POPULATION DYNAMICS FROM GAME THEORY

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Introduction.

We study a class of cubic dynamical systems on a n-simplex. They arise in biology at both ends of the evolutionary scale, in models of animal behaviour and molecular kinetics. The game theoretical aspects also suggest possible applications in the social sciences.

Game theory was introduced into the study of animal behaviour by Maynard Smith and Price [6, 7, 8] in order to explain the evolution of ritualised conflicts within a species, as for example when individuals compete for mates or territory. They defined the notion of an evolutionarily stable strategy (ESS) in a non-zero sum game. Each individual can play one of n+1 strategies, and different points of the n-simplex Δ represents populations with different proportions playing the various strategies. The pay-off represents fitness, or reproductive success, and an ESS is a point of Δ representing a population resistant to mutation, because mutants are less fit.

However, an ESS is a static concept, and so, following Taylor and Jonker [14], we introduce a dynamic into the game by assuming the hypothesis that the growth rate of those playing each strategy is proportional to the advantage of that strategy. This gives a flow on Δ whose flow lines represent the evolution of the population. In Section 1 we verify that if there is an ESS then it is an attractor of the flow, thereby sharpening a result of [14; see also 4]. The converse is not true : an attractor may not necessarily be an ESS because locally the flow may spiral in elliptically towards the attractor (an eventuality that is not always covered by the notion of ESS due to the linearity of its definition). We show there is also a global difference between an ESS and an attractor : if an ESS lies in the interior of Δ then it must have the whole interior as its basin of attraction and so there cannot be any other attractor, whereas if an attractor lies in the interior of Δ then its basin can be smaller, and the game may admit other competing attractors on the boundary. This is illustrated in Example 1, which gives a flow on a 2-simplex with a non-ESS attractor in the interior and an ESS attractor at a vertex, dividing Δ into two basins of attraction.

Meanwhile at the other end of the evolutionary scale studies by Eigen and Schuster [1] of the evolution of macromolecules before the advent of life have led to exactly the same types of equation. The resulting dynamics have been studied by Schuster, Sigmund, Wolff and Hofbauer [11, 12]. Here we are given n+1 chemicals, and different points in Δ represent mixtures of them in different proportions. The dynamic represents their enzymatic action upon each other, and an attractor represents a mixture that remains stable because of mutual cooperation. For instance the example mentioned above would represent a mixture of three chemicals, and if they happen to be added to the mixture in the right order, so that initial conditions fall into the basin of the interior attractor, then the mixture will develop into a stable cooperative mixture of all three chemicals; but if they are added in the wrong order, so that the initial conditions fall into the other basin, then only one of the chemicals will survive and the other two will be excluded. Schuster and Sigmund have also applied the dynamics to animal behaviour in the battle of the sexes [13].

One of the main benefits of the dynamic approach is that it allows the notion of structural stability [9, 10, 15] to be introduced into game theory : a game is stable if sufficiently small perturbations of its pay-off matrix induce topologically equivalent flows. A property is called robust if it persists under perturbations. In Section 2 we study the fixed points, since they seem to be the most important feature determining the nature of the flows. For example a stable game can have at most one fixed point in the interior of each face of Δ. We show that an isolated fixed point is robust, and give a sufficient condition for there to be robustly no fixed points (and hence no periodic orbits) in the interior of Δ. These constraints limit the type of bifurcations that can occur in parametrised games : for instance elementary catastrophes [15] cannot occur, but we give examples to show that exchanges of stability can occur if an interior fixed point runs into another one on the boundary, and that Hopf bifurcations [5] are also possible.

