$ is unordered by $\blacktriangleleft$.

Proof. Suppose it were possible that $u < v$ in $V = \partial_- B$. Fix sequences $\{x_k\}$, $\{y_k\}$ in B decreasing monotonically for $<$ to u, v respectively. For large k we have $x_k < v < y_k$, so by order convexity B contains the neighbourhood $[[x_k, y_k]]$ of v. But this contradicts v being in the boundary of B; therefore V is unordered by $<$. The second conclusion now follows because a strongly monotone map converts points related by $\blacktriangleleft$ to points related by $<$. The proof for $\partial_+ B$ is similar.

We return to the proof of theorem 2.1. Part (*e*) follows from the following general fact.

Proposition 2.6. Let $V \subset \boldsymbol{C}$ denote the lower or upper boundary of an order convex set $B \subset \boldsymbol{C}$. Let $u \in \boldsymbol{C}^0$ be any positive vector, $E \subset \boldsymbol{R}^n$ its orthogonal hyperplane and $P_E : \boldsymbol{R}^n \to E$ orthogonal projection. Then the map $g = P_E \mid V$ is a homeomorphism onto an open subset of E; both g and g^{-1} are Lipschitz with respect to the Euclidean distance function.

Proof. We assume $V = \partial_- B$, the proof for upper boundaries being similar. To see that g is injective suppose $g(x) = g(y)$. Then $x = y + \lambda u$ for some $\lambda \in \boldsymbol{R}$. Since $u > 0$ and no two points of V can be related by $<$, it follows that $\lambda = 0$; therefore g is injective.

The image of g is open in E and g^{-1} is continuous. To see this fix $a \in V$ and set $g(a) = b \in E$. Choose $c > a$ so that $[[a, c]] \subset B$ (compare the proof of part (*b*)). It is easy to show that $P_E[[a, c]]$ is a neighbourhood in E of b. For any $y \in P_E[[a, c]]$ let L_y denote the line through y parallel to u. Then $L_y \cap B$ has a greater lower bound $w \in L_y$ because B is bounded below, u is a positive vector, and L_y meets $[[a, c]]$. It is not hard to see that $w \in V$ and $g(w) = y$. Thus $g(V)$ is open in E. From this construction of w as $g^{-1}y$ it is easy to see that g^{-1} is continuous. This proves g is a homeomorphism onto an open set in E.

Since P_E has Lipschitz constant 1, so has g. We show that g^{-1} has a Lipschitz constant which depends only on u. Denote by S_E the set of all unit vectors in the linear subspace E. It is easy to see that S_E is disjoint from $\boldsymbol{C}$, and that there exists a number $\mu > 0$ with the following property. If $x \in S_E$, $\lambda \in \boldsymbol{R}$ and $x + \lambda u \notin \boldsymbol{C}$ then $|\lambda| < \mu$.

We show that $1 + \mu$ is a Lipschitz constant for g^{-1}. Fix two points a, b in E. Set $a = b = w \in E$ and $g^{-1}a - g^{-1}b = v$. Then $v = w + \rho u$ for some $\rho \in \boldsymbol{R}$. Notice that $v \notin \boldsymbol{C}$ because v is the difference between two points of the unordered set V. Consider the identity $v/|w| = w/|w| + (\rho/|w|)u$. Since $v/|w| \notin \boldsymbol{C}$ we find that $\rho/|w| < \mu$. From the triangle inequality we therefore get $|v|/|w| < 1 + \mu$. This completes the proof of proposition 2.6.

We now prove part (*f*) of theorem 2.1. Suppose $p \in \mathscr{E}$ and $V_-(p)$ is non-empty. Then there exists $a_* \in A_-(p)$ such that $a_* < p$; fix this a_*. By order convexity of $A_-(p)$ we have $[a_*, p] \backslash p \subset A_-(p) \subset \Gamma^0$.

Fix a number δ in the range

$$0 < \delta < \min\{|p_i - a_{*i}| : i = 1, \ldots, n\}$$

and define the following sets:

$$S_\delta(p) = \{x \in \boldsymbol{R}^n : x \leqslant p \quad \text{and} \quad |x - p| = \delta\}$$

where $|y|$ is the Euclidean norm of a vector y; and

$$L_\delta(p) = \{x \in S_\delta(p) : x < p\}.$$

It is easy to see that

$$L_\delta(p) \subset S_\delta(p) \subset [a_*, p]\backslash p \subset A_-(p).$$

One readily verifies that $S_\delta(p)$ is diffeomorphic to the closed simplex Δ^{n-1} via the map

$$h : \Delta^{n-1} \to S_\delta(p) \qquad h(x) = p - |x|^{-1}\,\delta x$$

recalling that Δ^{n-1} denotes $\{x \in \boldsymbol{R}^n_+ : \Sigma x_i = 1\}$. Moreover h maps the open simplex $\Delta^{n+1}\backslash\partial\Delta^{n-1}$ diffeomorphically onto $L_\delta(p)$.

For $t \geqslant 0$ define $U_t = \varphi_{-t}[[a_*, p]]$. Each U_t is an open subset of Γ^0 diffeomorphic to $[[a_*, p]]$ and therefore to $\boldsymbol{R}^n$. Observe that $U_t \supset U_s$ if $t > s$, because $[[a_*, p]]$ is invariant under φ_r if $r \geqslant 0$. Moreover the definition of $A_-(p)$ implies that $A_-(p) = \bigcup_{t\geqslant 0} U_t$, which is a nested union of open n cells. A theorem of Brown (1961) implies that such a union, and hence $A_-(p)$, is homeomorphic to $\boldsymbol{R}^n$.

