Competing species and homeomorphisms of the disk

Rafael Ortega

Asume that several species are competing and there is no coexistence state. Is it true that some of these species must go to extinction? This vague question admits a precise formulation in terms of differential equations and can be translated into the language of Topology. For few competitors (low dimension) the answer to this question is usually affirmative. We discuss a concrete situation (three species with seasonal effects). The proofs are based on Brouwer's arc translation lemma.

1. Competition models.

Population dynamics.
The logistic equation.
Cooperative and
competitive systems.
Seasonal effects and periodicity.
The carrying simplex.

2. Ecology or Topology?

The arc translation lemma and the theory of free homeomorphims.
A proof of the exclusion principle for three species.

Competing species and homeomorphisms of the disc

Rafael Ortega

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In Ecology the interaction between several species is modeled by systems of differential equations of the type

$$\dot{u}_i = \lambda_i\,(t, u_1, .. u_N)\,u_i, \quad i = 1, .. N,$$

where $u_i = u_i(t)$ is the size of the species. This is somehow similar to Newton's Second law in Mechanics. In contrast to that case the functions λ_i are only known at a qualitative level:

λ_i is positive, negative, increasing/decreasing in u_j

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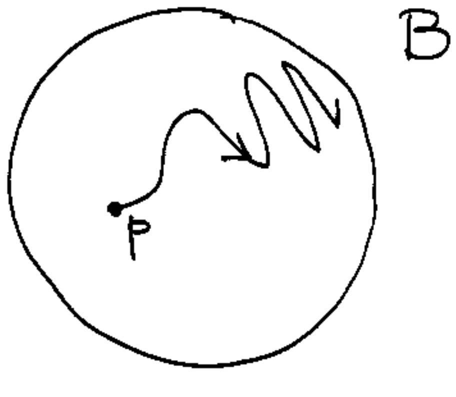
For this reason it is interesting to know which properties of the system can be known with this purely qualitative information. At this point Topology becomes useful.

We deal with a concrete question: the principle of competitive exclusion. If several species compete for the same niche, some of them must go to extinction. This is a vaguely stated principle in Ecology (see [Murray] and [McA] for more information). As we shall see the possible validity of this principle is related to the following problem: Assume that

$$h : B \to B \text{ is a homeomorphism}$$

of the unit ball $B = \{ x \in \mathbb{R}^d : \|x\| \leq 1 \}$ which preserves the orientation. Assume also that all fixed points are on the boundary, $\mathrm{Fix}(h) \subset \partial B$.

Can we say that all orbits $h^n(p)$ must go to ∂B?



A single population

The size of the population at time $t \geq 0$ is

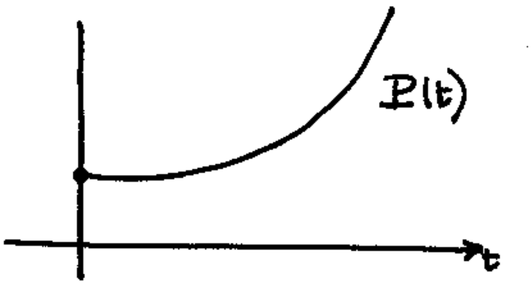
$$P = P(t) \geq 0$$

and the law of growth

$$\dot{P}(t) \sim P(t).$$

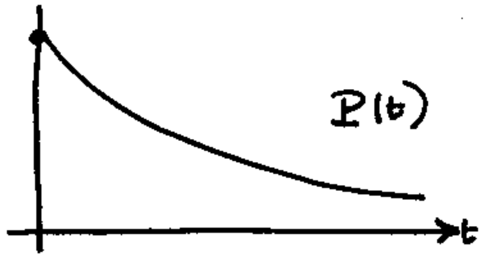
The simplest instance is $\dot{P} = \lambda P$ with $\lambda \in \mathbb{R}$ constant. This is Malthus' model. The quantity λ is related with the difference between the processes of birth and death

$\lambda > 0$



Malthusian growth

$\lambda < 0$



Extinction (radiactive disintigration)

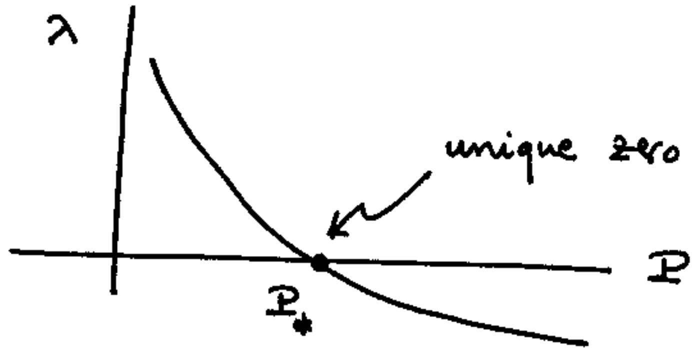
$\lambda = 0$

$P(t) =$ constant

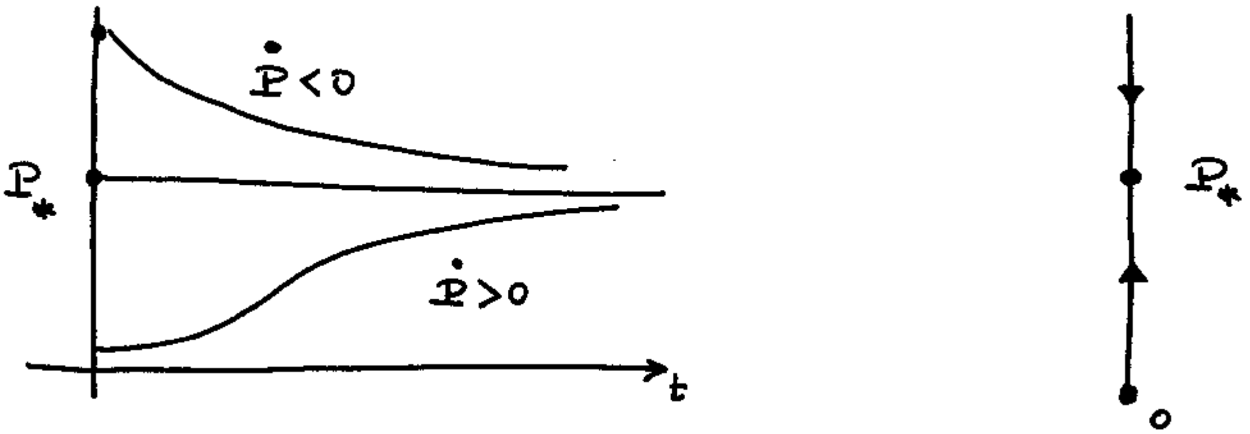
More sophisticated models take into account the limitations of the enviroment (resources are finite).

$$\dot{P} = \lambda(P)\, P$$

$\lambda : [0,\infty[\to \mathbb{R}$ decreasing, $\lambda > 0$ if P small,
$\lambda < 0$ if P large



Two equilibria $P \equiv 0$, $P \equiv P_*$



(We are assuming that λ satisfies conditions that guarantee uniqueness and existence for the initial value problem).

This class of models was initially considered by Verhulst (1838, 1845). He selected the simplest choice for λ,

$$\lambda(P) = a - bP, \quad a, b > 0,$$

arriving at the so-called logistic equation. Then he applied the model to some human populations. In particular he predicted that the Belgian population could never exceed 6.600.000 ($\equiv P_*$). This work was more or less forgotten. Around 1920 Pearl and Reed rediscovered the logistic equation. The model was then applied to Drosophila (fruit flies) showing a better agreement than with human populations. The next figure is taken from Lotka's book [Lotk], which appeared in 1924. For more information on Verhulst model the reader can go to [Maw].

Pearl, to an experimental population of fruit flies (Drosophila). In this case practically the entire range of the S-shaped curve defined by equation (12) is realized, and a glance at the plot in figure 5 shows that the agreement of the observed figures (represented by small circles) and the calculated curve is exceedingly satisfactory. Still closer is the agreement in the case of bacterial cultures studied

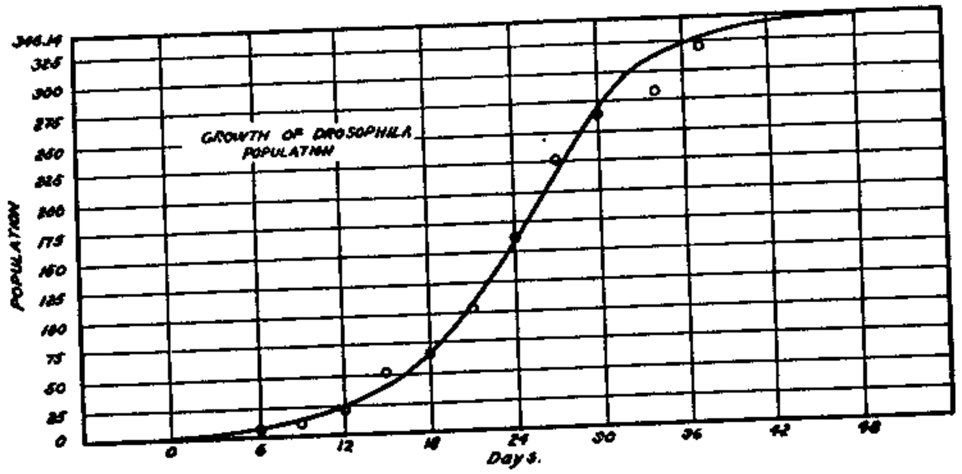
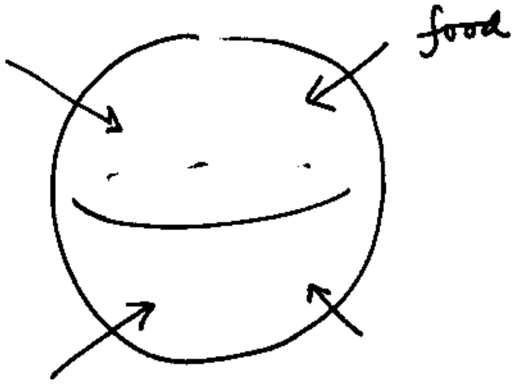


Fig. 5. Growth of a Population of Drosophila (fruit Flies) under Controlled Experimental Conditions, According to Pearl and Parker

To show another model with limited growth we consider a spherical cell. The logistic effect will be produced by the geometry: "the cell eats through the surface but waste energy in the whole volume".

The spherical shape is always preserved but the radius can change



$r = r(t)$ radius

$S(t) = 4\pi r(t)^2$

$V(t) = \frac{4}{3}\pi r(t)^3$

$$\dot{V} = f S - \nu V$$

$f > 0$ says how nutritive is the food

$\nu > 0$ measure the waste of energy per unit of volume

From $\gamma V^{2/3} = S$,

$$\dot{V} = f \gamma V^{2/3} - \nu V = V\left(f\gamma V^{-1/3} - \nu\right)$$

We can go back to the logistic model by taking the inverse of the radius as unknown, $\rho = \frac{1}{r}$,

$$\dot{\rho} = \rho\left(\frac{\nu}{3} - f\rho\right).$$

Seasonal effects

For many species the birth and death rates oscillate periodically along years according to the season. Probably winter will increase deaths while spring or summer may increase births. To model this effect we can assume that the function λ also depends upon time,

$$\lambda : \mathbb{R} \times [0, \infty[\longrightarrow \mathbb{R}, \quad \text{smooth enough}$$

$$\lambda(t+1, P) = \lambda(t, P)$$

$$\lambda(t, \cdot) \searrow$$

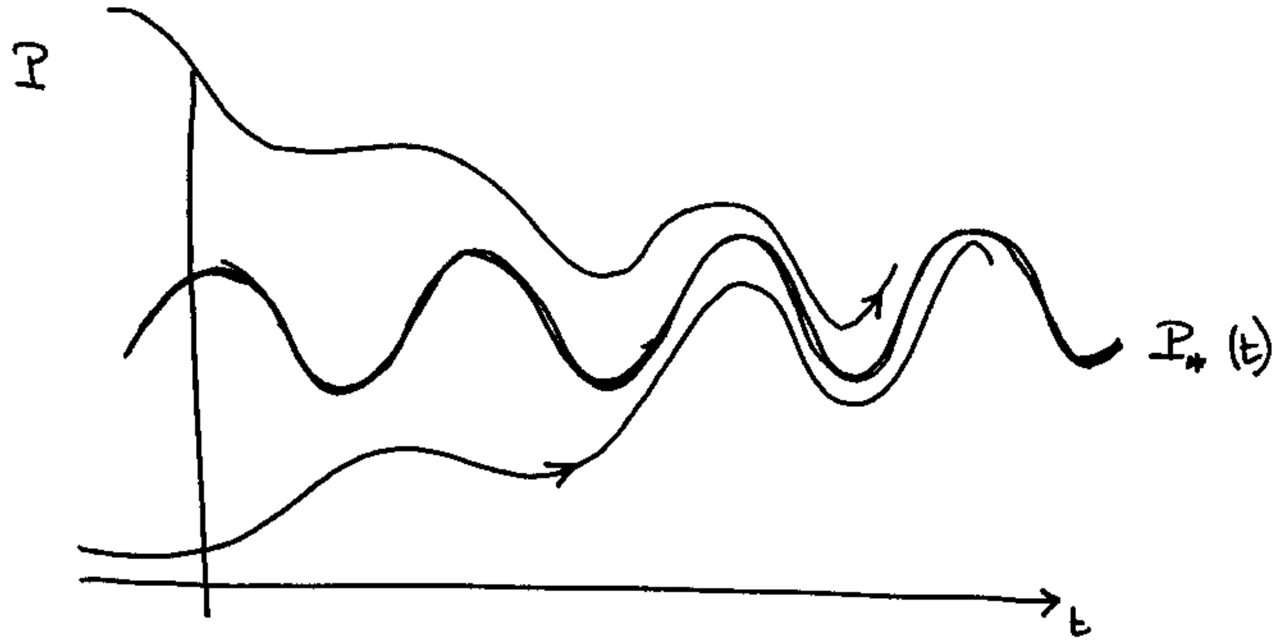
$$\int_0^1 \lambda(t, 0)\, dt > 0, \qquad \int_0^1 \lambda(t, +\infty)\, dt < 0$$

Example (logistic) $\quad \lambda(t, P) = (1 + \varepsilon \sin 2\pi t) - (2 + \varepsilon \cos 2\pi t) P$

It can be proved that the equation

$$\dot{P} = \lambda(t, P) P$$

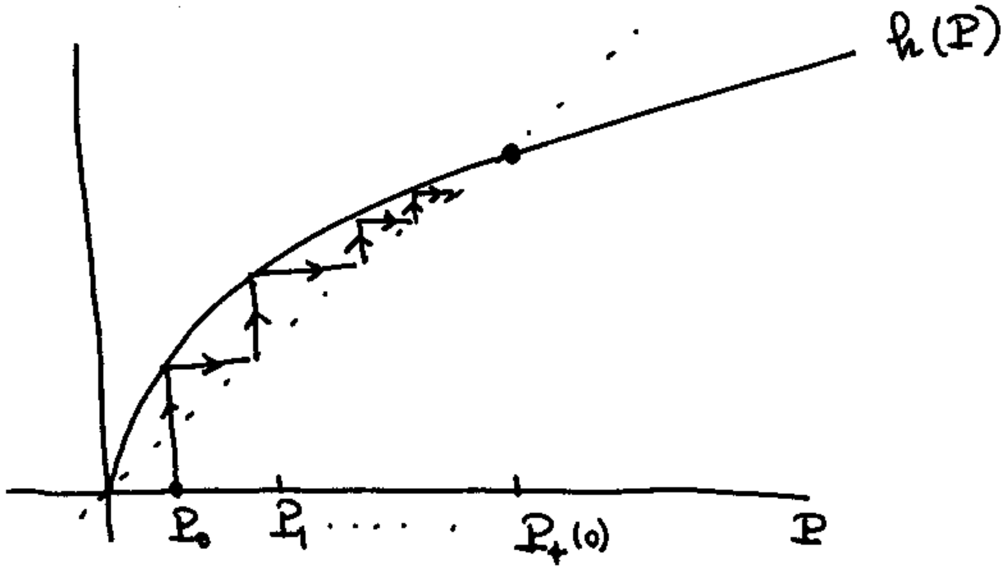
has a unique positive T-periodic solution which attracts all positive solutions [Season].