In Section 3 we begin to tackle the classification problem, up to topological equivalence. We conjecture that stable classes are dense, and finite in number for each n. These conjectures are plausible because a game is determined by its pay-off matrix, and therefore the space of games on an n-simplex is the same as the space of real $(n+1)\times(n+1)$ matrices. For $n = 1$ it is easy to verify the conjectures, and show there are only 2 stable classes (up to flow reversal). For $n = 2$ we conjecture further, that a stable game is determined by its fixed points, and that there are therefore 19 stable classes (up to flow reversal) as illustrated in Figure 11. This conjecture is surprising because it implies that for $n = 2$ there are no periodic orbits in stable games, and therefore no generic Hopf bifurcations. In fact at the end of the paper we prove that all Hopf bifurcations on a 2-simplex are degenerate (thereby correcting a mistake in [14]), and the proof involves going some way towards proving the last conjecture. On the other hand such a conjecture would be false in higher dimensions, because when $n \geq 3$ generic Hopf bifurcations do occur, as is shown by Example 6, which is an elegant example due to Sigmund and his coworkers [11]. In higher dimensions the number of stable classes proliferates, but this is primarily due to the combinatorial possibilities of what can happen on the boundary of Δ, and if the flow is given on the boundary there seem to be relatively few stable extensions to the interior. For example if there are no fixed points in the interior we conjecture the extension is unique and gradient-like on the interior. If there is a fixed point then periodic orbits may also appear, but I do not know if strange attractors can occur.

In applications where perturbations are meaningful it is best to use stable models since they have robust properties. In another paper [16] we analyse the original game of Maynard Smith [6, 8] about animal conflicts, which gives a flow on a tetrahedron since there are 4 strategies involved. The retaliator is the best strategy, but it turns out to be only a weak attractor because the game is unstable. When the game is stabilised it becomes a proper attractor, but at the same time another competing attractor appears, surprisingly, which is a mixture of hawks and bullies, and which has biological implications for the evolution of pecking orders.

Section 1. ESS's and attractors.

Suppose competing individuals in a population can play one of n+1 strategies, labelled $i = 0,1,\ldots,n$. Let x_i denote the proportion of the population playing strategy i. Then $x = (x_0, x_1, \ldots, x_n) \in \Delta$, where Δ denotes the n-simplex in $\mathbb{R}^{n+1}$ given by $\Sigma x_i = 1$, $x_i \geq 0$. Let $\mathring{\Delta}$ denote the interior of Δ given by $x_i > 0$, and $\partial\Delta$ its boundary. Let $X_0, X_1, \ldots, X_n$ denote the vertices of Δ. We shall use x to denote ambiguously the population, the point in Δ, the row matrix, and its transposed column matrix.

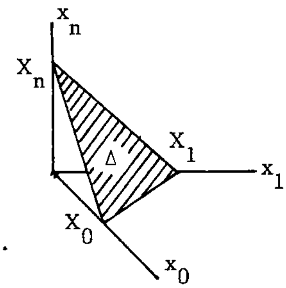


Figure 1.

The game is determined by the pay-off matrix $A = (a_{ij})$, which is a real $(n+1)\times(n+1)$ matrix. Pay-off means expected gain, and if an individual plays strategy i against another individual playing strategy j, then the pay-off to i is defined to be a_{ij}, while the pay-off to j is a_{ji}. This is a non-zero sum game, and therefore A is not necessarily skew-symmetric. If the population x is large the probability of an opponent playing j is x_j, and therefore

$$\text{pay-off to } i \text{ against } x = \sum_j a_{ij}x_j = (Ax)_i \ ,$$
$$\text{pay-off to } x \text{ against } x = \sum_i x_i(Ax)_i = xAx \ .$$

If two populations x, y play against each other

$$\text{pay-off to } x \text{ against } y = xAy.$$

Interpretation of the pay-off. There are three implicit assumptions : (i) Each individual plays a fixed pure strategy. If individuals were allowed to play mixed strategies then we should have to represent the population by a distribution on Δ rather than a point of Δ, and this leads to more complicated, but related, dynamics [see 2, 16]. However, in this paper we keep to pure strategies. (ii) Individuals breed true, in other words if an individual plays strategy i so do his offspring. Of course this avoids the question of sex, but in applications to sex-related strategies, one can assume that the related sex breeds true. (iii) Pay-off is related to reproductive fitness, in other words the more pay-off the more offspring. In other applications the pay-off can represent rewards, leading to sociological adaptation rather than biological evolution.