To prove the second statement of theorem 2.1(f) consider for each $x \in S_\delta(p)$ the ray R_x through x emanating from p. Since $A_-(p)$ is order convex and bounded, $R_x \cap A_-(p)$ is a bounded open interval with one endpoint at p. It is easy to see that the other endpoint, denoted by $g(x)$, belongs to $V_-(p)$, and that the resulting map $g : S_\delta(p) \to V_-(p)$ sends $S_\delta(p)$ homeomorphically onto the set

$$D(p) = \{x \in V_-(p) : x \blacktriangleleft p\}$$

while g maps $S^0_\delta(p)$ homeomorphically onto the set

$$D^0(p) = \{x \in V_-(p) : x < p\}.$$

Therefore

$$D(p) \approx S_\delta(p) \approx \Delta^{n-1}$$

where $\approx$ indicates homeomorphism, and also

$$D^0(p) \approx S^0_\delta(p) \approx \boldsymbol{R}^{n-1}.$$

Now observe that for any $x \in V_-(p)$ there is a number $t_x > 0$ such that $\varphi_t x \in D^0(p)$ for all $t \geqslant t_x$. To see this fix $y > x$ such that $y \in A_-(p)$, and choose $t_x > 0$ such that $\varphi_s y < p$ if $s \geqslant t_x$. Then for $t \geqslant t_x$ we have $\varphi_t x < \varphi_t y < p$.

We have shown that $V_-(p) = \bigcup_{t>0} \varphi_{-t} D^0(p)$. Now $D^0(p)$ is invariant under φ_t for $t > 0$ by monotonicity, therefore we have expressed $V_-(p)$ as a nested union of open $(n-1)$ cells. So by the aforementioned theorem of Brown $V_-(p)$ is an open n cell.

Consider now the case $p = \infty$. Denote by H the closed halfspace of $\boldsymbol{R}^n$ comprising all vectors of the form $y + \lambda u$, $y \in E$, $\lambda \geqslant 0$. For each $y \in E$ denote by μ_y the smallest number such that $y + \mu_y u \in A(\infty)$, which exists because Γ is compact and $A(\infty) = \boldsymbol{C}^0\backslash\Gamma$. It is easy to see that we obtain a homeomorphism $h : H \to$ closure of $A(\infty)$ by defining $h(y + \lambda u) = y + \lambda u + \mu_y u$. Since $h(E) = V_-(\infty)$ it follows that $V_-(\infty)$ is homeomorphic to $\boldsymbol{R}^{n-1}$. Since $h(H\backslash E) = A(\infty)$, the latter space is homeomorphic to $\boldsymbol{R}^n$. This completes the proof of theorem 2.1(f).

To prove part (g) for $p = \infty$ one verifies that $h(E)$ is a closed set, which we leave to the reader. Suppose now that p is finite and $x \blacktriangleleft p$ is the limit of a sequence $\{x_i\}$ in $V_-(p)$. In order to prove $x \in V_-(p)$ it suffices by invariance to prove $\varphi_1 x \in V_-(p)$. Now $\varphi_1 x$ is the limit of the sequence $\{\varphi_1 x_i\}$ in $V_-(p)$; and $\varphi_1 x < p$ by strong monotonicity. Therefore, replacing x by $\varphi_1 x$, we assume that $x < p$.

Clearly $x \notin A_-(p)$. Now the line segment L from x to p contains points in $A_-(p)$ because it intersects $[[a_*, p]]$ where a_* is as in the proof of part (f). It follows that there is a maximal point $y \geqslant x$ in L such that the segment xy does not meet $A_-(p)$. It is easy to see that the points of L strictly between y and p belong to $A_-(p)$, and $y \in V_-(p)$.

We now show $y = x$. Suppose not; then $x < y$. Pick i so large that $x_i < y$. Since $x_i \in V_-(p)$ there exists $u \in A_-(p)$ with $x_i < u < y$. But then $y \in A_-(p)$ by order convexity. This completes the proof of theorem 2.1(g).

Part (h) is left to the reader.

Part (f) of theorem 2.1 can be sharpened: if $A_-(p)$ is non-empty then it is diffeomorphic to $\boldsymbol{R}^n$. The proof is the same, using the fact that the theorem of Brown (1961) is valid (with practically the same proof) in the differentiable category.

It is an interesting open problem to determine conditions under which the $(n-1)$ cells $V_-(p)$ are smooth. Currently there are no examples known where they are not smooth. Being Lipschitz, they are differentiable almost everywhere.

The following result means that the open $(n-1)$ cells $V_-(p)$ and $V_+(p)$ have nice tubular neighbourhoods.

Proposition 2.7. Let $V \subset \boldsymbol{R}^n$ be an open $(n-1)$ cell which is unordered with respect to $\blacktriangleleft$. Then for any $u \blacktriangleright 0$ the map $h: V \times \boldsymbol{R} \to \boldsymbol{R}^n$ defined by $(x, \lambda) \to x + \lambda u$ is a homeomorphism onto an open n cell.

Proof. It suffices to prove that h is injective. If $h(x, \lambda) = h(y, \mu)$ then $x - y$ is a scalar multiple of u. Since $u > 0$ this multiple must be 0 because by hypothesis no two points of V are related by $\blacktriangleleft$.

The proofs of the following two corollaries are left to the reader. Let V be as in proposition 2.7.

Corollary 2.8. The union of V with the set of points related to points of V by $\blacktriangleleft$ or $\blacktriangleright$ is an open neighbourhood of V.

Corollary 2.9. Every point of V has a neighbourhood Q in $\boldsymbol{R}^n$ with the following property: if $x \in Q$ then the subsets of V comprising all points $\geqslant x$, and respectively all points $\leqslant x$, are compact.

3. Limit sets in eventually strongly monotone flows

The main goal of this section is to prove the following result concerning the flow φ in $\boldsymbol{C}$ of §2. Recall that φ is strongly monotone in $\boldsymbol{C}^0$.

Theorem 3.1. Let K be an alpha or omega limit set which is not a singleton. Then there exist $p \in \mathscr{E}$ and $q \in \mathscr{E} \cup \{\infty\}$ such that $p < K$, $K < q$ if q is finite, and $K \cap \Gamma^0 \subset V_+(p) \cap V_-(q)$. For every $x \in K$, p is the supremum of the equilibria $<x$, and q is the infimum of the equilibria $>x$ if such equilibria exist; otherwise $q = \infty$.