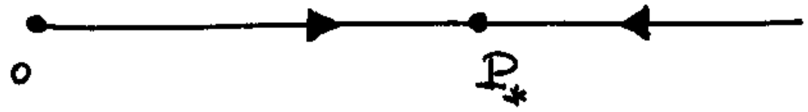
To understand the periodic model from another perspective we measure the size of the population once every year (say January 1st of year 0, 1, 2, ..) we obtain in this way a sequence $\{P_n\}$ which solves a difference equation

$$P_{n+1} = h(P_n)$$

where $h : [0,\infty[\to [0,\infty[$ is an increasing homeomorphism. This homeomorphism has two fixed points at $P=0$ and $P_*(0)$ and a graph of the type



To sum up we can say that the model of a population living in an enviroment with limited resources has the dynamics



Seasonal effects do not destroy this dynamics but change the dynamical system from continuous to discrete.

Interaction of several species : Competition models

Assume that

$$u = u(t) \geqslant 0, \quad v = v(t) \geqslant 0$$

measure the size of two different species competing for the same resources. They satisfy

$$\begin{cases} \dot{u} = \lambda(u,v)\,u \\ \dot{v} = \mu(u,v)\,v \end{cases}$$

where $\lambda, \mu : \mathbb{R}_+^2 \to \mathbb{R}$ are decreasing in each variable and are positive if $u+v$ is small and negative if $u+v$ is large. From now on, $\mathbb{R}_+ = [0,\infty[$.

The classical Lotka-Volterra competition model assumes

$$\lambda(u,v) = a - bu - cv$$
$$\mu(u,v) = d - eu - fv$$

where all the coefficients are positive. The interaction coefficients are c and e. They measure how harmful is each species for the other

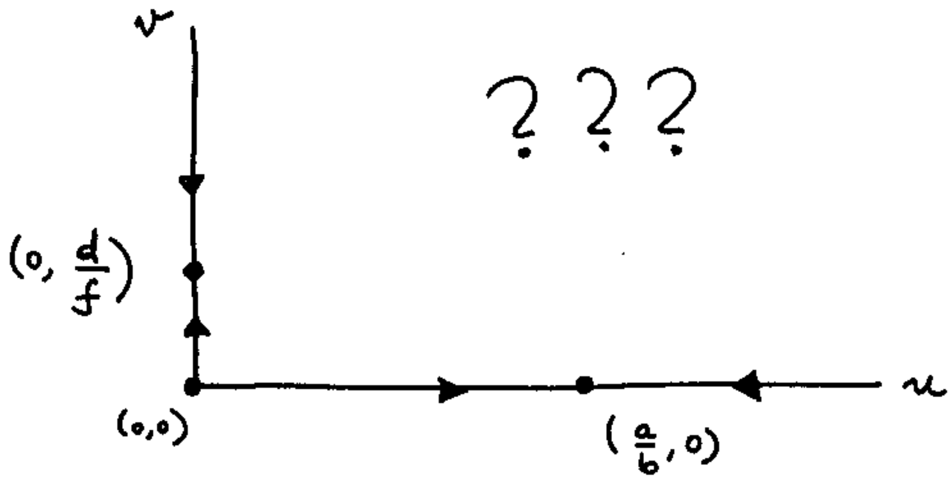
Notice that in the absence of one species ($v \equiv 0$) the other follow a logistic model, $\dot{u} = (a - bu)u$.

We are going to sketch the phase portrait on the phase space $\mathbb{R}^2_+$. This is the space of the orbits

$$\{ (u(t), v(t)) : t \in I \} \subset \mathbb{R}^2_+$$

where $u(t), v(t)$ is a maximal solution.

From previous discussions we know the behavior on $\partial \mathbb{R}^2_+$,

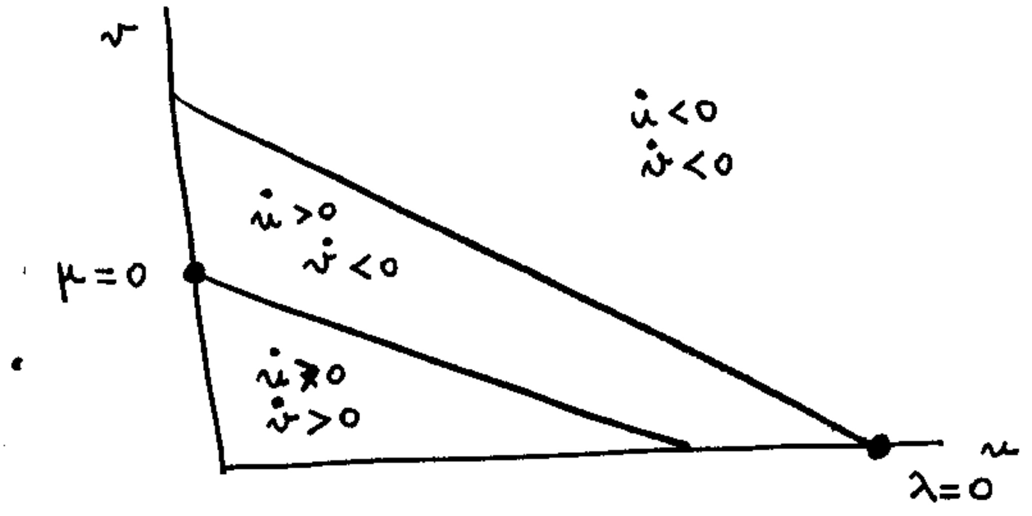


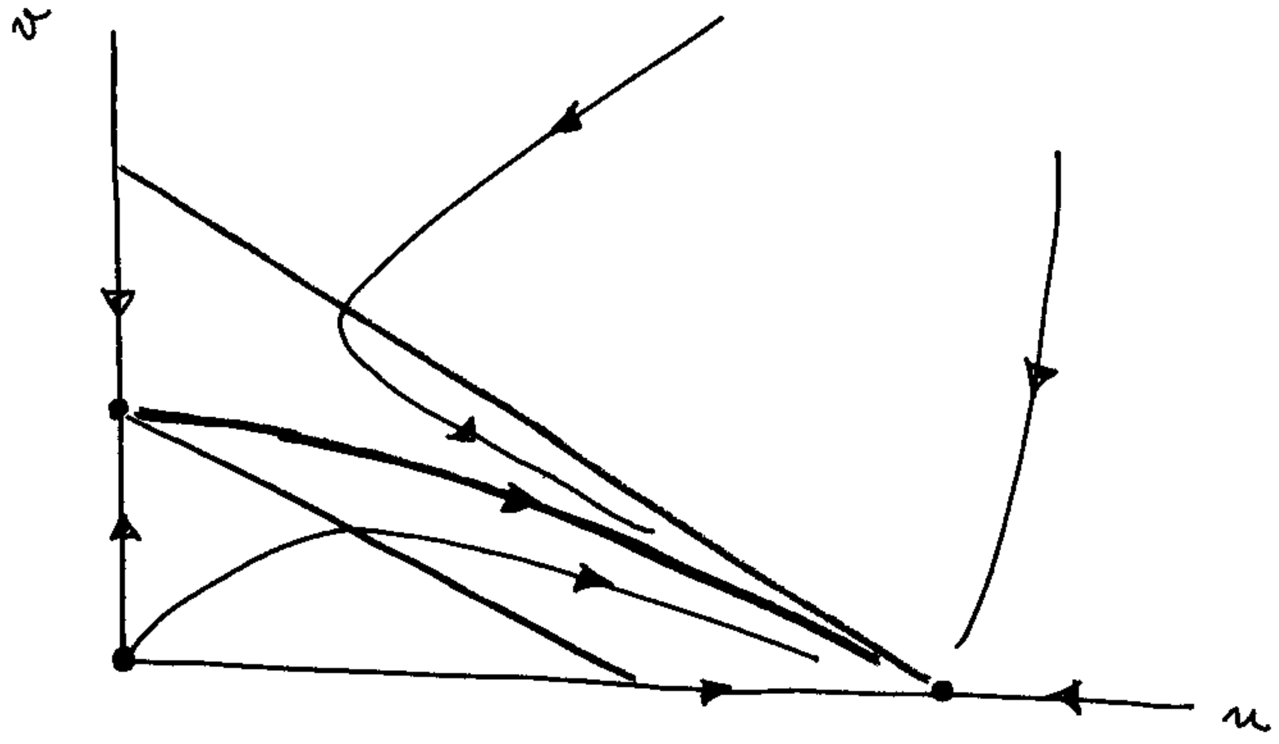
To understand the dynamics on int $(\mathbb{R}^2_+)$ we distinguish several cases depending on the position of the straight lines

$$\lambda = 0 \quad \text{and} \quad \mu = 0$$

We look at the sign of $\dot{u}$ and $\dot{v}$ in each region

i) The lines do not intersect in the first quadrant



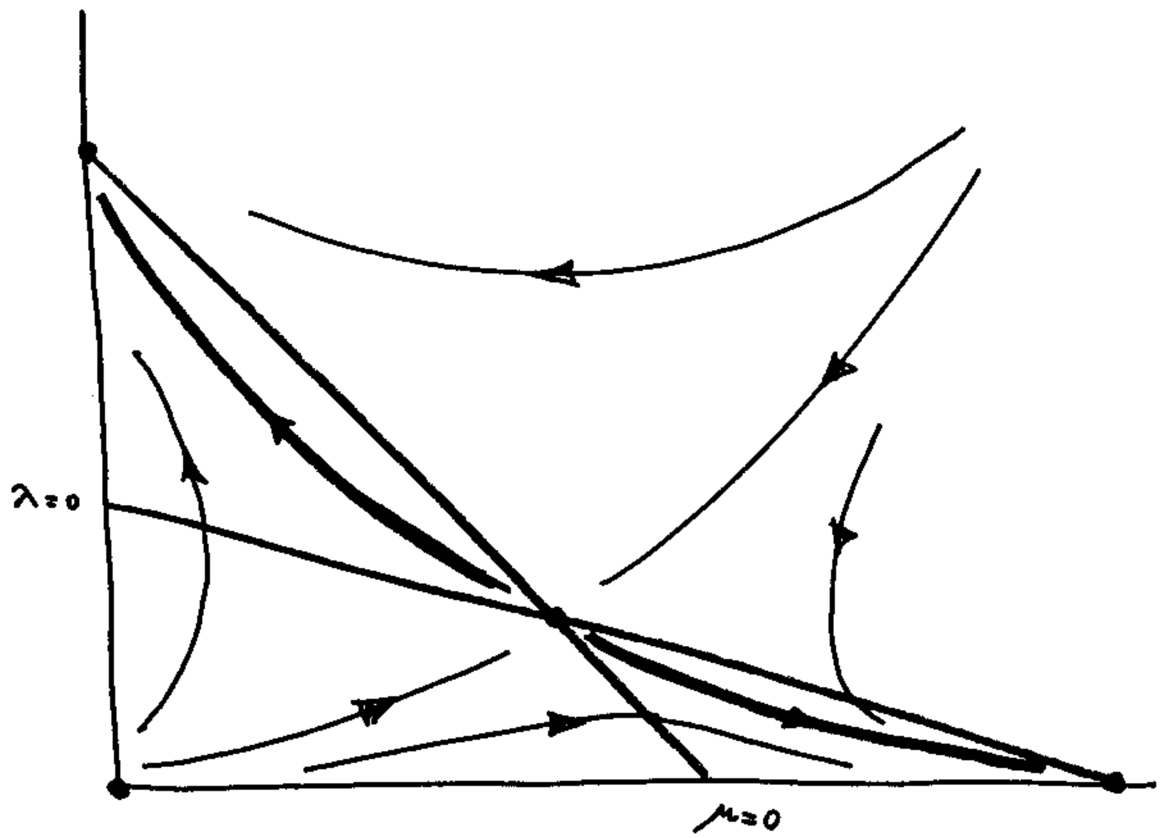


All positive orbits are attracted by the equilibrium $\left(\frac{a}{b}, 0\right)$.

u is the winner

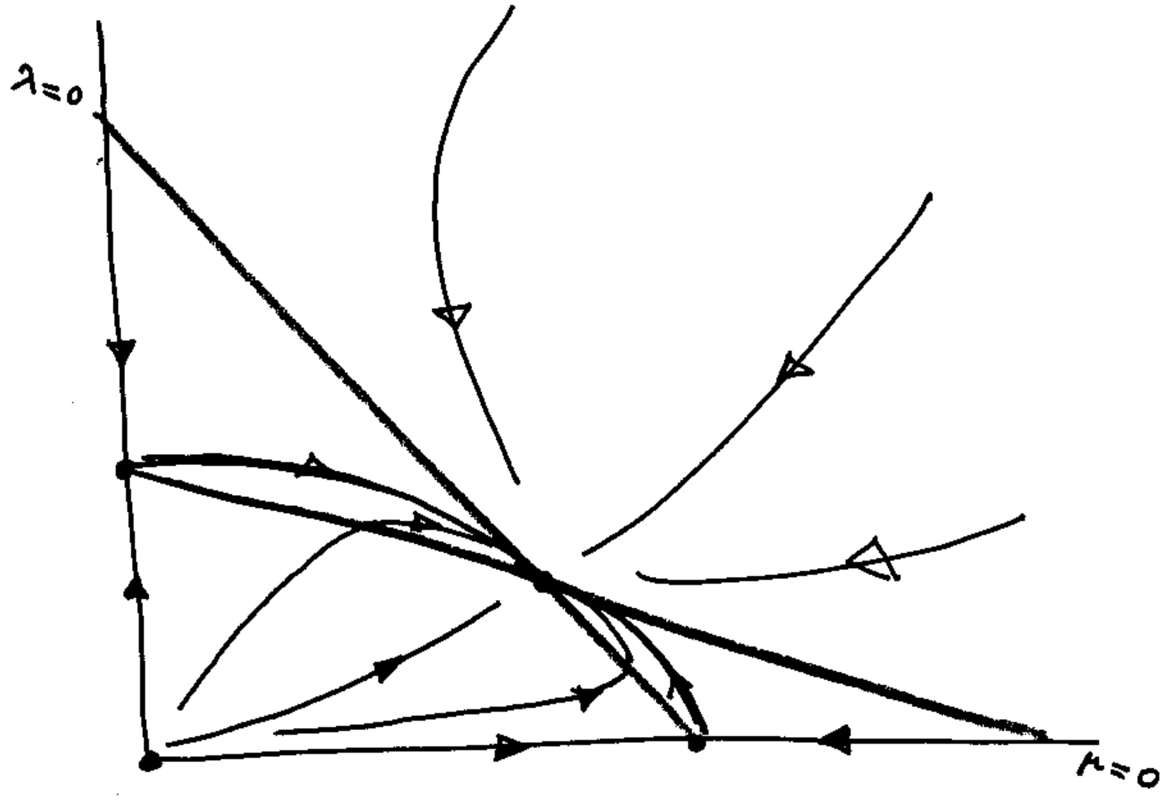
v dissapears

ii) The lines intersect at the first quadrant and equilibria are exterior



An equilibrium in int $(\mathbb{R}^2_+)$ (unstable coexistence). The stable manifold of this equilibrium divides the phase space in two regions, u or v can win depending on the region. Coexistence is almost impossible, only for initial conditions lying on the stable manifold

iii) The lines intersect at the first quadrant and equilibria are interior



The interior equilibrium is a global attractor, u and v will coexist

<u>Exercise</u> Draw the phase portrait when $\lambda = 0$ and $\mu = 0$ coincide.