Definition of evolutionarily stable strategy (ESS). Given $e \in \Delta$, call e an ESS of A if, $\forall x \in \Delta - e$,

$$\text{either } xAe < eAe$$
$$\text{or } xAe = eAe \text{ and } xAx < eAx.$$

In other words a mutant x strain will be less fit than e because it either loses out against e, or against itself. It will be convenient to write

$$fx = eAe - xAe, \qquad gx = eAx - xAx \ ,$$

so that the condition becomes $fx > 0$ or $fx = 0$ and $gx > 0$.

Definition of the dynamic. The main hypothesis is that the growth rate of those playing each strategy is proportional to the advantage of that strategy. By suitable choice of time scale we can make the factor of porportionality equal to 1.

$\therefore$ growth rate of x_i = (pay-off to i) - (pay-off to x)

$$\therefore \frac{\dot{x}_i}{x_i} = (Ax)_i - xAx$$

$$\therefore \boxed{\dot{x}_i = x_i[(Ax)_i - xAx]}$$

Maynard Smith suggests that if might be sometimes biologically more appropriate to divide the right-hand side by xAx. This would change the length but not the direction of the vector field, and so would not alter the phase portrait. The above dynamic does have the mathematical advantage of being polynomial, indeed cubic. The dynamic is defined on $\mathbb{R}^n$, but we are only interested in Δ.

Lemma 1. Δ and its faces are invariant.

Proof. The n-plane containing Δ given by $\Sigma x_i = 1$ is invariant because

$$(\Sigma x_i)^{\bullet} = \Sigma \dot{x}_i = xAx - (\Sigma x_i)xAx = 0 .$$

Similarly, given any q-dimensional face Γ then the q-plane containing Γ is invariant. Hence Δ and its faces are invariant.

Induced flow. Let φ_A denote the induced flow on Δ. Examples of such flows on a 2-simplex can be seen in Figure 11 below. The reverse flow is given by reversing the sign, $-\varphi_A = \varphi_{-A}$. If Γ is a face of Δ we write $\Gamma < \Delta$, and we shall use the symbol Γ to denote ambiguously both the subset of Δ and the subset of $\{0, 1, \ldots, n\}$ corresponding to the vertices; thus $i \in \Gamma$ is an abbreviation for $X_i \in \Gamma$. If $A|\Gamma = \{a_{ij}; i, j \in \Gamma\}$ denotes the corresponding submatrix, then the induced flow on Γ satisfies $\varphi_A|\Gamma = \varphi_{A|\Gamma}$.

Attractors. For the most part we shall only need to consider point attractors. Recall the definition : a point is an attractor of the flow if it is the ω-limit of a neighbourhood, and the α-limit of only itself. Its basin of attraction is the (open) set of points of which it is the ω-limit. It is hyperbolic if its eigenvalues have negative real part.

Theorem 1. An ESS is an attractor, but not conversely. This result was first proved in [14] under the extra hypothesis that the ESS was regular, and giving the extra conclusion that the attractor was hyperbolic. Another proof is given in [4]. The Theorem shows that from the point of view of smooth dynamics an attractor is a more general notion than an ESS, and better characterisation of the resistance to mutation. Theorem 2 and Example 1 below show that there are also global differences between them.

Proof of Theorem 1. Suppose we are given an ESS e of A. We shall show that

$$V = \prod x_i^{e_i}$$

is a Lyapunov function for φ_A. In other words we shall prove there is a neighbourhood N of e such that

$$\left.\begin{array}{ll} (1) & \nabla V.(e-x) > 0 \\ (2) & \dot{V} > 0 \end{array}\right\} \quad \forall x \in N - e$$

By (1) V increases radially towards e, and so e is the maximum and there are no stationary points of V in N-e. By (2) all orbits inside a level curve of V tend to e, and so e is an attractor, as required. The proof of the two conditions is divided into two cases, according as to whether e lies in the interior or boundary of Δ.