Recall that a point $x \in \Gamma$ is non-wandering if for every neighbourhood $N \subset \Gamma$ of x and every number $T > 0$ there exists $t > T$ such that $(\varphi_t N) \cap N \neq \varnothing$ (= the empty set). All other points of Γ are wandering. The set of non-wandering points, denoted by Ω, is a compact invariant subset of Γ which contains all limit points.

Lemma 3.2. If $x \in \Omega \cap \Gamma^0$ then every neighbourhood of x contains a point $z > x$ such that $\omega(z)$ contains an equilibrium $\geqslant x$.

Proof. By proposition 2.3(c) every neighbourhood of x contains a point $z > x$ with $\omega(z) \cap \boldsymbol{C}^0 \subset \mathscr{E}$. Because x is non-wandering there are convergent sequences $y_i \to x$ in Γ^0 and $t_i \to \infty$ in $\boldsymbol{R}$ such that $\varphi(t_i, y_i) \to x$, and we can take $t_i > 0$ and $y_i < z$. Passing to a subsequence we assume $\varphi(t_i, z)$ converges as $i \to \infty$ to a point q. Since φ is monotone, $\varphi(t_i, y_i) < \varphi(t_i, z)$. Since the relation $\leqslant$ is closed, $x \leqslant q$. Therefore $q \in \omega(z) \cap \boldsymbol{C}^0$, and so $q \in \mathscr{E}$.

Lemma 3.3. Let K be a limit set. If $q > 0$ is an equilibrium and $x \blacktriangleleft q$ for some $x \in K$, then $K < q$.

Proof. By strong monotonicity $\varphi_t x < q$ for $t > 0$, so there are points of K that are $<q$. Suppose $K = \alpha(v)$. It follows that for any $t \in \boldsymbol{R}$ there exists $s < t$ such that $\varphi_s v < q$, and therefore $\varphi_t v < q$ by monotonicity. Thus the entire orbit of v is $<q$ so $\alpha(v) \leqslant q$. In fact $\alpha(v) \blacktriangleleft q$, since $q \in \alpha(v)$ would imply $K = q$; otherwise K would contain two points related by $\blacktriangleleft$, contradicting proposition 2.3(e). Therefore by invariance of K and q and strong monotonocity, $\alpha(v) < q$. A similar argument applies if $K = \omega(v)$.

Proof of theorem 3.1. For each $x \in K \cap \Gamma^0$ pick $z_x > x$ and $q_x \geqslant x$ such that $q_x \in \mathscr{E} \cap \omega(z_x)$; this is possible by lemma 3.2. I claim that the set R of those x in $K \cap \Gamma^0$ for which $q_x \neq x$ is dense in $K \cap \Gamma^0$. Suppose that this is not so. Then $x = \omega(z_x)$ for every x in some relatively open subset U of $K \cap \Gamma^0$ by proposition 2.3(a) and strong monotonicity, and therefore $U \subset \mathscr{E}$. Fix $y \in U$. Since y is not isolated in K and K is compact and unordered, there must be a compact neighbourhood N of y in U so small that $N \blacktriangleleft b < z_y$ where b is the least upper bound of N. Now $N \subset \mathscr{E}$ and so N is invariant. By strong monotonicity $\varphi_t b > N$ for $t > 0$, whence $\varphi_t b > b \blacktriangleright y$ for $t > 0$. Also $\varphi_t z_y > \varphi_t b$ for $t > 0$. But this entails $\varphi_t z_y > b \blacktriangleright y$ for $t > 0$, contradicting $\varphi_t z_y \to y$. Therefore $q_x \blacktriangleright x$ for some $x \in U$, proving that R is dense in $K \cap \Gamma^0$.

It now follows from lemma 3.3 that $K < q_x$ for every $x \in R$. Let $q \in \mathscr{E}$ be the greatest lower bound of the set of equilibria $>K$; then $q \geqslant K$. In fact $q \notin K$, otherwise K would equal q, contrary to hypothesis, by an application of proposition 2.3(a) and strong monotonicity. Thus $q \blacktriangleright K$, and by strong monotonicity we conclude $q > K$.

By choosing the $z_x < q$ we see that $q_x \leqslant q$ and therefore $q_x = q$ for all $x \in R$. Recalling that $\omega(z_x) = q_x$ we find that $z_x \in A_-(q)$ for all $x \in R$. Since z_x can also be taken arbitrarily near x, and $x \notin A_-(q)$ for $x \in R$, it follows that $R \subset V_-(q)$. Since the intersection of $V_-(q)$ with the set L of points $\blacktriangleleft q$ is closed in L by theorem 2.1(g), and K is a compact subset of L, it follows that $K \cap \Gamma^0 \subset V_-(q)$.

Uniqueness of q follows from disjointness of $V_-(p)$ and $V_-(p')$ for $p \neq p'$ (theorem 2.1(c)).

To prove the last sentence of theorem 3.2, observe that we have already shown

$q > x$. Suppose $q' > x$ is an equilibrium. Since $x \in V_-(q)$ there must exist a point $b \in A_-(q)$ such that $x < b < q'$. Since $\varphi_t b \to q$ as $t \to \infty$ and $\varphi_t b < q'$ for all $t > 0$ it follows that $q \leqslant q'$.

The existence of p is proved similarly.

4. Competing species

In this section we prove theorem 1.1 concerning the flow ψ of the system:

$$\dot{x}^i = F^i(x) = x^i N^i(x) \qquad (i = 1, \ldots, n)$$

in the non-negative orthant $\boldsymbol{C}$, under the hypotheses of competition, irreducibility, and dissipation. Recall that $\Gamma \subset \boldsymbol{C}$ is a compact invariant set with non-empty interior Γ^0, such that for every compact set $S \subset \boldsymbol{C}$, the distance from $\psi_t x$ to Γ goes to 0 as $t \to \infty$, uniformly in $x \in S$. It follows that Γ is unique.