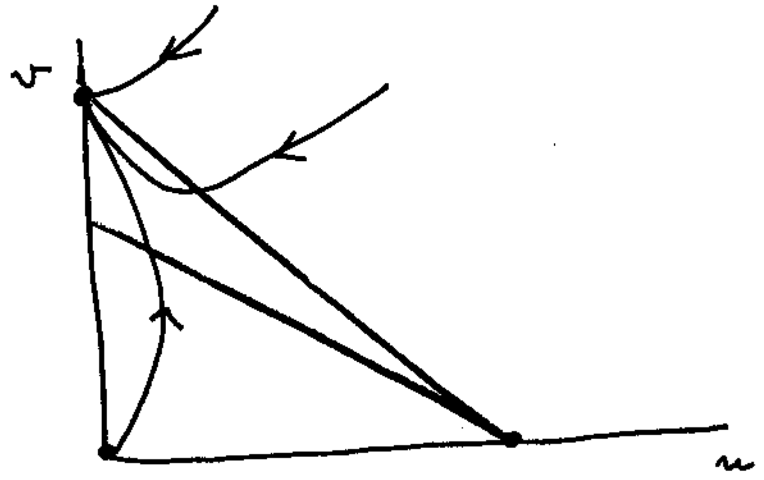
The reader who is not familiar with the qualitative theory of differential equations can find more details in [Murray], (Section 3.5) and in [Hirsch-Smale]. Also she (or he) can use the computer and some of the programs in the web to draw phase portraits

The previous model has been employed recently to explain the extinction in Europe of Neanderthal men [Flo]. It seems that they lived in Europe for more than 60.000 years, but they were replaced by the Early Modern men 40.000 years ago. The extinction took place in a period ranging between 5.000 and 10.000 years. The main assumption in [Flo] is that the parameters of the two species are the same excepting for the mortality rate, which is slightly larger in Neanderthal's case.

u = Neanderthal , v = Early Modern

$$\lambda(u,v) = \alpha - \beta u - \gamma v, \quad \mu(u,v) = \alpha - \gamma u - s\beta v$$

$$0.992 < s < 0.997$$



This is in agreement with the principle of competitive exclusion. It corresponds to the phase portrait of case i). In case ii) there is remote possibility of coexistence while in case iii) coexistence always occurr. In view of this we could formulate a more precise exclusion principle.

Assume that $u_1, \dots, u_N$ are different species competing for the same habitat. This means that they solve the system

$$\dot{u}_i = \lambda_i(u_1, .. u_N)\, u_i \,, \quad i = 1, .., N$$

where $\lambda_i : \mathbb{R}^N_+ \to \mathbb{R}$ is decreasing in each variable, positive if $\sum u_i$ small and negative if $\sum u_i$ large. In addition assume that there no coexistence equilibria (that is, constant solutions lying in $\operatorname{int}(\mathbb{R}^N_+)$).

Is it true that for some $i \in \{1, .., N\}$, $u_i(t) \to 0$ as $t \to +\infty$?

When we take into account the seasonal effects,

$\lambda_i = \lambda_i(t, u_1, .. u_N)$, $\quad \lambda_i(t+1, u_1 .. u_N) = \lambda_i(t, u_1, .. u_N)$

equilibria must be replaced by 1-periodic solutions lying in $\operatorname{int}(\mathbb{R}^N_+)$.

From differential equations to homeomorphisms

Consider the system

$$(*) \qquad \dot{u}_i = \lambda_i(t, u_1, \dots, u_N)\, u_i \;, \quad i = 1, \dots, N$$

defined on $\mathbb{R}^N_+$. It satisfies

(Λ_1) λ_i is continuous and 1-periodic in t and there is uniqueness for the initial value problem associated to $(*)$

(Λ_2) $\lambda_i(t, u_1, \dots, u_N)$ is strictly decreasing with respect to u_j for each i, j

(Λ_3) $\int_0^1 \lambda_i(t, 0)\, dt > 0 \,, \quad \int_0^1 \lambda_i(t, Re_i)\, dt < 0$

for some $R > 0$ and $i = 1, \dots, N$. Here $\{e_1, \dots, e_N\}$ is the canonical basis of $\mathbb{R}^N$.

The assumption (Λ_1) is standard in the theory of differential equations. The uniqueness just says that the system is deterministic. The assumption (Λ_2) says that the system is competitive while (Λ_3) reflects the logistic character of each species in absence of competitors.

Extinction means that every solution of $(*)$ satisfies

$$\lim_{t \to +\infty} u_i(t) = 0$$

for some $i \in \{1, \dots, N\}$. Notice that the index i can change with the solution.

A coexistence state means ~~the~~ a 1-periodic solution of (*) lying in $\mathrm{int}(\mathbb{R}^N_+)$.

Given $p \in \mathbb{R}^N_+$, $u(t,p)$ is the solution of (*) satisfying $u(0) = p$. Experts in differential equations can proved easily that this solutions are defined in intervals of the type $]\alpha, +\infty[$ where $-\infty \leq \alpha = \alpha(p) < 0$.

Next we consider the map

$$h : \mathbb{R}^N_+ \longrightarrow \mathbb{R}^N_+ , \quad h(p) = u(1,p)$$

which tells us the size of the population after one period. To understand the dynamics of (*) it is sufficient to look at the difference equation

$$p_{n+1} = h(p_n).$$

We can construct a dictionary differential equation / map h,

1 - periodic solution $\longleftrightarrow$ fixed point of h

coexistence state $\longleftrightarrow$ fixed point in $\mathrm{int}(\mathbb{R}^N_+)$

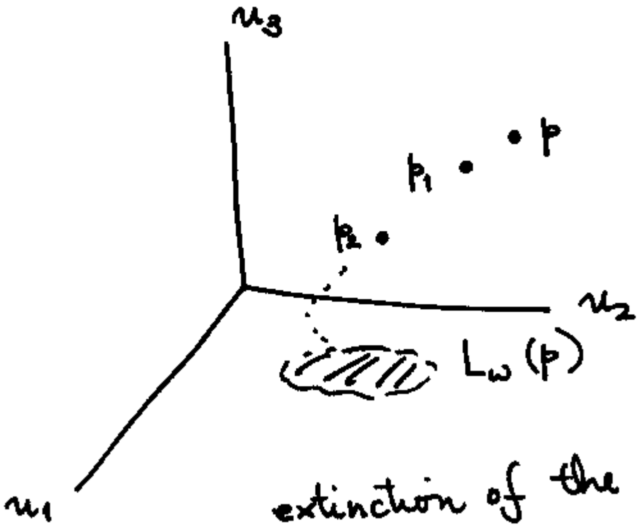
Extinction $\longleftrightarrow$ For each $p \in \mathbb{R}^N_+$ there exists $i \in \{1, \ldots, N\}$ such that $L_\omega(p) \subset \{u_i = 0\}$

. . . . .

Here $L_\omega(p)$ denotes the ω-limit set

$$L_\omega(p) = \{ q \in \mathbb{R}^N_+ : \exists \{n_k\} \to \infty,\ h^{n_k}(p) \to q \}.$$

Our main question can be reformulated:
Assume $Fix(h) \subset \partial \mathbb{R}^N_+$, can we say that every ω-limit set lies in a face of $\partial \mathbb{R}^N_+$?



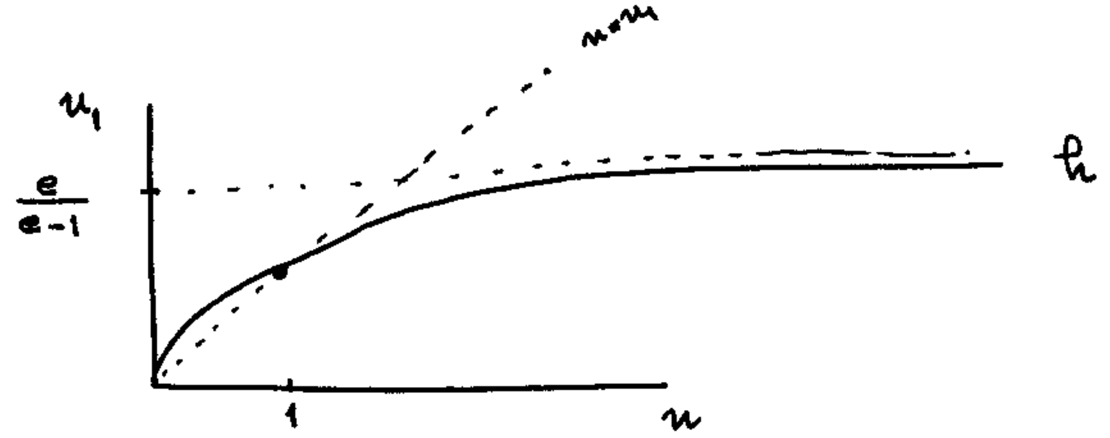
extinction of the 3^{rd} species

Next we state some useful properties of the map h. For the proofs we refer to [[redacted]] and to [OT], [COT].

1) $h : \mathbb{R}^N_+ \to \mathbb{R}^N_+$ is one-to-one, continuous and orientation-preserving

It is important to notice that sometimes h is not onto. For example, if $N=1$, $\lambda_1(t,u) = (1-u)$,

$$u(t,p) = \frac{p}{p + (1-p)e^{-t}} \quad \text{and} \quad h(\mathbb{R}_+) = [0, \frac{1}{1-e^{-1}}[$$

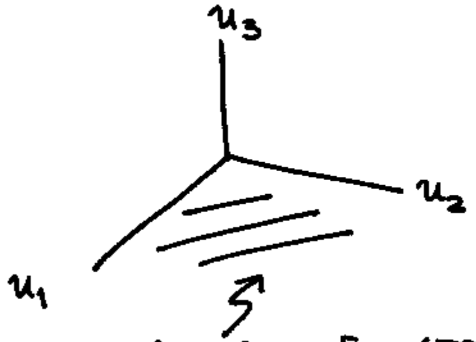


We employ the notation $\mathcal{U} = h(\mathbb{R}^N_+)$.

2) For each non-empty subset I of $\{1, \dots, N\}$ we consider $E_I = \{x \in \mathbb{R}^N_+ : x_i = 0, i \in I\}$.

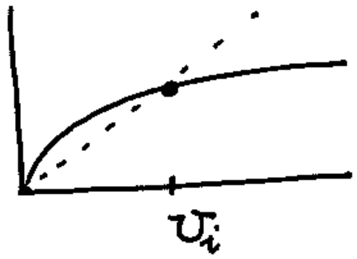
Then $h(E_I) \subseteq E_I$.

$N = 3$, $I = \{1, 2\}$

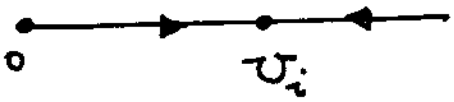


this face E_I corresponds to a subsystem where the third species is not present

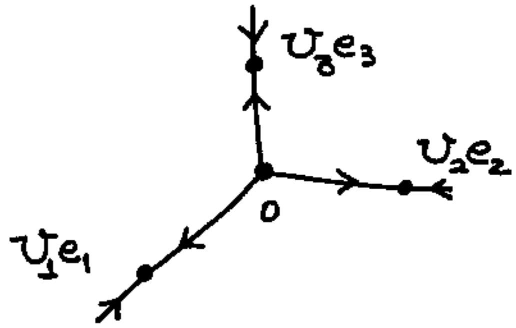
3) When I is a singleton, $I = \{i\}$, the restriction of h, $h_I : E_I \to E_I$, has a graph of the type



and so the dynamics on E_I is of the type



This just say that every species is of logistic type in the absence of the others. In particular h has always at least $N+1$ fixed points



It can be proved that the box

$$B := [0, v_1] \times \dots \times [0, v_N]$$

is contained in $\mathcal{U}$.

~~4) Given $p, p^* \in \mathbb{R}^N_+$ with $p \lneq p^*$ then p~~

4) Given $p, \hat{p} \in \mathbb{R}^N_+$ with $p \lneq \hat{p}$ and $\hat{p} \in \mathcal{U}$, then $p \in \mathcal{U}$ and

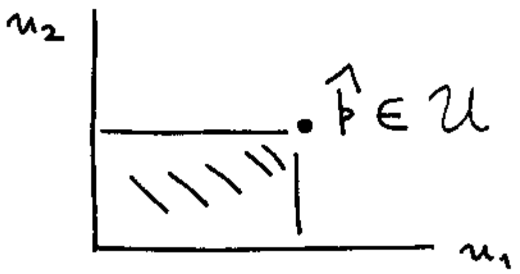
$$h^{-1}(p) \ll h^{-1}(\hat{p}).$$

Here we are employing the following notations about the partial ordering in $\mathbb{R}^N$,

$$p \lneq \hat{p} \quad \text{means} \quad \hat{p} - p \in \mathbb{R}^N_+, \; p \neq \hat{p}$$

$$p \ll \hat{p} \quad \text{means} \quad \hat{p} - p \in \operatorname{int}(\mathbb{R}^N_+)$$

The set $\mathcal{U}$ has a very special geometry

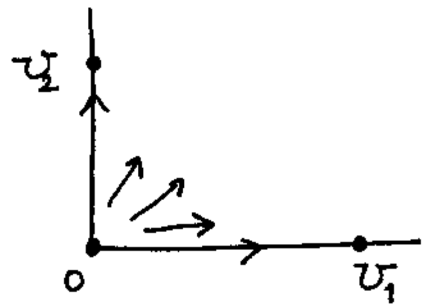


The ~~re~~ monotonicity of h^{-1} is related to the competitive character of the system. To understand this it is convenient to think first about cooperative species. In this case h should be increasing (the more initial population, the better after one year). Next we can ~~think that~~ see a competitive system as a cooperative system with the reversed time. Indeed, if we would make a movie of the evolution of two competing species and then show it from the end to the beginning, it would seem that the species are cooperative.

5) The origin is a repeller: there exists $r>0$ such that if $\|p\|<r$ then $\{h^{-n}(p)\}_{n\geq 0}$ is well defined and

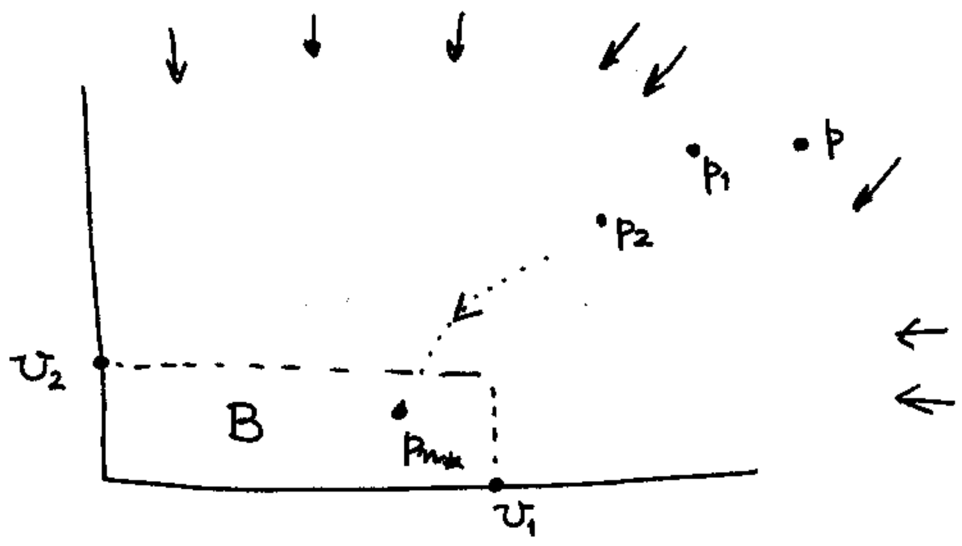
$$\lim_{n\to\infty} h^{-n}(p)=0$$

uniformly in $\|p\|<r$.