<u>Proof of (1) when $e \in \mathring{\Delta}$.</u> Let $N = \mathring{\Delta}$. If $x \in \mathring{\Delta} - e$ then $V > 0$ and

$$V_i \equiv \frac{\partial V}{\partial x_i} = V\frac{e_i}{x_i}$$

$\therefore \nabla V.(e-x) = \Sigma V_i(e_i - x_i) = V\Sigma\frac{e_i}{x_i}(e_i - x_i) = V\Sigma\frac{(e_i - x_i)^2}{x_i}$, since $\Sigma e_i = \Sigma x_i = 1$. $\therefore \nabla V.(e-x) > 0$, since $x \neq e$.

<u>Proof of (2) when $e \in \mathring{\Delta}$.</u> Recall that

$$fx = eAe - xAe, \quad gx = eAx - xAx .$$

Given $x \in \mathring{\Delta} - e$, and $t \in \mathbb{R}$, let $x_t = tx + (1-t)e$. Then $x_t \in \Delta$ for $|t|$ sufficiently small, since $e \in \mathring{\Delta}$.

$\therefore f(x_t) \geq 0$, since e an ESS. But $f(x_t) = tfx$.

$\therefore tfx \geq 0$ for $|t|$ sufficiently small. $\therefore fx = 0$.

$\therefore gx > 0$ since e an ESS.

$\therefore \dot{V} = \Sigma V_i \dot{x}_i = V\Sigma\frac{e_i}{x_i}x_i((Ax)_i - xAx) = Vgx > 0.$

This completes the proof of Theorem 1 for the case $e \in \mathring{\Delta}$.

Notice that in this case, since $N = \mathring{\Delta}$, the basin of attraction of e contains $\mathring{\Delta}$. But the basin $\subset \mathring{\Delta}$, because $\partial\Delta$ is invariant. $\therefore$ the basin $= \mathring{\Delta}$.

<u>Proof of (1) when $e \in \partial\Delta$.</u> Suppose $e \in \mathring{\Gamma}$, $\Gamma < \Delta$.

Let $N_1 = \mathring{\Gamma} \cup \mathring{\Delta}$,

$G = \partial\Delta - \mathring{\Gamma} = \Delta - N_1$.

If $x \in N_1 - e$ then $x_i \neq 0$, $i \in \Gamma$.

$$\therefore V_i = \begin{cases} V\frac{e_i}{x_i}, & i \in \Gamma \\ 0, & i \notin \Gamma \end{cases}$$

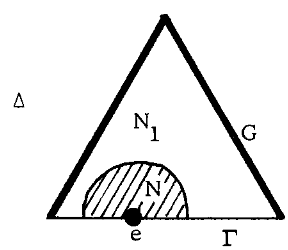


Figure 2.

$\therefore \nabla V.(e-x) = \sum_{i \in \Gamma} V\frac{e_i}{x_i}(e_i - x_i) = V\sum_{i\in\Gamma}\frac{(e_i - x_i)^2}{x_i} + V(1 - \sum_{i\in\Gamma} x_i) > 0$, because the first term > 0 and the second term ≥ 0. (Note that the proof given in [4] for this step does not work, and the proof given for the next step is incomplete).

<u>Proof of (2) when $e \in \partial\Delta$.</u> If $x \in N_1$ then $\dot{V} = \sum_{i\in\Gamma} V\frac{e_i}{x_i}x_i((Ax)_i - xAx) = Vgx$, since $e_i = 0$, $i \notin \Gamma$. Therefore we have to find a neighbourhood N of e in N_1 such that g is positive on $N - e$, but the problem this time is that f may not vanish on N. Let $G_0 = G \cap f^{-1}0$. (Notice $G_0 \supset \partial\Gamma$). Then $g > 0$ on G_0 by the ESS condition. $\therefore g > 0$ on an open neighbourhood G_1 of G_0 in G. Let $G_2 = G - G_1$. Then G_2 closed in G, and therefore compact. Since $f > 0$ on G_2, the function $\frac{g}{f}$ is defined and continuous on G_2, and therefore bounded since G_2 compact. Choose ε, $0 < \varepsilon < \frac{1}{2}$ such that $|\frac{g}{f}| < \frac{1}{2\varepsilon}$ on G_2.