Lemma 4.1. Γ, Γ^0 and the closure of Γ^0 are invariant and order convex; the closure of Γ^0 is a compact neighbourhood of the origin in $\boldsymbol{C}$.

Proof. We have already noted invariance. To prove Γ order convex we first show that if $x \in \boldsymbol{C} \backslash \Gamma$ and $y \geqslant x$ then $y \notin \Gamma$. To see this observe that $\omega(x)$ is a compact subset of Γ, but $\alpha(x)$ cannot be compact: if it were, the closure of the entire orbit of x would be a compact invariant set not contained in Γ. Therefore there is a sequence $t_k \to \infty$ such that $|\psi_{-t_k} x| \to \infty$ or, equivalently, $|\varphi_{t_k} x| \to \infty$. By monotonicity, if $y \geqslant x$ then also $|\varphi_{t_k} y| \to \infty$.

To see that Γ is order convex suppose $a, c \in \Gamma$ and $a \leqslant b \leqslant c$. Then $b \in \boldsymbol{C}$. If $b \notin \Gamma$ then, by the foregoing, the forward orbit of b under φ is unbounded, and the same would hold for c. But this contradicts compactness and invariance of Γ. This proves order convexity of Γ. Since the interior and closure of an order convex set are order convex, it follows that Γ^0 and its closure are order convex. Finally, the closure of Γ^0 contains 0 and a point $b > 0$, so it contains $[0, b]$ which is a neighbourhood of 0 in $\boldsymbol{C}$.

As usual φ denotes the flow obtained from ψ by time reversal. All the results of §§2 and 3 apply to φ. In order to interpret those results in terms of ψ we make some definitions. Let p be an equilibrium for ψ and $R(p)$ its basin of repulsion. We define the following sets:

$$\begin{aligned} R_-(p) &= \text{the basin of lower repulsion} \\ &= \{x \in R(p) : \exists T \in R_+ \text{ such that } \psi_t x > p \text{ if } t \geqslant T\} \\ &= A_-(p) \text{ for } \varphi \text{ (as defined in §3)} \end{aligned}$$

$$\begin{aligned} R_+(p) &= \text{the basin of upper repulsion} \\ &= \{x \in R(p) : \exists T \in R_+ \text{ such that } \psi_t x < p \text{ if } t \geqslant T\} \\ &= A_+(p) \text{ for } \varphi \end{aligned}$$

$$\begin{aligned} M_-(p) &= \text{the lower repulsion boundary} \\ &= \partial_- R_-(p) \\ &= \text{lower boundary of } R_-(p) \\ &= V_-(p) \text{ for } \varphi \end{aligned}$$

$$\begin{aligned} M_+(p) &= \text{the upper repulsion boundary} \\ &= \partial_+ R_+(p) \\ &= \text{upper boundary of } R_+(p) \\ &= V_+(p) \text{ for } \varphi. \end{aligned}$$

For the fictional equilibrium ∞ we define analogous sets:

$$\begin{aligned} R(\infty) &= \text{the basin of repulsion of } \infty \\ &= \boldsymbol{C}\backslash\Gamma = A(\infty) \text{ for } \varphi \end{aligned}$$

$$R_-(\infty) = R(\infty)$$

$$R_+(\infty) = \varnothing$$

$$\begin{aligned} M_-(\infty) &= \text{the lower repulsion boundary of } \infty \\ &= \partial_- R(\infty) = V_-(\infty) \text{ for } \varphi \end{aligned}$$

$$M_+(\infty) = \varnothing.$$

Interpreting theorem 2.1 in terms of ψ we have the following result.

Theorem 4.2. Let p, q denote elements of $\mathscr{E} \cup \{\infty\}$. Then

(*a*) the sets $R(p)$, $R_-(p)$, $R_+(p)$, $M_-(p)$ and $M_+(p)$ are invariant;

(*b*) $R(p)$, $R_-(p)$ and $R_+(p)$ are order convex; $R_-(p)$ and $R_+(p)$ are relatively open in $\boldsymbol{C}$;

(*c*) $R_-(p) \cap R_-(q)$ and $M_-(p) \cap M_-(q)$ are empty if $p \neq q$;

(*d*) $M_-(p)$ is unordered with respect to $\blacktriangleleft$, and $M_-(p) \cap \Gamma^0$ is unordered with respect to $<$;

(*e*) let $P_E : \boldsymbol{R}^n \to E$ be orthogonal projection onto a hyperplane E orthogonal to a vector >0. Then $P_E \mid M_-(p)$ is a homeomorphism $g_E : M_-(p) \to U$ onto an open subset $U \subset E$; g_E and $(g_E)^{-1}$ are Lipschitz;

(*f*) if $R_-(p)$ is non-empty then $R_-(p)$ is an open n cell and $M_-(p)$ is an open $(n-1)$ cell;

(*g*) if $x \in \operatorname{clos} M_-(p)$ and $x \blacktriangleleft p$ then $x \in M_-(p)$;

(*h*) results analogous to (*c*), (*d*), (*e*) and (*f*) hold for $M_+(p)$ and $R_+(p)$.

Despite the symmetry in their definitions, the open $(n-1)$ cells $M_-(p)$ and $M_+(p)$ have somewhat different geometries as subsets of $\boldsymbol{C}$, owing to the special role the relation $\geqslant$ plays in the definition of $\boldsymbol{C}$. For example, if $p \in \partial\boldsymbol{C}$ then $M_-(p)$ is empty, but $M_+(p)$ may be non-empty. On the other hand $M_-(p)$ may intersect $\partial\boldsymbol{C}$ (even if $p \in \boldsymbol{C}^0$), whereas one can show that $M_+(p)$ does not.

Interpreting theorem 3.1 in terms of ψ we get the following basic result.