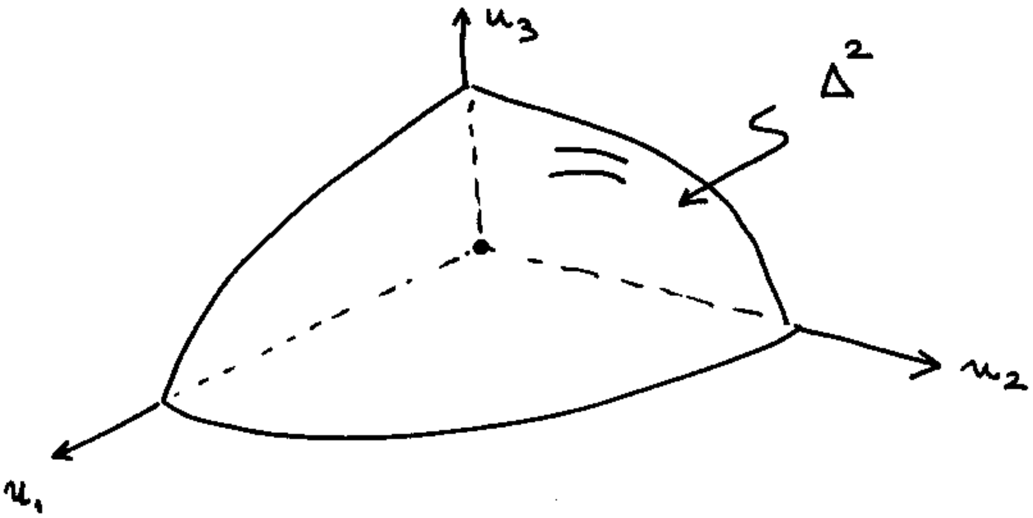
when the total population is small there are enough resources and it grows

7) ∞ is a repeller. For each $p \in \mathbb{R}^N_+$ there exists $n_* = n_*(p)$ such that $h^n(p) \in B$ if $n \geq n_*$



Reduction of dimension: the carrying simplex

In principle a competitive system leads to a dynamical system in $\mathbb{R}^N_+$, where N is the number of species. M. W. Hirsch observed in [H] that these systems always contain an invariant cell of dimension N-1 (the carrying simplex) which is invariant and attracts all the orbits of the system



Therefore it is enough to understand the dynamics on Δ and so the dimension is reduced in one unity. Previously Smale [Sm] had made an interesting observation which can be thought as a sort of converse for autonomous competitive systems. He considered the linear simplexes

$$\Delta_1 = \{ x \in \mathbb{R}^N_+ \mid \sum_1^N x_i = 1 \}$$

and

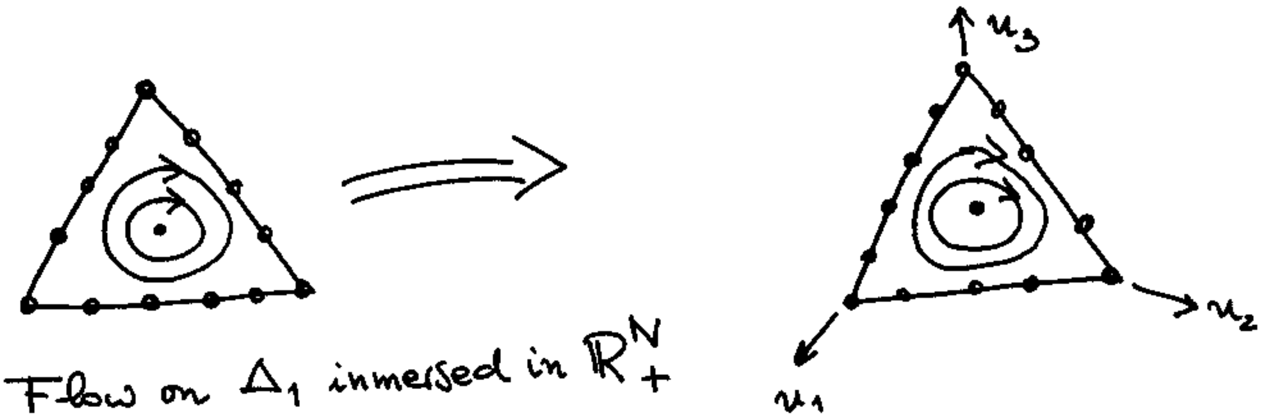
$$\Delta_0 = \{ x \in \mathbb{R}^N_+ \mid \sum_1^N x_i = 0 \}$$

and an arbitrary C^∞ vector field $h : \Delta_1 \to \Delta_0$.
Then it is possible to construct a C^∞-system

$$\dot{u}_i = \lambda_i(u_1 \cdots u_N) u_i$$

satisfying (Λ_2) and (Λ_3) and such that Δ_1 is a global attractor with dynamics governed by

$$\dot{x} = (x_1 \cdot x_2 \cdot \ldots \cdot x_N) h_0(x), \quad x \in \Delta_1$$

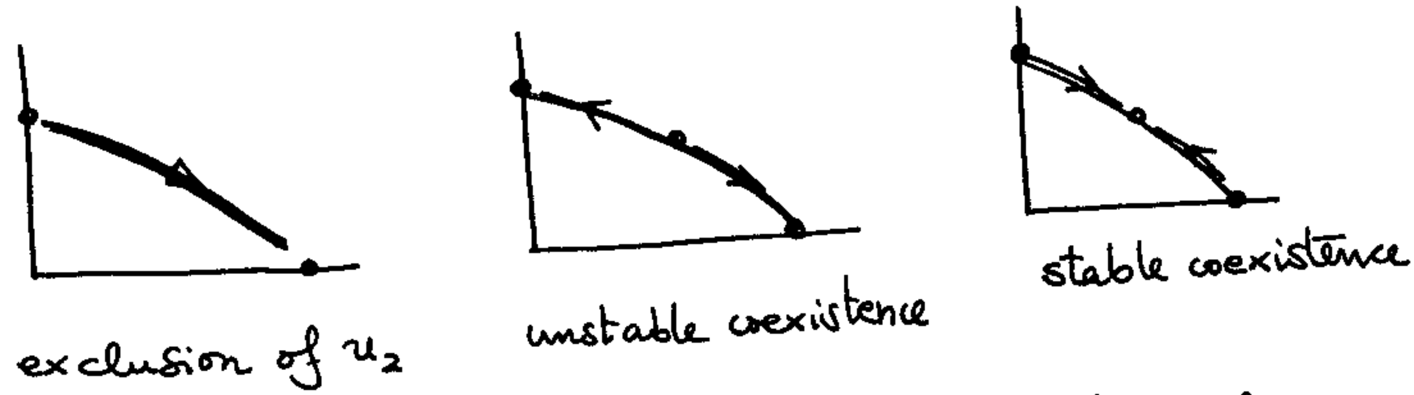


Flow on Δ_1 inmersed in $\mathbb{R}^N_+$

Roughly speaking Smale's result says that any dynamics in $\mathbb{R}^{N-1}$ can be realized as a competitive system of N species. It must be noticed that in Smale's construction all the points on $\partial\Delta_1$ are equilibria. This is due to the term $x_1 \cdot x_2 \cdots x_N$.

The rest of this lesson will be devoted to understand the construction of the carrying simplex. Besides [H] there are constructions with some variants in [Smith], [OT] and [WangJ].
Before doing this it is interesting to go back to the competitive autonomous systems in the plane

and identify the carrying simplex in each situation



If we recall the dynamics outside Δ^1 we observe that this arc Δ^1 is the boundary of the region of repulsion of the origin. This will be valid in the general case.

From now on we work with the map

$$h : \mathbb{R}^N_+ \longrightarrow \mathbb{R}^N_+$$

satisfying properties 1)-6). Since h is not necessarily onto some orbits may be undefined for the past. Given $p \in \mathbb{R}^N_+$ the orbit is denoted by

$$\{ h^n(p) \}_{n \in I_p}$$

where $I_p = \mathbb{Z}$ or $I_p = \{ n \in \mathbb{Z} : n \geq \alpha \}$ with $\alpha = \alpha(p) \leq 0$. In view of 6) all orbits are bounded in the future (they enter into B) but they can be undefined or unbounded in the past. We define the set of bounded orbits

$$\Sigma = \{ p \in \mathbb{R}^N_+ : I_p = \mathbb{Z} \text{ and } \sup_{n \in \mathbb{Z}} \| h^n(p) \| < \infty \}$$
$$= \{ p \in \mathbb{R}^N_+ : I_p = \mathbb{Z} \text{ and } \sup_{n \leq 0} \| h^n(p) \| < \infty \}.$$

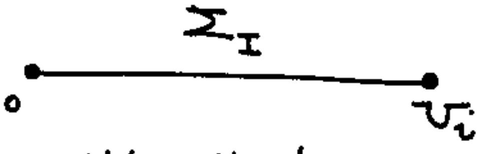
Given $I \subset \{1, .., N\}$, $I \neq \phi$, we apply 2) and obtain the restriction to the face

$$h_I : E_I \longrightarrow E_I .$$

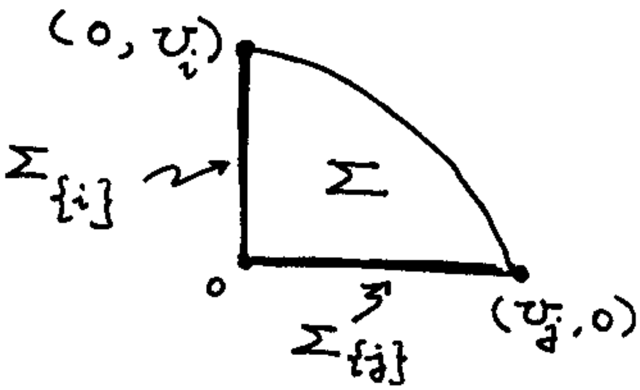
This is the Poincaré map of the restricted system, when the competitors u_i, $i \in I$, have disappeared. Hence the map h_I enjoys the properties 1) to 6). The set Σ_I has an obvious meaning and we observe that, by the invariance of E_I under h_I,

$$\Sigma_I = \Sigma \cap E_I .$$

From property 3) we observe that if $I = \{i\}$ then Σ_I is a segment



We draw a possible situation with two species



The boundary of Σ (relative to $\mathbb{R}^N_+$) will be denoted by Δ. The next result describes Δ (it is an $N-1$ cell) and its dynamical properties.

<u>Theorem</u> The map

$$q \in \Delta \mapsto \frac{q}{\|q\|} \in \Delta_1$$

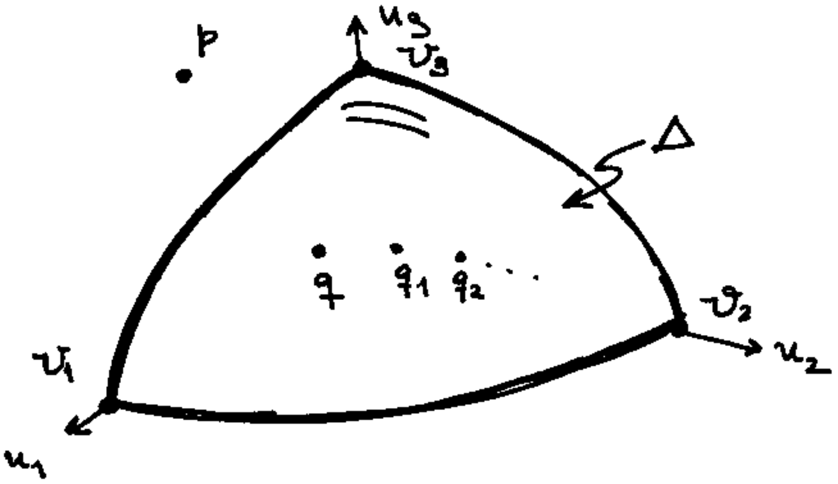
is a homeomorphism. Moreover Δ is invariant under h, $h(\Delta) = \Delta$, and given $p \in \mathbb{R}^N_+ - \{0\}$ there exists $q \in \Delta$ such that

$$h^n(p) - h^n(q) \longrightarrow 0 \text{ as } n \to +\infty.$$

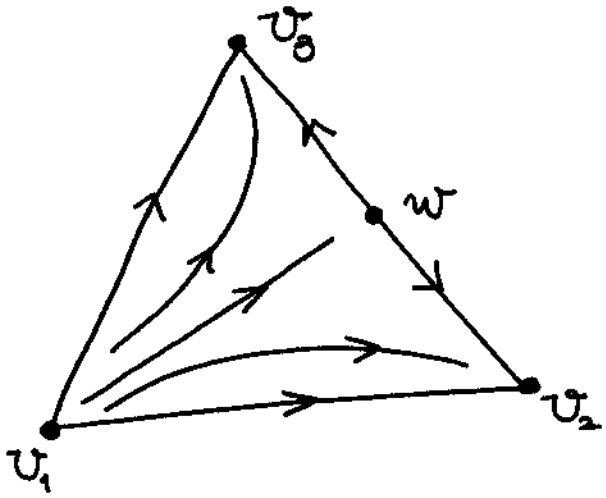
(Recall that $\|x\| = \sum_1^N |x_i|$ and

$$\Delta_1 = \{x \in \mathbb{R}^N_+ : \|x\| = 1\}).$$

We observe that, in particular, the limit set $L_\omega(p)$ of any $p \in \mathbb{R}^N_+ - \{0\}$ is contained in the carrying simplex Δ.



As an example we can imagine that the dynamics on the carrying simplex is



In this case there are no coexistence states and u_1 will dissapear. Depending on the initial condition it may hapen that u_2 or u_3 also disappear or they can coexist at the fixed point $w = (0, w_2^*, w_3^*)$.

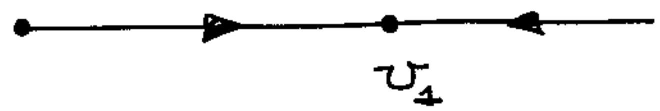
The proof of the Theorem will be obtained after studying the properties Σ. We will need some extra properties of h. They are summed up in the next lemma. Their proof uses some elementary facts of differential equations and we refer to Propositions 2.5 and 2.7 in [OT].

<u>Lemma</u> Given $p, q \in \mathbb{R}^N_+ - \{0\}$ the following properties hold,

i) $p \lneqq q$, $q \in \Sigma \Longrightarrow I_p = \mathbb{Z}$ and $h^{-n}(p) \to 0$ as $n \to +\infty$

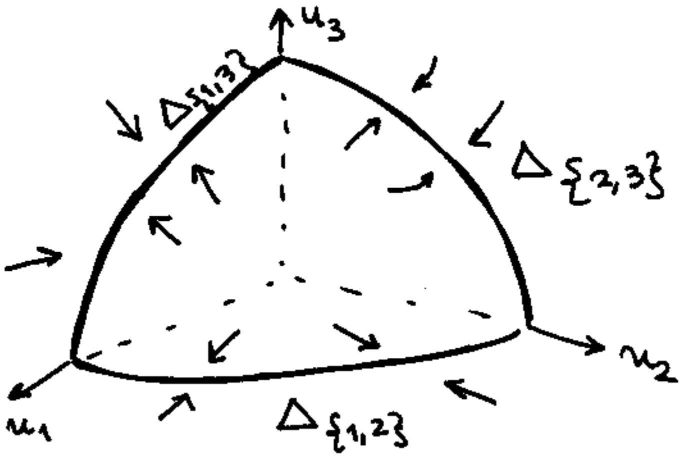
ii) $\exists n_0 : n \geq n_0$, $h^n(p) \leq h^n(q) \Longrightarrow h^n(p) - h^n(q) \to 0$ as $n \to +\infty$.