$\therefore \varepsilon|gx| < \frac{1}{2}fx$, $\forall x \in G_2$. Let N be the neighbourhood of e in N_1 given by

$$N = \{x_t = tx + (1-t)e;\ x \in G,\ 0 \leq t < \varepsilon\} .$$

Now

$$g(x_t) = t^2 gx + t(1-t)fx.$$

If $0 < t < \varepsilon$ and $x \in G_1$ then on the right-hand side the first term >0 and the second term ≥ 0. On the other hand if $x \in G_2$ then the second term >0, and the first term is smaller, because

$$|tgx| < \varepsilon |gx| < \tfrac{1}{2}fx, \text{ by above, } < (1-t)fx, \text{ since } t < \varepsilon < \tfrac{1}{2}.$$

Therefore in both cases $g > 0$. This completes the proof of Theorem 1 for the case $e \in \partial\Delta$. Finally the negative converse, that an attractor is not necessarily an ESS, is established by Example 1 below. A similar counterexample is given in [14], but ours has the extra subtlety of illustrating a global difference between the basins of attraction of an ESS and an attractor, as indicated by the following theorem.

<u>Theorem 2.</u> <u>If an ESS lies in $\mathring{\Delta}$ then its basin of attraction is $\mathring{\Delta}$, and there are no other attractors. If an attractor lies in $\mathring{\Delta}$ then its basin may be smaller than $\mathring{\Delta}$, and there may be other attractors in $\partial\Delta$ (but not in $\mathring{\Delta}$).</u>

<u>Proof.</u> We have already shown in the proof of Theorem 1 that an ESS in $\mathring{\Delta}$ has basin $\mathring{\Delta}$; therefore there cannot be another attractor in Δ otherwise its basin would have to be a non-empty open set in Δ disjoint from $\mathring{\Delta}$, which is impossible since $\mathring{\Delta}$ is dense in Δ. The second half of Theorem 2 is established by Example 1 below, which illustrates an attractor in $\mathring{\Delta}$ with another in $\partial\Delta$, and hence the basin of the former must be smaller than $\mathring{\Delta}$. There cannot be another attractor in $\mathring{\Delta}$, otherwise by Lemma 2 below the line joining the two attractors would be pointwise fixed, so neither would be an attractor.

<u>Lemma 2.</u> <u>If there are two fixed points in $\mathring{\Delta}$ then the line joining them is pointwise fixed.</u>

<u>Proof.</u> Given $x \in \mathring{\Delta}$,

$$\dot{x} = 0 \iff (Ax)_i = xAx, \ \forall i$$

$$\iff (Ax)_i \text{ independent of } i, \text{ since } \Sigma x_i = 1 .$$

Given e, x fixed in $\mathring{\Delta}$, and $t \in \mathbb{R}$, then x_t is also fixed since

$$(Ax_t)_i = (A(tx+(1-t)e))_i = t(Ax)_i + (1-t)(Ae)_i$$

is independent of i. This completes the proof of Lemma 2.

<u>Example 1.</u> <u>Non-ESS attractor.</u>

$$A = \begin{pmatrix} 0 & 6 & -4 \\ -3 & 0 & 5 \\ -1 & 3 & 0 \end{pmatrix}$$

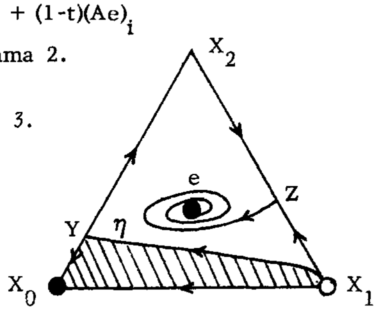


Figure 3.