Theorem 4.3. Let K be a limit set of ψ which is not a singleton. Then there exist $p \in \mathscr{E}$, $q \in \mathscr{E} \cup \{\infty\}$ such that $p < K$, $K < q$ if q is finite, and $K \cap \Gamma^0 \subset M_+(p) \cap M_-(q)$. For every $x \in K$, p is the supremum of the equilibria $<x$ and q is the infimum of the equilibria $>x$ if such equilibria exist; otherwise $q = \infty$.

In preparation for the proof of theorem 1.1 we define the family of sets $\mathscr{F} = \{M_-(q) : q \in \mathscr{E} \cup \{\infty\}\}$. By theorem 4.2 the elements of $\mathscr{F}$ are pairwise disjoint, invariant open $(n-1)$ cells in $\boldsymbol{C}$. Each of these cells is a Lipschitz submanifold which is unordered with respect to $\blacktriangleleft$; its intersection with $\boldsymbol{C}^0$ is unordered with respect to $<$.

Lemma 4.4. Let M be one of the invariant $(n-1)$ cells of $\mathscr{F}$. Suppose $x \in \boldsymbol{C}^0 \backslash M$ is such that $\omega(x) \subset M \cap \boldsymbol{C}^0$ and $\psi_t x <$ some point of M for some $t \in \boldsymbol{R}$. Then there exists $y \in M \cap \boldsymbol{C}^0$ and $t_0 > 0$ such that $|\psi_t y - \psi_t x| \to 0$ as $t \to \infty$ and $\psi_t y > \psi_t x$ for all $t \in \boldsymbol{R}$. An analogous result holds if $\psi_t x >$ some point of M for some $t \in \boldsymbol{R}$.

Proof. We first show that $\psi_t x <$ some point of M for all $t \in \boldsymbol{R}$. Since M is invariant and $\psi_{-s} \mid \boldsymbol{C}^0$ is strongly monotone for $-s < 0$, it suffices to show that there exist arbitrarily large $t > 0$ such that $\psi_t x \blacktriangleleft$ some point of M. To this end fix $z \in \omega(x)$. It is easy to see that z, like every point of $M \cap \boldsymbol{C}^0$, has a neighbourhood N in $\boldsymbol{C}^0$ so small that every point of $N \backslash M$ is related to some point of M by $<$ or $>$; see proposition 2.7. Choose a sequence $t_i \to \infty$ so that $\psi_{t_i} x \in N$ and $\psi_{t_i} x \to z$ as $i \to \infty$. It is impossible that $\psi_{t_i} x$ be related by $\geqslant$ to points of M for arbitrarily large i, since then it would follow by strong monotonicity that $\psi_t x$ is $\geqslant$ some point of M for all $t \in \boldsymbol{R}$, which is contrary to the hypothesis. Therefore for all large i we have $\psi_{t_i} x \blacktriangleleft$ some point of M. This verifies the claim that every point on the orbit of x is related by $<$ to some point of M.

By local compactness of M, z has a neighbourhood N_1 in N such that for any $p \subset N_1$, the set $S_+(p) \subset M$ comprising all points of M that are $\geqslant p$ is a compact subset of $M \cap N$. There exists $r > 0$ with $\psi_r x \in N_1$. Since it suffices to prove the lemma with x replaced by $\psi_r x$, we assume $x \in N_1$. For every $t \geqslant 0$ set $B_t = S_+(\psi_t x)$; from the first paragraph of this proof we know that B_t is non-empty. Therefore if $\psi_t x \in N_1$ then B_t is compact and non-empty.

Observe that because ψ_{-s} is monotone for $s > 0$, it follows that $\psi_{-s} B_{t+s} \subset B_t$ whenever $t \geqslant 0$ and $s > 0$.

Let $\{t_i\}$ be an unbounded increasing sequence of numbers such that $t_0 = 0$ and $\psi_{t_i} x \in N_1$. For each $i = 0, 1, 2, \ldots$, put $L_i = \psi_{-t_i} B_{t_i}$, which is a non-empty compact subset of B_0. Notice that if $0 < t < t_i$ then $\psi_t L_i = \psi_{-(t_i - t)}(B_{t_i}) \subset B_t$. This proves $L_i \subset \psi_{-t} B_t$ for $0 < t < t_i$, and $L_i \subset L_{i-1}$. Set $L = \bigcap L_i$. Then L is a non-empty compact set in $M \cap \boldsymbol{C}^0$ such that $\psi_t L \subset B_t$ for all $t \geqslant 0$. We shall see that any $y \in L$ fulfils the requirements of lemma 4.5.

Fix $y \in L$. Since $\psi_t y \in B_t$ for all $t \geqslant 0$ it follows that $\psi_t x \leqslant \psi_t y$ for all $t \geqslant 0$. But $\psi_t x \neq \psi_t y$ because $x \notin M$ and $y \in M$, and M is invariant. Therefore $\psi_t x \blacktriangleleft \psi_t y$ for all $t \geqslant 0$. Since any $r \in \boldsymbol{R}$ can be written as $-\tau + t$ with $-\tau < 0 < t$, it follows from strong monotonicity of $\psi_{-\tau}$ that $\psi_r x < \psi_r y$ for all $r \in \boldsymbol{R}$.

To see that $|\psi_t x - \psi_t y| \to 0$ as $t \to \infty$, suppose that this is not so. Then there is a sequence $s_j \to \infty$ such that $\psi_{s_j} x \to a \in \omega(x) \subset M \cap \boldsymbol{C}^0$ and $\psi_{s_j} y \to b \in M$; then necessarily $a \blacktriangleleft b$. Applying ψ_{-1} to a and b we obtain points $u \in M$ and $v \in M$ with $u < v$. There exists $v_0 \in M$ so near v that $u < v_0$, contradicting M being unordered for $<$.