Proof of the theorem It will be obtained by induction on the dimension N. We observe that for $N=1$ the result follows from the dynamics



$$\Sigma = [0, U_1], \quad \Delta = \{U_1\}.$$

From now on we assume that the result is valid in dimension $\leq N-1$. In particular, for each $I \subset \{1, .., N\}$ with no more than $N-1$ elements the result hold when $\Delta_I = \partial_{E_I} \Delta_I$.



"The dynamics on the faces is known by induction"

Next we describe some properties of Σ.

(i) $h(\Sigma) = \Sigma$

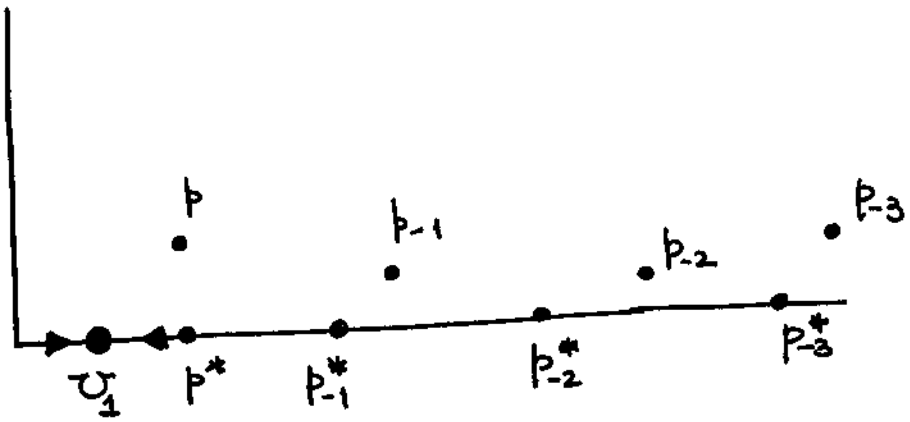
This is a direct consequence of the defintion of Σ.

(ii) $\Sigma \subset B = [0, U_1] \times .. \times [0, U_N]$

Assume that $p \in \mathbb{R}^N_+$ is such that, for some i, $p_i > v_i$. Then $p \geq p^* = (0, \dots 0, \overset{i}{p_i}, 0 \dots 0)$ and we deduce from 4) that

$$h^{-n}(p^*) \leq h^{-n}(p), \quad n \geq 0$$

as long as $h^{-n}(p)$ is well defined. From 3) we know that either $h^{-n}(p^*)$ is undefined for some n or $h^{-n}(p^*) \to +\infty$. This shows that p cannot belong to Σ.



(iii) Σ is closed

Assume that $p_m \in \Sigma$, $p_m \to p$. From the previous steps we know that

$$h^{-n}(p_m) \in B \quad \text{for each } m, n \geq 0.$$

Letting $m \to \infty$ we deduce that also $h^{-n}(p) \in B$ for each $n \geq 0$. ~~Since $\mathcal{U} = h(\mathbb{R}^N_+)$ contains B~~

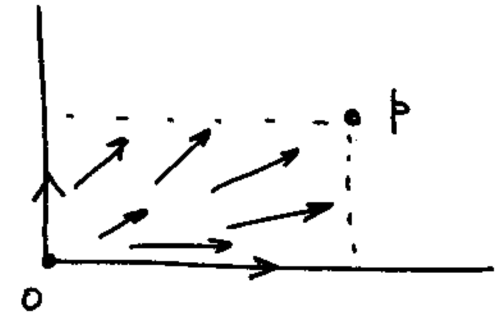
This reasoning is only correct if we know that $h^{-n}(p)$ is well defined. This is achieved by induction since $\mathcal{U} = h(\mathbb{R}^N_+)$ contains B.

At this moment we know that Σ is compact. Hence $h: \Sigma \to \Sigma$ is a homeomorphism and so Δ is invariant under h.

Next we introduce a subset of Σ which will play an important role. It is the region of repulsion of the origin

$$\mathcal{R} = \{ p \in \mathbb{R}^N_+ : I_p = \mathbb{Z} \text{ and } h^{-n}(p) \to 0 \text{ as } n \to +\infty \}.$$

In view of 5) we can say that $\mathcal{R}$ is an open set (relative to $\mathbb{R}^N_+$) which contains the origin. Let us recall the first part of the Lemma, it says that all the points below $p \in \Sigma$ lie in $\mathcal{R}$



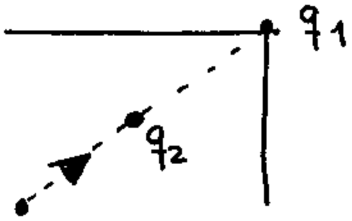
We are ready to prove that $q \mapsto \frac{q}{\|q\|}$ is one-to-one on Δ. By a contradiction argument assume that

$$q_1, q_2 \in \Delta, \quad \frac{q_1}{\|q_1\|} = \frac{q_2}{\|q_2\|} = w \in \Delta_1 \text{ and } q_1 \neq q_2.$$

Say $q_1 = \lambda_1 w$, $q_2 = \lambda_2 w$, $\lambda_1 > \lambda_2$. We distinguish two cases:

i) $w \in \partial \mathbb{R}^N_+$. Then $q_1, q_2 \in \Delta_I$ for some proper subset $I \subset \{1,..,N\}$. By induction it is not possible.

ii) $w \gg 0$. Then $q_1 \gg q_2$ and since $q_1 \in \Sigma$ we deduce that $q_2 \in \mathcal{R}$. Thus $h^{-n}(q_2) \to 0$ as $n \to \infty$. This is a contradiction since Δ is invariant.



(Indeed this distinction of cases is not needed).

Next we prove that $q \mapsto \frac{q}{\|q\|}$ maps Δ onto Δ_1. Given $r \in \Delta_1$ we observe that, for small $\varepsilon > 0$, $\varepsilon r \in \mathcal{R} \subset \Sigma$. In consequence there exists $\varepsilon_* > 0$ such that $\varepsilon_* r \in \Delta$. This is the point which is mapped into r.

Finally we are going to prove the attractivity property. Given $p \in \mathbb{R}^N_+ - \Sigma$ we define, for each $n \geq 1$,

$$K_n = \{ q \in \Delta : h^n(q) \leq h^n(p) \}.$$

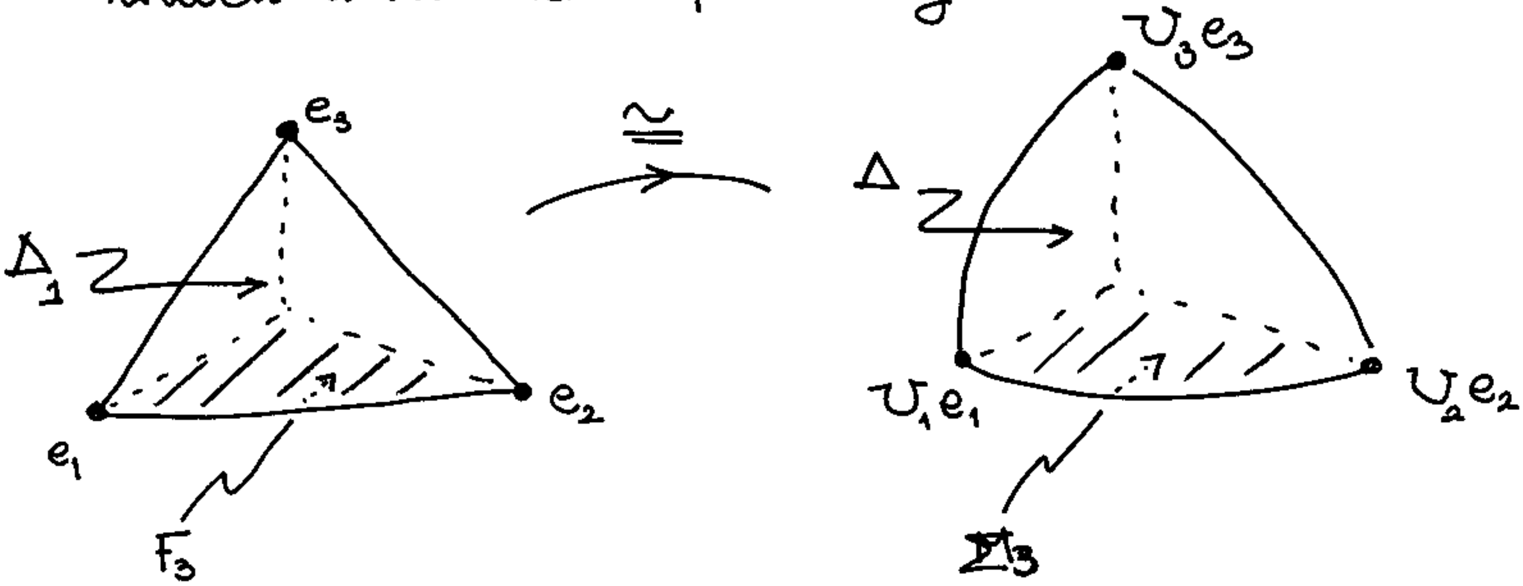
The set K_n is non-empty since $h^n(p)$ is outside Σ. Moreover, $K_{n+1} \subseteq K_n$ and so we have a decreasing sequence of compact sets. Any point q in $\bigcap_n K_n$ satisfies $h^n(q) \leq h^n(p)$, $n \geq 0$, and so $h^n(q) - h^n(p) \to 0$.

The map on the carrying simplex and a reformulation of the exclusion principle

Assume that we are given a competitive system and we have constructed the carrying simplex Δ. The restriction of h to the simplex will be denoted by

$$h_\Delta : \Delta \longrightarrow \Delta .$$

We observe that h_Δ is a homeomorphism, since it is byective and continuous on the compact space Δ. An important property of h_Δ is that it preserves orientation. To justify this we observe that Δ can be immersed on a topological manifold $M \cong \mathbb{S}^{N-1}$ and h_Δ admits an extension to M which is orientation preserving



We first recall that

$$\Delta \longrightarrow \Delta_1 \, , \; p \longmapsto \frac{p}{\|p\|}$$

is a homeomorphism and $\mathrm{int}_{\mathbb{R}^N_+}(\Sigma)$ is the bounded component of $\mathbb{R}^N_+ - \Delta$.

The inverse
$$\Delta_1 \longrightarrow \Delta, \; \xi \longmapsto \Psi(\xi)\xi$$

with $\Psi : \Delta_1 \longrightarrow]0,\infty[$ continuous.

For each $i \in \{1,..,N\}$ define
$$F_i = \{ \xi \in \mathbb{R}^N_+ : \xi_i = 0 \, , \; \|\xi\| \leq 1 \}.$$

The map
$$\xi \in F_i \longmapsto \Psi\left(\frac{\xi}{\|\xi\|}\right)\xi \in \Sigma_{\{i\}}$$

is a homeomorphism and so

$$M = \Delta \cup \Sigma_{\{1\}} \cup .. \cup \Sigma_{\{N\}}$$

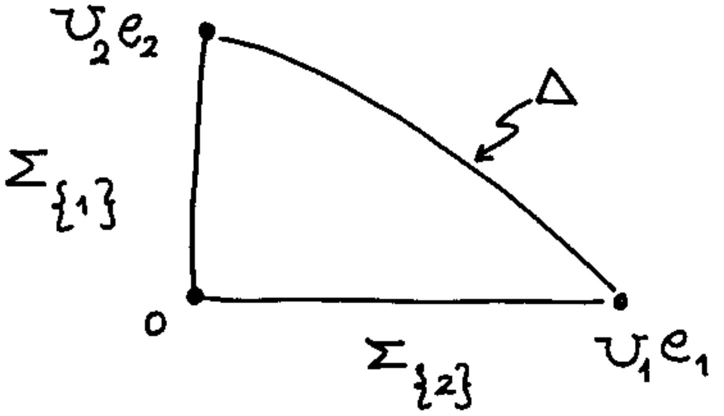
is a topological sphere. Now we observe that

$$h : M \longrightarrow M$$

is a homeomorphism extending h_Δ.

Moreover $h_{\{i\}}$ is orientation-preserving as a homeomorphism of $\Sigma_{\{i\}}$. Indeed it is the Poincaré map of a competitive system with N-1 species and hence isotopic to the identity.

The idea of the previous proof is taken from [Campos].

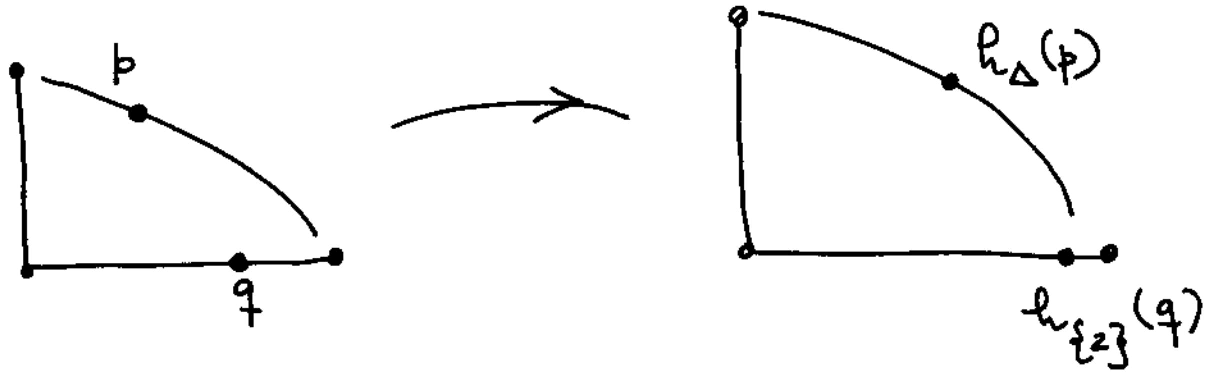


$\cong \mathbb{S}^1$

$h_{\{i\}}$ orientation-preserving

$$\Downarrow$$

h_Δ orientation-preserving



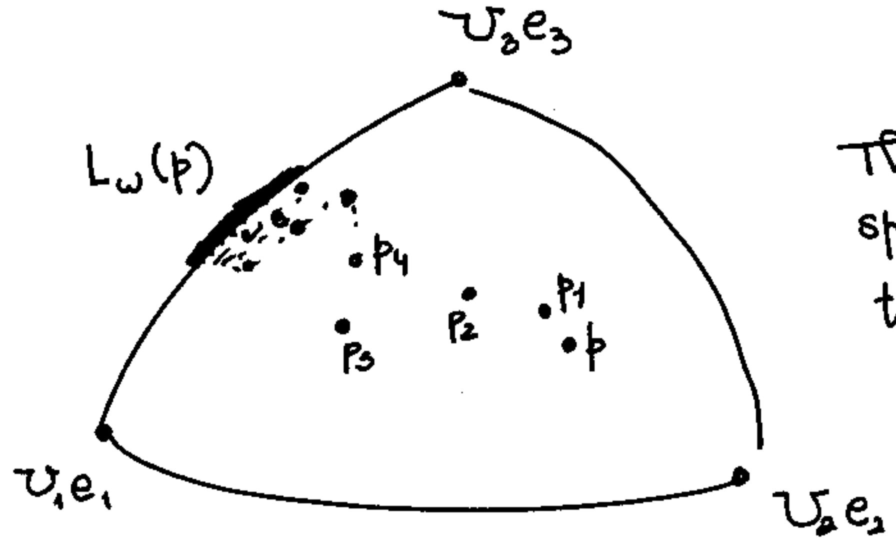
The exclusion principle can now be described as follows, given:

$h_\Delta : \Delta \longrightarrow \Delta$ orientation-preserving homeomorphism

with

$\mathrm{Fix}(h_\Delta) \subset \partial\Delta$ Non-existence of coexistence states,

Can we say that for each $p \in \Delta$ the limit set $L_\omega(p)$ lies in $\partial\Delta \cap \{u_i = 0\}$ for some i?