φ_A is a flow on the triangle $X_0X_1X_2$. There is an attractor at the barycentre $e = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ with eigenvalues $\frac{1}{3}(-1 \pm i\sqrt{2})$. However, e is <u>not</u> an ESS because $fX_0 = 0$ but $gX_0 = -\frac{4}{3}$. On the other hand X_0 is another attractor which <u>is</u> an ESS. The other fixed points are a repellor at X_1, and saddles at X_2, $Y = (\frac{4}{5}, 0, \frac{1}{5})$ and $Z = (0, \frac{5}{8}, \frac{3}{8})$. As visual notation for all the figures in this paper we use a solid dot for an attractor and an open dot for a repellor, and we always put in the insets and outsets of the saddles, as in Figure 3. (Here insets and outsets are short for the usual more cumbersome terms "stable and unstable manifolds"). In the proof of Theorem 7 below we show that

$$V = x_0^4 x_1^5 x_2^{-10}(-4x_0 - 5x_1 + 10x_2)$$

is a global Lyapunov function for the flow in $\check{\Delta}$. Therefore the inset η of Y flows away from the repellor X_1, and all other orbits in $\mathring{\Delta}$-e flow away from X_1 and towards one or other of the two attractors, e and X_0. Hence η separates Δ into the basins of attractions of the two attractors, as illustrated in Figure 3, where the basin of X_0 is shown shaded. If also follows from the proof of Theorem 7 that this example is in fact stable. This example completes the proof of Theorems 1 and 2.

Figure 3 illustrates qualitatively why an attractor need not be an ESS, and reveals exactly where the notion of ESS fails. The local reason that e is not an ESS is that the orbits spiral in somewhat elliptically; therefore a mutant X_0-strain will initially have a slight advantage over e, but it will also stimulate the growth of an X_2-strain that will soon wipe out that advantage, and which will in turn be wiped out by an X_1-strain, and so on, as the orbit spirals in towards e. Meanwhile the global reason that e is not an ESS is that its basin is not the whole of $\check{\Delta}$.

In the application to chemical reactions, e represents cooperative behaviour, while X_0 represents exclusive behaviour. The fact that both types of behaviour occur in the same example shows that one cannot divide all stable systems into cooperative or exclusive, as might be suggested by the emphasis on this dichotomy in [11].

Section 2. Stability, fixed points and bifurcations.

Equivalence. Let M_{n+1} denote the space of games with n+1 strategies, which we identify with the space of real (n+1)x(n+1) matrices. Define $A, B \in M_{n+1}$ to be equivalent, written $A \sim B$, if there exists a face-preserving homeomorphism of Δ onto itself throwing φ_A-orbits onto φ_B-orbits. Here face-preserving means that each face is mapped onto another face, not necessarily onto itself.

Stability. Call A stable if it has a neighbourhood of equivalents in M_{n+1}. Note that this is a form of structural stability, with the proviso that we are confining ourselves to a special type of dynamical system, and to a restricted form of equivalence. A stable class is an equivalence class of stables. (Note that each stable class is open in M_{n+1}, but may have some unstable equivalents on its boundary, so the full equivalence class may be slightly larger than the stable class.)

Conjecture 1. Stables are dense in M_{n+1}.

Conjecture 2. For each n there are only a finite number of stable classes.

In other words we are suggesting that this is a well-behaved piece of mathematics. Although the dynamical systems involved are non-linear and possess some unexpected properties, nevertheless they appear to be qualitatively fairly simple, and there are so few of them that it seems plausible to try and classify them, at least in the lower dimensions. When n = 1 it is easy to verify the conjectures are true (see Section 3 below). When n = 2 we go some way towards proving them (see Theorems 6, 7). For all n the limitations on the possible configurations of fixed points impose considerable constraints on the types of flows and bifurcations that can occur, and so we begin by examining the fixed points.

Theorem 3. A stable game has at most one fixed point in the interior of each face of Δ (including $\mathring{\Delta}$).

Before we prove Theorem 3 consider some examples. In Example 1 above there are 6 fixed points, one in the interior of each face except the edge X_0X_1. Figure 11 below illustrates all the different possible configurations of fixed points that can occur in stable games on a 2-simplex. The following example shows that for any n it is possible to have a stable game with exactly one fixed point inside every face. If a game is unstable there may be more than one fixed point - for instance A = 0 has every point fixed.

Example 2. Let I denote the identity matrix. Then φ_I has a fixed point at the barycentre of each face. The vertices are attractors, the barycentre e of Δ a repellor, and the rest are saddles.

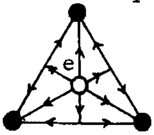


Figure 4.