Proof of theorem 1.1. We take $\mathscr{F}$ to be the family of $(n-1)$ cells defined above, namely the lower boundaries of attraction of the weak sources in $\boldsymbol{C}^0$ and of ∞. The properties of the elements of $\mathscr{F}$ listed in parts (b), (c) and (d) of theorem 1.1 were proved in theorem 4.2.

We prove part (a). Let $x \in \boldsymbol{C}^0$ have a persistent trajectory which does not converge to a stationary point; set $K = \omega(x) \subset \boldsymbol{C}^0$. By theorem 4.3 there is a weak source q such that $K \subset M_-(q)$. Since $M_-(q)$ is non-empty, q must be in $\boldsymbol{C}^0 \cup \{\infty\}$, so

$M_-(q)$ belongs to $\mathscr{F}$. We show that the forward trajectory of x is asymptotic to the trajectory of some $y \in M_-(q)$. If $x \notin M_-(q)$ then pick any $z \in K$. By corollary 2.8 z has a neighbourhood U in $\boldsymbol{C}^0$ such that every point of $U \backslash M_-(q)$ is related by $<$ or $>$ to some point of $M_-(q)$. Because $K = \omega(x)$ there exists $s > 0$ with $\psi_s x \in U$. Then there exists $v \in M_-(q)$ related by $<$ or $>$ to $\psi_s x$. By lemma 4.4 we choose v so that the forward trajectories of v and $\psi_s x$ are asymptotic. Set $y = \psi_{-s} v$; then $y \in M_-(q)$ by invariance, and $|\psi_t x = \psi_t y| \to 0$ as $t \to \infty$. If $x \in M_-(q)$ then set $y = x$.

5. Further results

Let ψ denote the flow in $\boldsymbol{C}$ of system (1) of §1, generated by the C^1 vector field F. In this section we prove the results stated in §1 after theorem 1.1, and some other results.

Theorem 2.1′. Every positive limit set lies in an invariant open $(n-1)$ cell in which the flow ψ is conjugate, via a Lipschitz homeomorphism, to the flow of a Lipschitz vector field in an open $(n-1)$ cell in $\boldsymbol{R}^{n-1}$.

Proof. Let $M \in \mathscr{F}$ (the family of $(n-1)$ cells defined in §1). Let $g: M \to E$ denote the restriction to M of the orthogonal projection $P: \boldsymbol{R}^n \to E$ where $E \subset \boldsymbol{R}^n$ is a hyperplane orthogonal to a positive vector. Then g and g^{-1} are Lipschitz homeomorphisms by theorem 2.1(e) because we can take M to be $A_-(p)$ of theorem 2.1, define a flow $\theta = \{\theta_t\}$ in $g(M)$ by $\theta_t = P\psi_t g^{-1}$. Differentiating by t one finds

$$\frac{\mathrm{d}}{\mathrm{d}t}(\theta_t x) = PF(g^{-1}(\theta_t x)).$$

This implies θ is the flow of the locally Lipschitz vector field PFg^{-1} in the open $(n-1)$ cell $g(M)$.

The following result sharpens theorem 4.3.

Theorem 5.1. Let $K \subset \boldsymbol{C}^0$ be a positive limit set of ψ which is not a singleton. Suppose K is contained in the open $(n-1)$ cell $M_-(p)$ for some $p \in \mathscr{E} \cup \{\infty\}$. Then there exists a negatively invariant closed $(n-1)$ cell D such that $K \subset D \subset M_-(p)$, and $D \blacktriangleleft p$ if p is finite. In fact D depends only on p, and D contains every compact invariant set in $M_-(p) \cap \boldsymbol{C}^0$.

Proof. First assume that p is finite. Define

$$D(p) = \{x \in M_-(p) : x \blacktriangleleft p\}$$
$$D^0(p) = \{x \in M_-(p) : x < p\}.$$

We identify $M_-(p)$ with the set $A_-(p)$ defined for the time reversal φ of ψ. In the proof of theorem 2.1(f) we showed that $D(p)$ is a closed $(n-1)$ cell and $D^0(p)$ is an open $(n-1)$ cell, and both are positively invariant under φ; thus they are negatively invariant under ψ. It also follows from that proof that the sets $\{\psi_t D(p)\}_{t \in \boldsymbol{R}}$ form a nested family of closed $(n-1)$ cells whose union is $M_-(p)$. Therefore K, being compact, is contained in one of them; and being invariant, K is contained in all of them. In particular K, and every compact invariant set, lies in $\psi_{-1}D(p)$. We set $D = \psi_{-1}D(p)$. By strong monotonicity of ψ_{-1} it follows that $D < p$ if p is finite.

Now suppose $p = \infty$ and define the set

$$\Sigma = \text{clos}(M_-(\infty) \cap \boldsymbol{C}^0).$$

It is not hard to prove the following properties of Σ: it is a closed invariant subset of Γ, and thus compact. Moreover, every ray in $\boldsymbol{C}$ emanating from the origin meets Σ in a unique point, so that radial projection maps Σ bijectively on the simplex Δ^{n-1}; and this map is a homeomorphism. Setting $D = \Sigma$ completes the proof of theorem 5.1.

Theorem 1.3′. Let p be an equilibrium satisfying one of the following conditions:

(*a*) $p > 0$ and p is a source;

(*b*) $p > 0$ and some compact invariant set is $\gg p$;

(*c*) $p = 0$ and p is asymptotically stable.

Then there is an equilibrium $\gg p$.

Proof. (*a*) If $p > 0$ is a source then p must be in the interior of the fundamental attractor Γ. Consider a ray emanating from p in a direction parallel to a vector $v \blacktriangleright 0$: eventually the ray must enter $A(\infty)$. Therefore there is a unique number $c(v) > 0$ such that $p + c(v)v \in M_-(\infty) =$ the lower boundary of the basin of repulsion of ∞. Define a map $h : \Delta^{n-1} \to M_-(\infty)$ by $h(x) = p + c(x)x$. One easily proves h continuous and injective. Thus the image of h is a closed $(n-1)$ cell B in $M_-(\infty)$. Geometrically we can describe B as the boundary in $M_-(\infty)$ of the set of points $\blacktriangleright p$ in $M_-(\infty)$. It is important to note that $B \subset \boldsymbol{C}^0$ because $p > 0$.