The second species goes to extinction

Notice that i can depend upon p (The looser ~~will~~ may depend upon initial conditions)

A result in abstract dynamics

$$B = \{ x \in \mathbb{R}^d : \|x\| \leq 1 \}$$

$h : B \to B$ orientation-preserving homeomorphism

$$\mathrm{Fix}(h) \subset \partial B$$

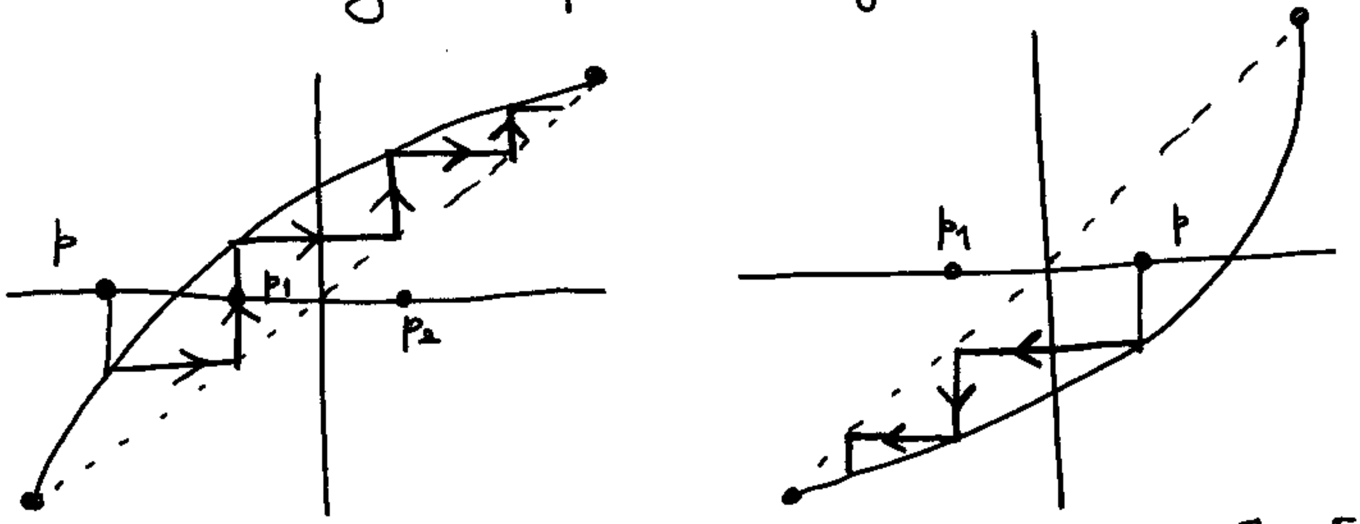
What can be said about the dynamics of h?

Dimension $d = 1$

$B = [-1, 1]$, $h : [-1,1] \to [-1,1]$ continuous and increasing

$$\mathrm{Fix}(h) = \{-1, 1\}$$

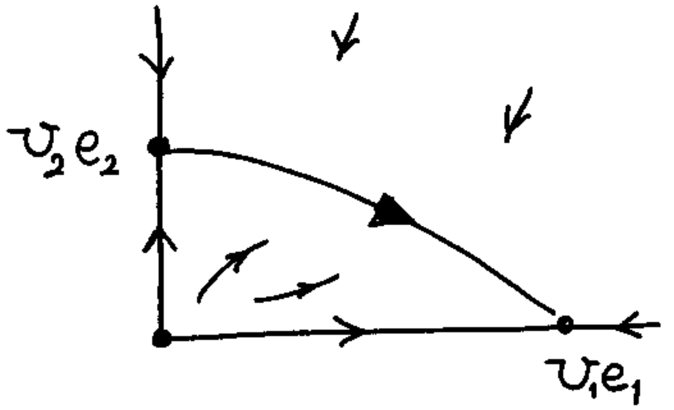
There are only two possible dynamical behaviors



$h^n(p) \longrightarrow 1 \quad \forall p \in]-1,1[$ $\qquad$ $h^n(p) \longrightarrow -1 \quad \forall p \in]-1,1[$

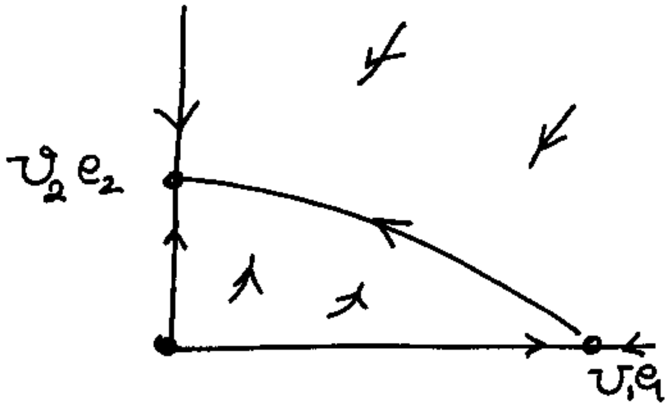
<u>Consequence</u> : the exclusion principle holds for two competitors

$$\mathrm{Fix}\,(h_\Delta) = \{ v_1 e_1 , v_2 e_2 \}$$



$\forall p \in \mathrm{int}\,(\mathbb{R}^2_+)$

$h^n(p) \longrightarrow (v_1, 0)$



$\forall p \in \mathrm{int}\,(\mathbb{R}^2_+)$

$h^n(p) \to (0, v_2)$

Notice that winner and looser are independent of the initial conditions.
This result is due to de Mottoni and Schiaffino [MS]

<u>Dimension $d = 2$</u>

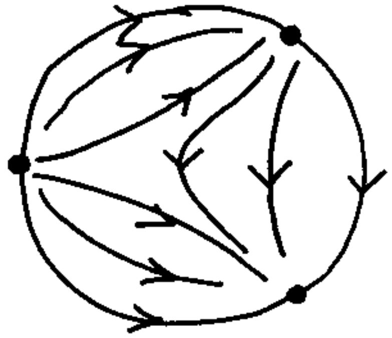
$h : B \to B$ orientation preserving

$\mathrm{Fix}\,(h) \subset \partial B.$

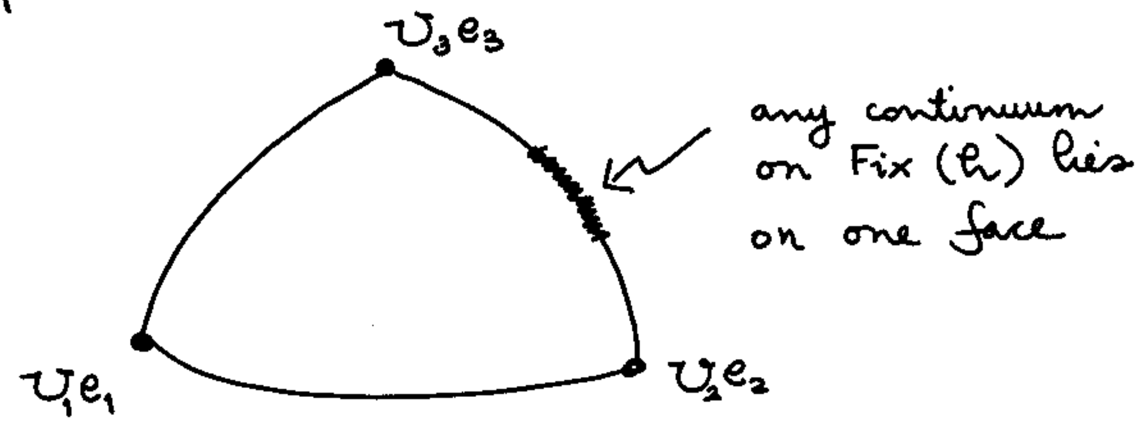
Then, for every $p \in B$, $L_\omega(p)$ is a continuum contained in $\mathrm{Fix}\,(h)$.

This result was obtained in [COT]. When h is analytic $L_\omega(p)$ is always a singleton [CDO].

Example:



Consequence: The exclusion principle holds for three competitors as soon as the semi-trivial solutions $v_1(t)e_1$, $v_2(t)e_2$, $v_3(t)e_3$ are isolated as T-periodic solutions



Notice that now the species going to extinction may depend upon initial conditions.

There are pathological examples for $N=3$ which do not satisfy the exclusion principle (see [COT]).

Dimension $d \geqslant 3$

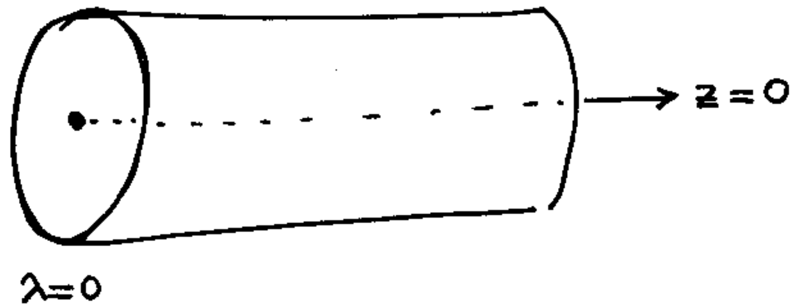
An example of $h : B \to B$ orientation preserving

$$\mathrm{Fix}(h) \subset \partial B$$

and $L_\omega(p) \subset \mathrm{int}(B)$ for some $p \in B$.

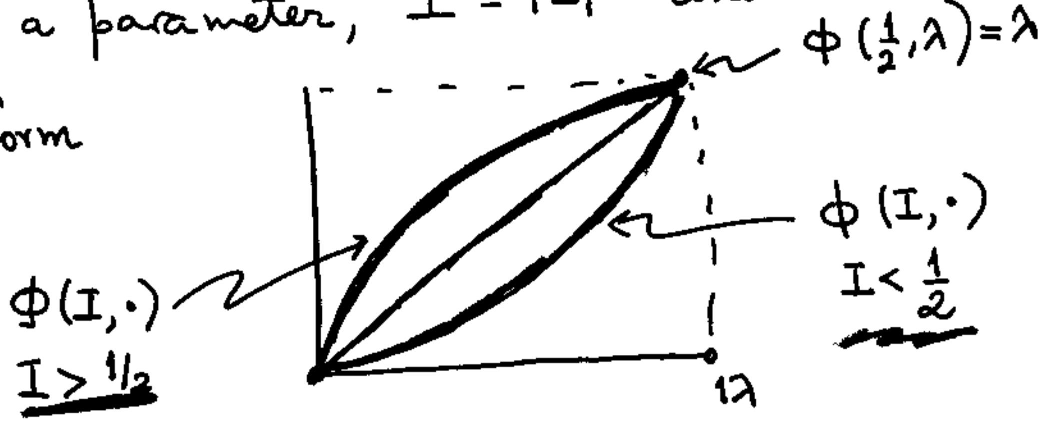
We change B by a solid cylinder with coordinates

$$(z,\lambda), \quad z \in \mathbb{C},\ |z| \leqslant 1,\ \lambda \in [0,1]$$



$$h : (z,\lambda) \mapsto (z_1,\lambda_1), \quad z_1 = e^{i\omega I} z,\ \lambda_1 = \phi(I,\lambda)$$

where ω is a parameter, $I = |z|^2$ and ϕ has the form



The quantity I is a first integral (constant along orbits) and so the cylinders $|z| = \text{constant}$ are invariant. We describe the dynamics on each cylinder

$I = 0$

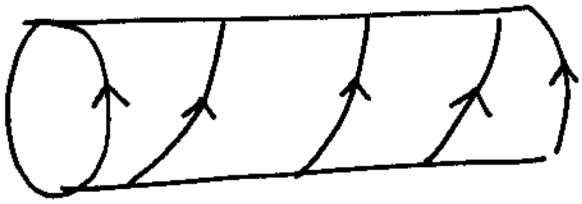
$0 < I < \frac{1}{2}$

orbits travel from $\lambda = 1$ to $\lambda = 0$

$I = \frac{1}{2}$

Invariant circles

$\frac{1}{2} < I \leq 1$



orbits travel from $\lambda = 0$ to $\lambda = 1$

when ω is not a multiple of π,

$$\mathrm{Fix}(h) = \{ (0,0), (0,1) \} \subset \partial B$$

If $I = \frac{1}{2}$, ~~also~~ $L_\omega(p) \subset \mathrm{int}\,(B)$

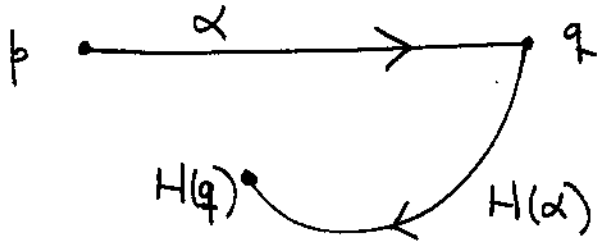
Brouwer's theory of translation arcs

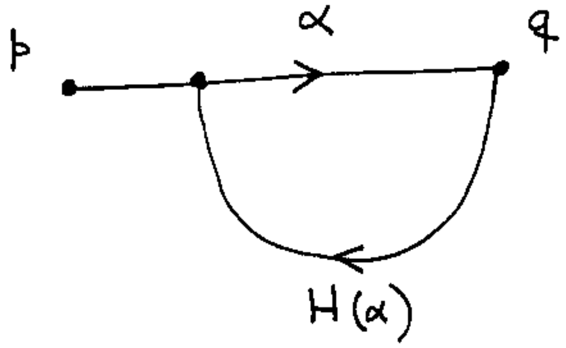
A set $\alpha \subset \mathbb{R}^2$ homeomorphic to $[0,1]$ will be called an arc. The end points are denoted by p and q

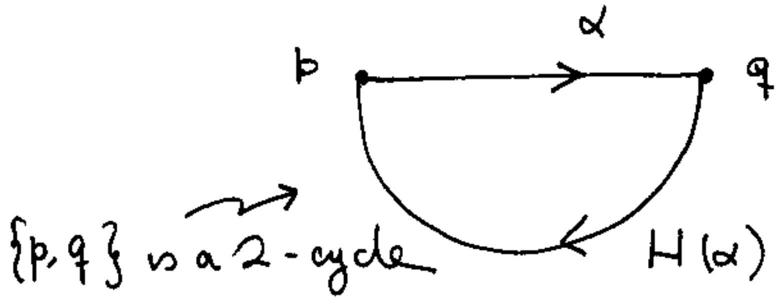
The ordering $\{p, q\}$ determines an orientation of α. We employ the notation $\dot{\alpha} = \alpha - \{p, q\}$.