Now B is negatively invariant; in fact for $t < 0$ we have $\psi_t B > p$ because ψ_t is strongly monotone in $\boldsymbol{C}^0$. This implies $\psi_t B \subset B \backslash \partial B$, since $\partial B = h(\partial \Delta^{n-1}) = \{y \in B : y \not\gg p\}$. A well known application of Brouwer's fixed-point theorem implies that any semiflow in a closed cell has an equilibrium. Therefore ψ has an equilibrium $q \in B \backslash \partial B$; thus $q \gg p$.

(*b*) One uses the existence of a compact invariant set $\gg p$ to conclude that $p \in \text{Int}\,\Gamma$; the rest of the proof is the same as that of part (*a*).

(*c*) From asymptotic stability of the origin there must exist a point $x > 0$ in Γ such that for some $T > 0$ we have $\psi_T x < x$. Set $y = \psi_T x$. Then for the time reversal φ of ψ we have $\varphi_T y > y$. Therefore by proposition 2.3 the omega limit set of y for φ is an equilibrium q—for both φ and ψ—and $q > y > 0$.

Theorem 1.4′. Let $n = 3$ and let $K \subset \boldsymbol{C}^0$ be a positive limit set. Then one of the following holds:

(*a*) K is an equilibrium;

(*b*) K is a one-dimensional set containing an equilibrium, and if K does not consist entirely of equilibria then the Čech cohomology group $\tilde{H}^1(K)$ is non-trivial;

(*c*) K is a cycle which bounds a positive invariant disc, and this disc contains an equilibrium.

Proof. Suppose (*a*) does not hold. Then K lies in some invariant 2-cell M, either $\partial \boldsymbol{C}$ or an element of $\mathscr{F}$. It is a well known consequence of the Poincaré–Bendixson theorem that K is at most one dimensional. Since K is connected and not a singleton it cannot be zero dimensional; thus $\dim K = 1$. Statement (b) is proved for general planar flows in Hirsch and Pugh (1987). Suppose K does not contain an equilibrium. Then the theorem of Poincaré–Bendixson applied to the flow in M implies that K is a cycle, which must bound a disc in M by Schoenflies' theorem; and the disc contains a stationary point by Brouwer's fixed-point theorem, so that (c) holds.

Theorem 1.6′. Suppose $n = 3$. Assume there is a unique positive equilibrium p and p is hyperbolic, and there are no positive cycles. Then every persistent trajectory converges to p.

Proof. Suppose $K \subset \boldsymbol{C}^0$ is the ω-limit set of a persistent trajectory. It suffices to show that K is an equilibrium.

By theorem 1.2 K lies in an invariant open 2-cell M and K is the ω limit set of a trajectory in M. Referring to theorem 1.4 we see that the proof is complete once we rule out the possibility that K is a one-dimensional set which contains an equilibrium and separates M. Suppose that K had this form; then $p \in K$. Therefore p, being hyperbolic, must be a saddle. Otherwise p would be a source or a sink; and K, being a limit set containing p, would reduce to p, contradicting K having dimension 1. Thus p is a saddle. It follows that K contains points other than p on the stable and unstable manifolds of p (see, e.g., Freedman and Waltman 1985).

Let $y \neq p$ be a point in the intersection of K with the unstable manifold of p. Then $\omega(y) \subset K$; since there are no positive cycles, $\omega(y)$ contains p; therefore $\omega(y)$ contains a point $z \neq p$ in the stable manifold of p. By considering the way the forward orbit of y meets an arc in M transverse at z to the orbit of z, one proves that z is on the forward orbit of y. This shows that p is a homoclinic equilibrium for the flow in M: one branch of its unstable manifold coincides with a branch of its stable manifold. This branch together with p forms a Jordan curve L in M.

Since M is homeomorphic to the plane, L bounds an invariant disc D in M. By hypothesis D contains no cycles and no equilibrium except p. It follows from the Poincaré–Bendixson theorem that p is in both the alpha and omega limit set of every point u in the interior of D. Since p is hyperbolic it is impossible for either the forward or the backward trajectory of u to converge to p. Therefore both these trajectories spiral toward the boundary L of D from the interior of D. But this implies they must cross, which is impossible. This contradiction proves that $K = p$ after all.

Next we prove theorem 1.7. Recall that for this theorem Σ denotes $\mathrm{clos}[\partial_- R(\infty) \cap \boldsymbol{C}^0]$.

Theorem 1.7′. In system (1) assume additionally that the origin is a source for the flow in $\boldsymbol{C}$, and that at every equilibrium in $\boldsymbol{C}\backslash 0$ we have $\partial N^i/\partial x^j < 0$ for all i, j. Then every trajectory in $\boldsymbol{C}\backslash 0$ is asymptotic to one in Σ and Σ is homeomorphic to Δ^{n-1} by radial projection.

Proof. The proof goes by induction on n. If $n = 1$ then Γ is an interval $[0, b]$ for some number $b > 0$. By hypothesis every positive equilibrium is an attractor, so b is the unique positive equilibrium. It is clear that all trajectories are attracted to $\Sigma = \{b\}$, and the last sentence of the theorem is trivial.

From now on we assume $n > 1$. The induction hypothesis is that the theorem holds for systems in $\boldsymbol{R}^m$ if $m < n$.

Let H denote a k-dimensional face of $\boldsymbol{C}$, $1 \leqslant k \leqslant n-1$, defined by setting $n-k$ coordinates equal to zero. By relabelling the remaining k coordinates we identify H with $\boldsymbol{R}^k$. The hypotheses of theorem 1.7 are inherited by the restriction of the system to H. Therefore by the induction hypothesis we conclude that every trajectory in $H \backslash 0$ is attracted to $H \cap \Sigma$.

From the application of the theorem to each face of $\boldsymbol{C}$ one proves easily that $\Sigma \cap \partial \boldsymbol{C} = \operatorname{clos}[M_+(0) \cap \partial \boldsymbol{C}]$. We denote this set by $\partial\Sigma$. Observe that no points of $\partial\Sigma$ are related by $\blacktriangleleft$.

We now prove that $\Sigma = \operatorname{clos} M_+(0)$. It suffices to prove that $\Sigma \cap \boldsymbol{C}^0 = M_+(0) \cap \boldsymbol{C}^0$. Every ray from the origin through a point of $\boldsymbol{C}^0$ meets $M_+(0)$ and Σ in points x and y, respectively, and it suffices to prove $x = y$. Suppose that for some ray $x \neq y$. Then $0 \blacktriangleleft x \blacktriangleleft y$, and both x and y are in Γ. I claim that for every $v \in [[x, y]]$, $\alpha(v)$ is an equilibrium. Suppose not; then by theorem 3.1 applied to the time reversal φ of ψ, $\alpha(v) \cap \boldsymbol{C}^0 \subset M_+(0) \cap M_-(\infty)$. I claim that $\alpha(v)$ is disjoint from the closure of $\boldsymbol{C}^0 \cap M_+(0)$. To see this, suppose there exists $z \in \alpha(v) \cap \operatorname{clos}[\boldsymbol{C}^0 \cap M_+(0)]$. Then from strong monotonocity of φ and the fact (easily proved) that the closure of $M_+(0) \cap \boldsymbol{C}^0$ is unordered for $\blacktriangleleft$, it follows that z is a common omega limit point under φ of x and v. Then by proposition 2.3(d), z is a weak sink for φ and thus a weak source for ψ. Now under the hypothesis the vector field F has negative divergence in a neighbourhood of every equilibrium in $\boldsymbol{C} \backslash 0$, and it is easily proved that at a weak source the divergence of F is $\geqslant 0$. Therefore the origin is the only candidate for a weak source for ψ, so $z = 0$. But z, being in $M_+(0)$, is >0, so we have reached a contradiction. This shows that $\alpha(v)$ is disjoint from the closure of $\boldsymbol{C}^0 \cap M_+(0)$. A similar argument proves $\alpha(v)$ disjoint from $\operatorname{clos}(\boldsymbol{C}^0 \cap \Sigma)$. Therefore $\alpha(v) \subset [M_+(0) \cup \Sigma] \cap \partial \boldsymbol{C}$. It now follows from the preceding paragraph that $\alpha(v) \subset \partial\Sigma$. Since $\partial\Sigma$ is unordered, monotonicity of φ implies that every $w \in \alpha(v)$ is a common omega limit point under φ of both v and x. By proposition 2.3(c) such a w must be a weak sink for φ, and w is therefore a weak source for ψ which is >0; as we have seen, this implies $w = 0$, a contradiction. This proves that $\alpha(v)$ is an equilibrium for every $v \in [[x, y]]$. We show next that this leads to another contradiction.

Let $J \subset [[x, y]]$ be a simply ordered arc. For every $v \in J$ denote by $p(v)$ the equilibrium which is $\omega(v)$. The map sending v to $p(v)$ is injective, otherwise some $p(v)$ would be a weak source different from 0. By monotonicity the set of $p(v)$ is simply ordered by $\leqslant$. Let H denote a face of $\boldsymbol{C}$ having minimal dimension among all faces such that $H \backslash \partial H$ contains uncountably many $p(v)$. Then there exists a sequence $\{v_i\}$ in J and a point $v_* \in J$ such that $\{p(v_i)\}$ is a simply ordered sequence of distinct points in $H \backslash \partial H$ converging to $p(v_*) \in H \backslash \partial H$.

The flow $\theta = \varphi \mid H$ is strongly monotone for the vector ordering in H, i.e. if we identify H with the open positive cone in $\boldsymbol{R}^m$ then $\varphi \mid H$ is strongly monotone; this follows from the hypothesis and proposition 2.2. We reach a contradiction by applying the following result.

Lemma 5.2. Let θ be the flow of a vector field G in an open set $W \subset \boldsymbol{R}^m$ satisfying $\partial G^i / \partial x^j > 0$ for all $i, j = 1, \ldots, m$. Then there cannot exist a simply ordered convergent sequence of distinct equilibria.

Proof. Suppose to the contrary that $q \in W$ is the limit of such a sequence q_i. Since the matrix $DG(q)$ has only positive entries, by the Perron–Frobenius theorem it has a positive eigenvalue λ, and λ has a positive eigenvector u; moreover any eigenvector $\blacktriangleright 0$ is a multiple of u. Fix $t > 0$ and set $A = D\theta_t(q)$. Then $e^{t\lambda}$ is an eigenvalue >1 of A, and every positive eigenvector of A is a multiple of u. On the other hand, the unit vectors $(q - q_i)/|q - q_i|$ have a subsequence converging to a fixed-point eigenvector w for A, as is easily proved from the first-order Taylor approximation to θ_t at q. Since $\{q_i\}$ is simply ordered, w or $-w$ is $\blacktriangleright 0$. But w is not a multiple of u because w belongs to the eigenvalue 1. This contradiction completes the proof.

We have proved, by contradiction, that $\operatorname{clos} M_+(0) = \Sigma$. We now complete the proof of theorem 1.7. Let $K = \omega(x)$ for some $x \blacktriangleright 0$. Since 0 is a source, $0 \notin K$. Therefore K, being invariant, cannot meet the basin of repulsion $R(0)$. Similarly K cannot meet $R(\infty)$. Let $y \in K$. We showed above that the ray from the origin through y meets Σ in a unique point y_0, and every other point of the ray is in $R(0) \cup R(\infty)$. Therefore $y = y_0$, proving $K \subset \Sigma$.

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