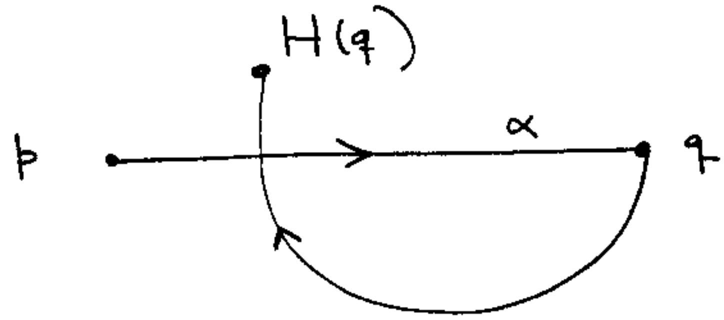
Given a homeomorphism $H : \mathbb{R}^2 \to \mathbb{R}^2$, α is a translation arc if

$$H(p) = q, \quad H(\alpha - \{q\}) \cap (\alpha - \{q\}) = \phi$$









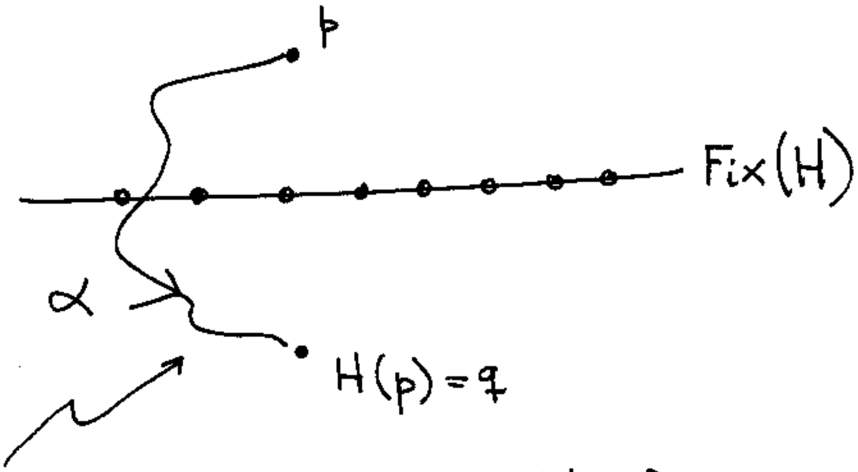
Not a translation arc

Remarks:

- A translation arc cannot contain fixed points
- There are homeomorphisms which do not admit translation arcs

H = identity

H = symmetry



any arc joining p and H(p) must cross Fix (H)

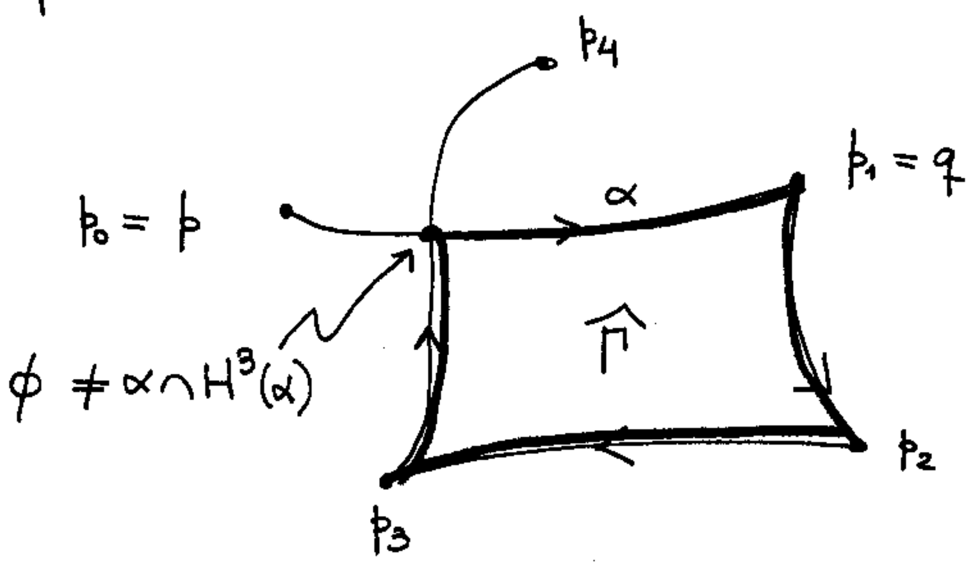
Lemma 1 (Brouwer) Assume that H is orientation preserving and α is a translation arc with

$$\alpha \cap H^n(\alpha) \neq \emptyset$$

for some $n \geq 2$.

Then there exists a Jordan curve $\Gamma \subset \mathbb{R}^2$ such that $I(H, \hat{\Gamma}) = \deg(id - H, \hat{\Gamma}) = 1$.

(Here $\hat{\Gamma}$ is the bounded component of $\mathbb{R}^2 - \Gamma$ and deg is the Brouwer degree, I fixed point index. In particular H has not fixed points on Γ)

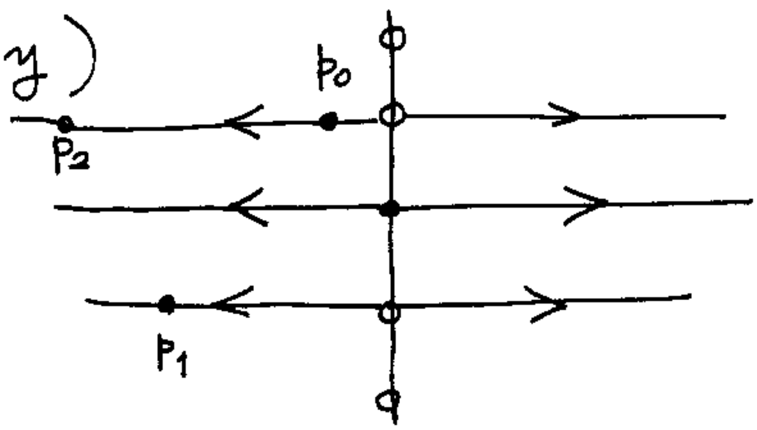


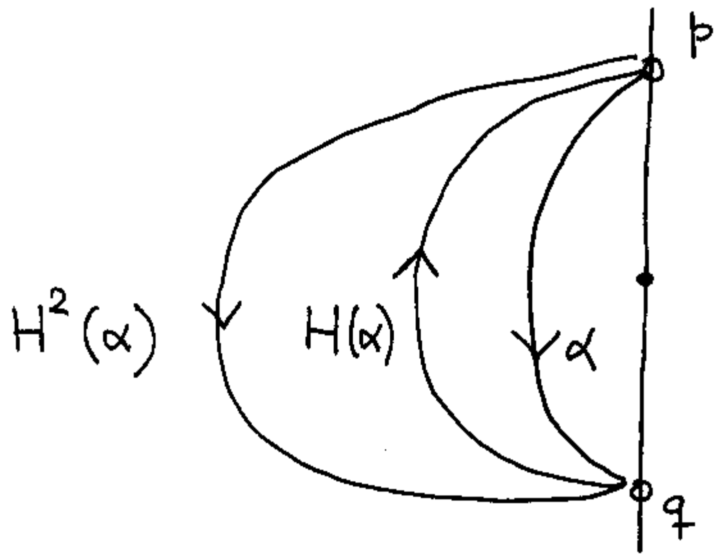
<u>Example</u> (The lemma is not valid when H is orientation reversing)

$H(x, y) = (2x, -y)$

$\mathrm{Fix}(H) = \{(0,0)\}$

$\mathrm{Fix}(H^2) = \{0\} \times \mathbb{R}$





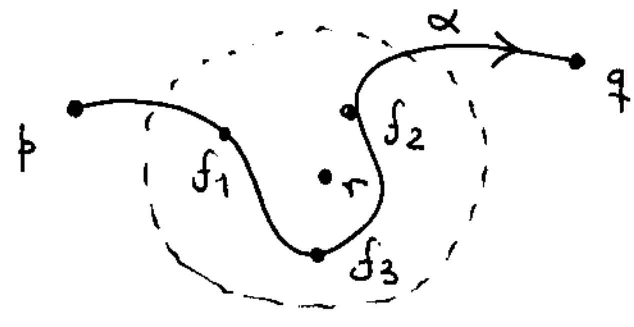
$H^2(\alpha) \cap \alpha \neq \emptyset$

The fixed point index of the origin is -1. Hence, for any Jordan curve Γ with $0 \notin \Gamma$

$$I(H, \hat{\Gamma}) = \begin{cases} 0 & \text{if } 0 \notin \hat{\Gamma} \\ -1 & \text{if } 0 \in \hat{\Gamma} \end{cases}$$

<u>Lemma 2</u> (Existence of translation arcs).
Assume that H has no fixed points and $r \in \mathbb{R}^2$. Then there exists $\varepsilon > 0$ such that given any finite set $F \subset B(r, \varepsilon)$, there exists a translation arc with

$$F \subset \dot{\alpha}.$$



Proof of the theorem

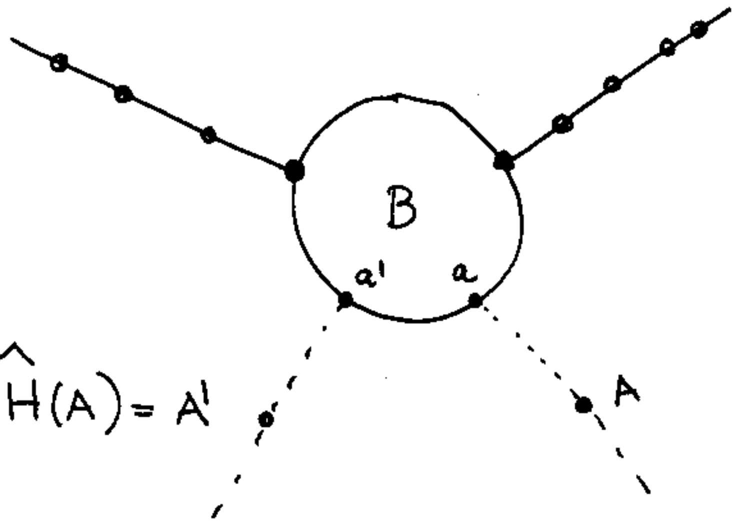
$B = \{x \in \mathbb{R}^2 : \|x\| \leq 1\}$, $h : B \to B$ orientation preserving homeomorphism

$Fix(h) \subset \partial B$

$\forall p \in B$, $L_\omega(p)$ is a continuum contained in $Fix(h)$.

First Step Radial extension of h

$$\hat{H}(x) = \begin{cases} h(x) & \text{if } \|x\| \leq 1 \\ \|x\| \, h\left(\frac{x}{\|x\|}\right) & \text{if } \|x\| > 1 \end{cases}$$



We observe that $\mathbb{R}^2 - Fix(\hat{H})$ is simply connected and hence $\cong \mathbb{R}^2$. Let H be the map on $\mathbb{R}^2$ given by

$$\begin{array}{ccc} \mathbb{R}^2 - \mathrm{Fix}(\hat{H}) & \xrightarrow{\hat{H}} & \mathbb{R}^2 - \mathrm{Fix}(\hat{H}) \\ \| 2 & & \| 2 \\ \mathbb{R}^2 & \dashrightarrow & \mathbb{R}^2 \\ & H & \end{array}$$

We observe that H is orientation preserving and has no fixed points. Both lemmas apply.

<u>Second Step</u> $L_\omega(p) \subset \mathrm{Fix}(h)$

Assume by contradiction that, for some $p \in B$, there exists $p_* \in L_\omega(p)$, $h(p_*) \neq p_*$.
~~We apply Lemma 2 and~~ This implies that, for some $x \in \mathbb{R}^2$, ~~there exists $r \in L_\omega(x, H)$~~.

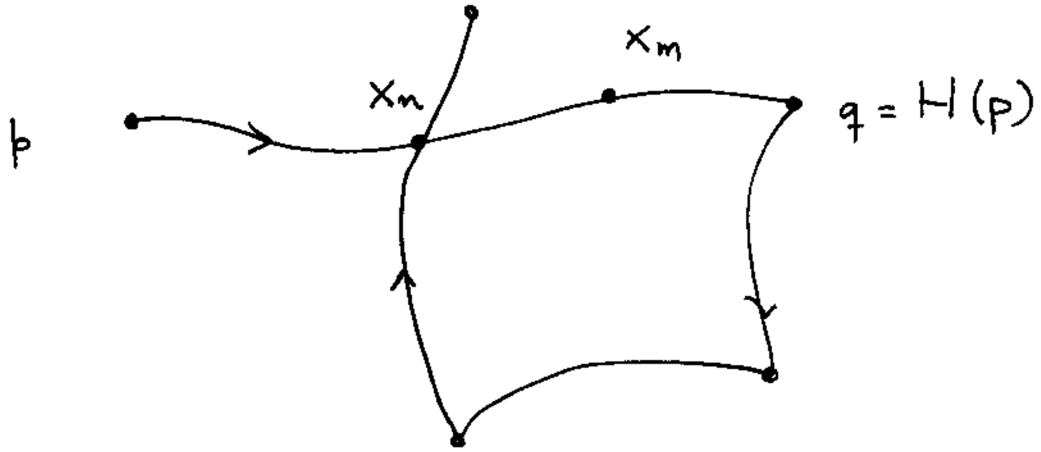
Φ $\qquad L_\omega(x, H) \neq \phi$.

Pick $r \in L_\omega(x, H)$ and find ε corresponding to Lemma 2. We can find $n > m$ large enough, $n \neq m+1$, such that

$$x_n = H^n(x),\ x_m = H^m(x) \in B(r, \varepsilon)$$

Hence there exists a translation arc for H, α, with $x_n, x_m \in \mathring{\alpha}$. It is clear that

$$H^{n-m}(\alpha) \cap \alpha \neq \phi$$



$$H^{n-m}(x_m) = x_n \in \alpha \cap H^{n-m}(\alpha).$$

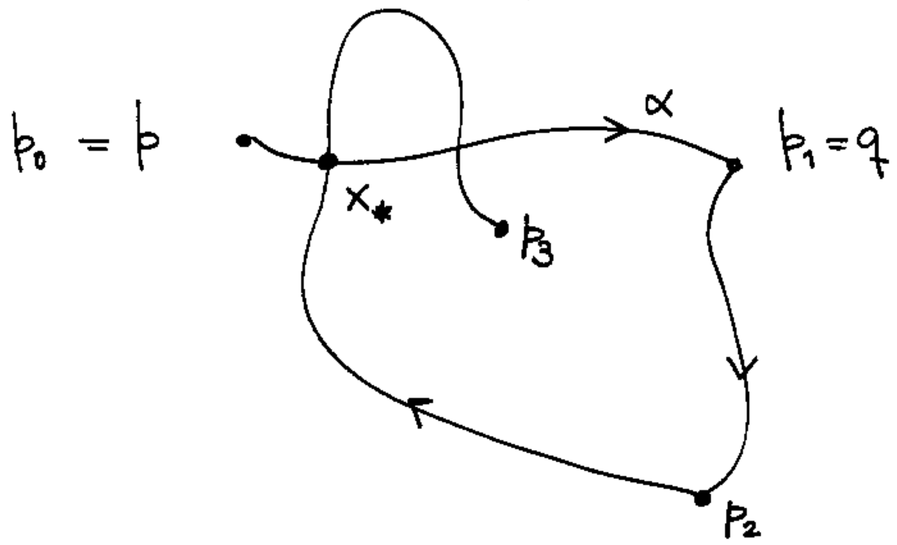
From Lemma 1 H must have a fixed point. This is the searched contradiction.

Third Step $L_\omega(p)$ is a continuum

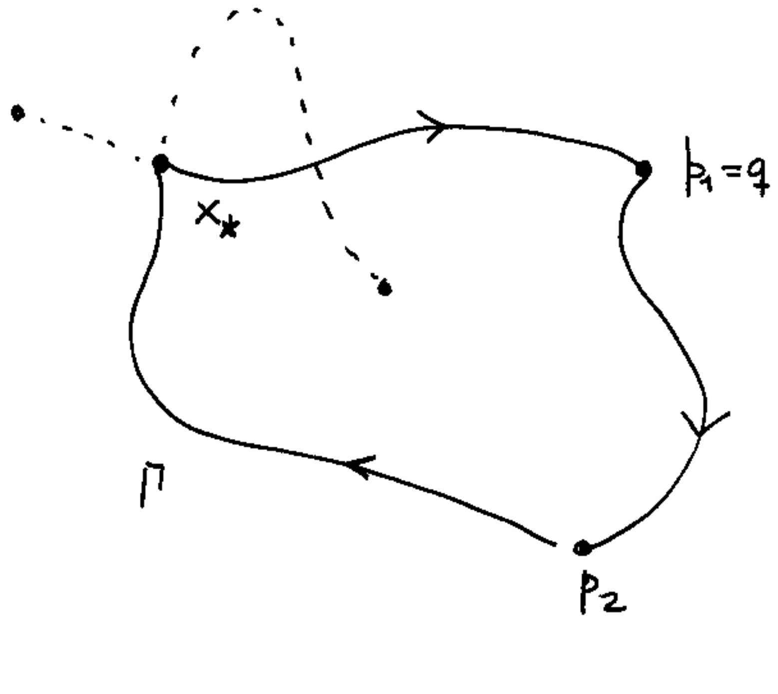
Exercise X metric space, $h: X \to X$ homeomorphism $\exists x \in X$: $\{h^n(x) : n \geq 0\}$ relatively compact in X, $L_\omega(x, h) \subset Fix(h)$. Then $L_\omega(x, h)$ is a continuum.

"Intuitive" proof" of Lemma 1

Consider the situation

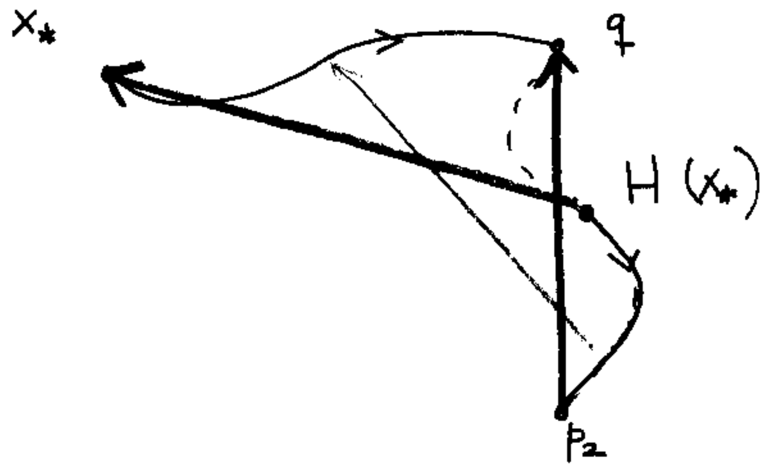


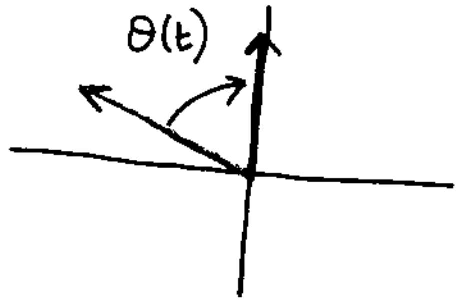
We observe that $H^2(\alpha) \cap \alpha$ has two points in this case. We select the first point (with respect to the orientation of $H^2(\alpha)$) and observe that $\Gamma = \widehat{x_* q} \cup H(\alpha) \cup \widehat{p_2 x_*}$ is a Jordan curve



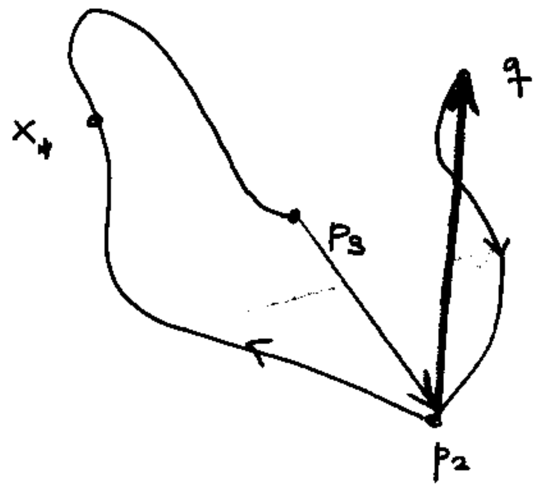
To compute $\deg(id - H, \hat{\Gamma})$ we think of the winding number of the path $t \longmapsto \alpha(t) - H(\alpha(t))$ where $\alpha(t)$ is a parameterization of Γ.

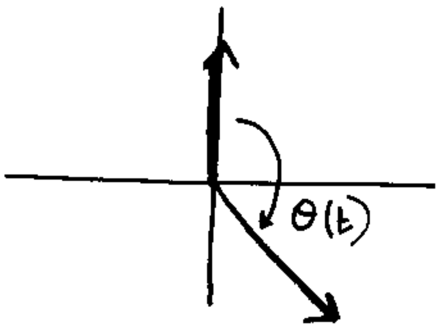
We observe that $\widehat{x_* q}$ is mapped onto a subarc $\widehat{H(x_*)\, p_2}$ of $H(\alpha)$





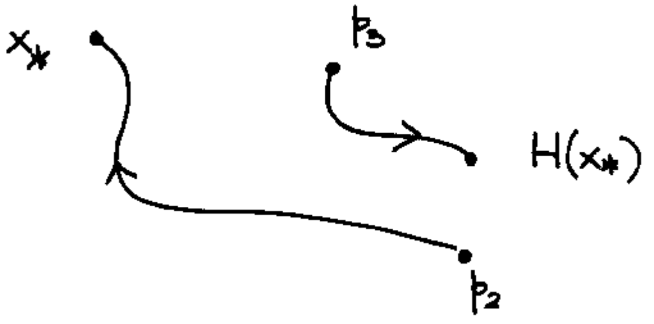
Next $H(\alpha)$ is mapped onto $H^2(\alpha)$



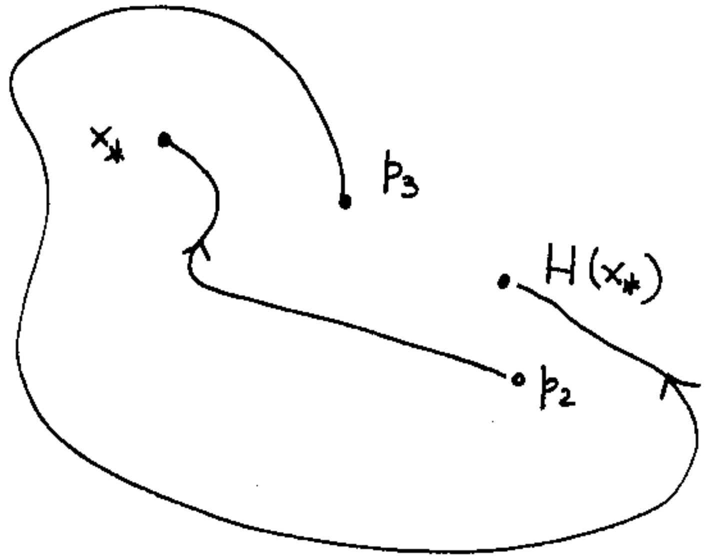


Now the key argument comes: the arc $\widehat{p_2 x_*}$ is mapped onto an arc $\widehat{p_3 H(x_*)}$. There are two possibilities:

(i)

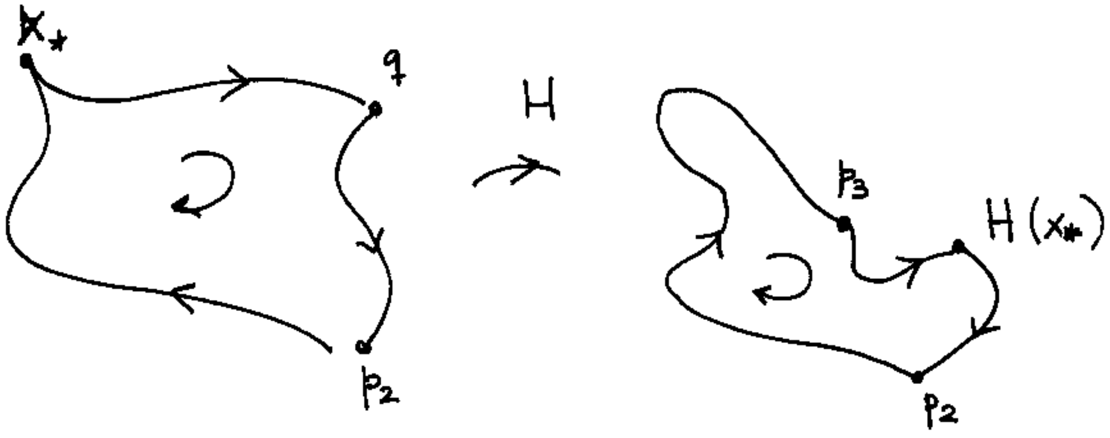


(ii)

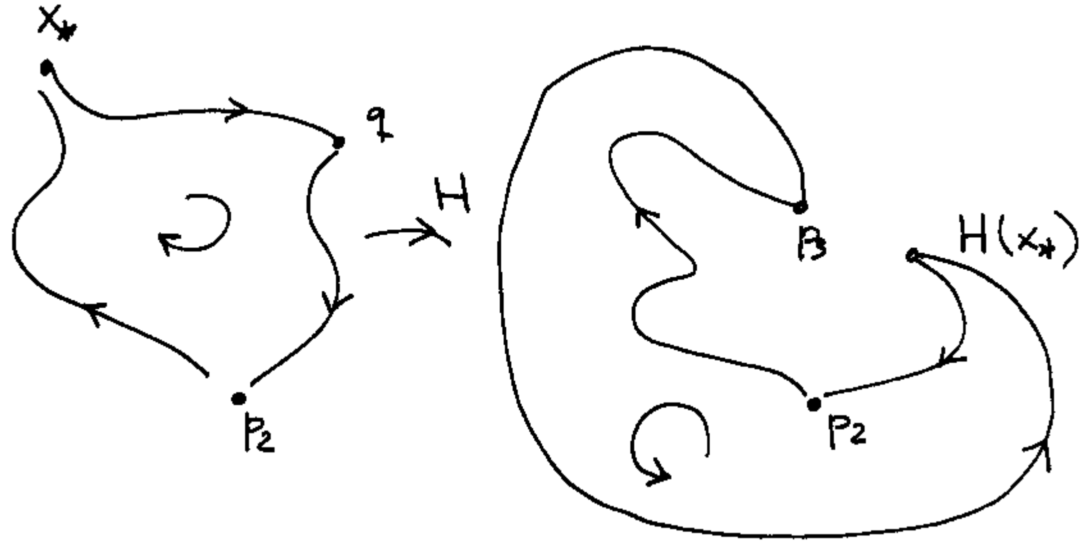


In the first case the degree would be 1 and in the second 0. The second case would imply that Γ and $H(\Gamma)$ have reversed orientations

(i)



(ii)

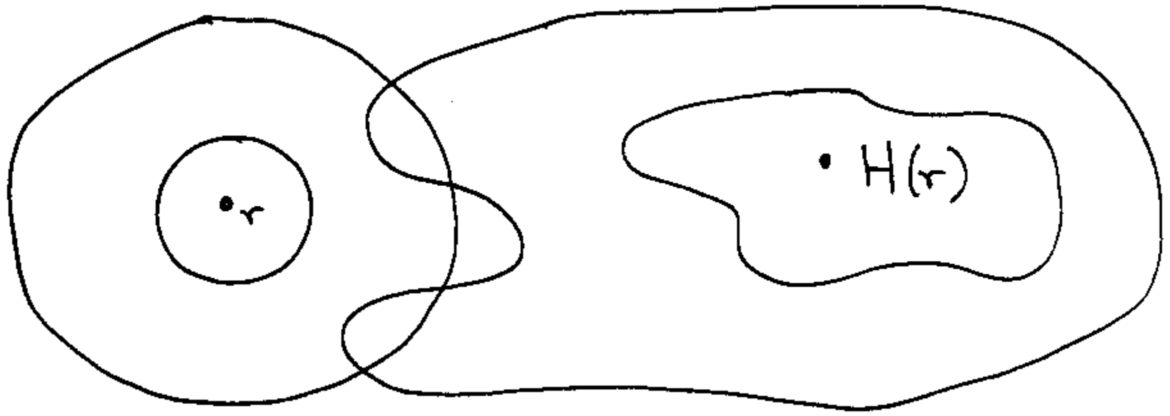


A rigorous proof can be found in [Brown].

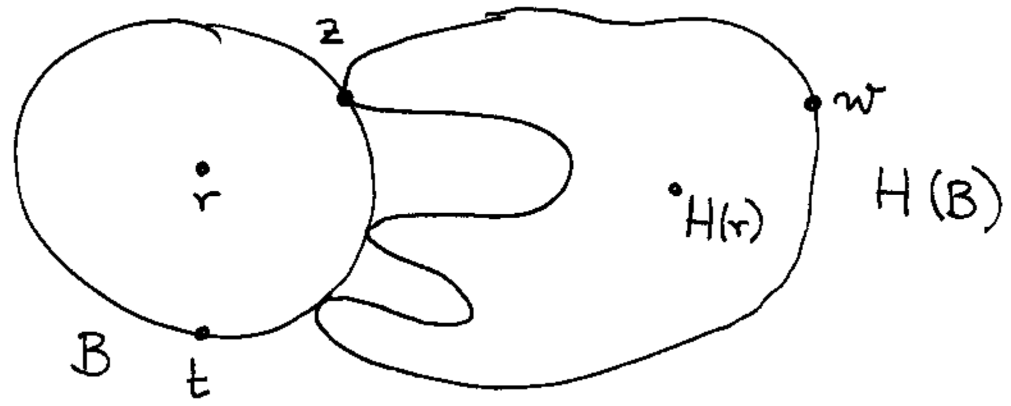
Proof of Lemma 2

Consider the family of disks

$\{\bar{B}(r,\varepsilon)\}_{\varepsilon>0}$. For small ε they do not intersect its image under H while for large ε they contain $H(r)$

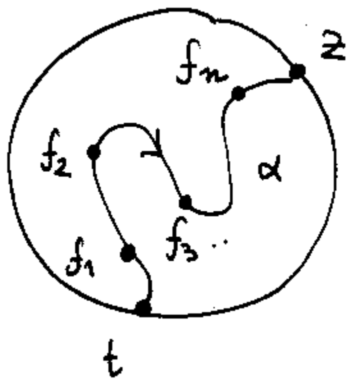


Let $\varepsilon_* > 0$ be the first value of ε such that the intersection of $\bar{B}$ and $H(\bar{B})$ is not empty. Certainly $\overline{B} \cap H(\overline{B}) \subset \partial B \cap H(\partial B)$

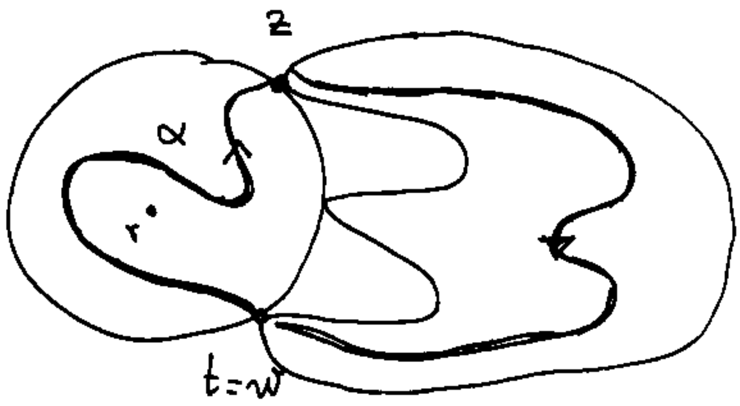


Pick $z \in \overline{B} \cap H(\overline{B})$ and $t = H^{-1}(z) \in \partial B$, $w = H(z) \in H(\partial B)$. Assume that F is contained in $\mathrm{int}(B)$. We draw an arc going from t to z and such that

$$F \subset \dot{\alpha} \subset \mathrm{int}(B)$$



The image of α must join z and w and $H(\dot{\alpha}) \subset \mathrm{int}\, H(B)$. We observe that w and t could coincide but $z \neq t, w$ since there are no fixed points. Hence



$$H(\alpha - \{z\}) \cap (\alpha - \{z\}) = \phi$$

This proof is a modification of a proof in [Brown 2].

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