Proof. Consider the reverse flow φ_{-I}. If $x \in \Delta - e$ then $fx = 0$ and $gx = |e-x|^2 > 0$. Therefore e is an ESS. Therefore by Theorem 1 e is an attractor, and by Theorem 2 there are no other fixed points in $\mathring{\Delta}$. Hence e is a repellor for φ_I. Similarly there is a fixed point at the barycentre of each face, and no others. One can verify that this particular example is in fact a gradient flow, $\dot{x} = \nabla(\sigma_3 - \sigma_2^2)$, where σ_k is the kth symmetric function of the x_i's. Hence, by induction on the faces, it is structurally stable [9], and therefore stable.

Notation. Let u denote ambiguously the row vector $u = (1, 1, \ldots, 1)$ and its transposed column vector.

Proof of Theorem 3. Suppose $n \geq 1$, otherwise the result is trivial. Let $Q, \subset M_{n+1}$, denote the set of matrices all of whose symmetric $q \times q$ minors are non-zero, for $1 \leq q \leq n + 1$. Then Q is open dense in M_{n+1} being the complement of an algebraic subset. Therefore any stable class meets Q. Therefore it suffices to prove the result for games in Q, since the result is invariant under equivalence, and so let $A \in Q$. Therefore A^{-1} exists since $\det A \neq 0$. If $x \in \mathring{\Delta}$ is a fixed point of φ_A then $(Ax)_i$ is independent of i, by the proof of Lemma 2.

$\therefore$ Ax = multiple of u. $\therefore$ x = multiple of $A^{-1}u$.

But the vector subspace $[A^{-1}u]$ of $\mathbb{R}^{n+1}$ generated by $A^{-1}u$ pierces Δ in at most one point, and so x is unique. Therefore φ_A has at most one fixed point in $\mathring{\Delta}$. The same holds for each face of Δ, using the fact that the corresponding minor is non-zero. This completes the proof of Theorem 3.

Robustness. A property of φ_A is called robust if it is preserved under perturbations; in other words the property is shared by φ_B for all B in a neighbourhood of A. Otherwise it is called transient. For example if A is stable then all topological properties of φ_A are robust, and if A is unstable some property of φ_A is transient. But we shall also consider robust properties of unstable games, as illustrated in the following theorem, which we need for both bifurcations (see the Corollary below) and applications [16].

Theorem 4. (i) Having an isolated fixed point in $\mathring{\Delta}$ is robust. (ii) If (adjA)u has both positive and negative components then φ_A has no fixed points and no periodic orbits in $\mathring{\Delta}$, and this is robust.

Remarks : In part (i) it is necessary that the fixed point be isolated, otherwise consider the example $A = 0$; here every point is fixed but A has arbitrarily small perturbations with no fixed points in $\mathring{\Delta}$. Nevertheless the result is surprising because isolated fixed points are not robust amongst dynamical systems in general. For example consider the dynamic $\dot{y} = y^2$, $y \in \mathbb{R}$ (the fold catastrophe); here the origin $y = 0$ is an isolated fixed point, but the perturbation $\dot{y} = y^2 + \varepsilon$, $\varepsilon > 0$, has none.

In part (ii) the hypothesis on (adjA)u is necessary because otherwise the absence of fixed points in $\mathring{\Delta}$ is not robust (for instance put $\varepsilon = 0$ in Example 3 below).

Proof of Theorem 4(i). Suppose φ_A has an isolated fixed point $e \in \mathring{\Delta}$. Notice this implies no other fixed points in $\mathring{\Delta}$ by Lemma 2. There are three cases accordingly as to whether the rank, $r(A) = n+1, n,$ or less.

Case 1 : $r(A) = n+1$. Here e is a multiple of $A^{-1}u$. Let $L_A = [A^{-1}u]$, the vector subspace of $\mathbb{R}^{n+1}$ generated by $A^{-1}u$. Then $e \in L_A \cap \mathring{\Delta}$. Therefore $L_A \neq 0$, and

L_A pierces $\mathring{\Delta}$ in e. Therefore if B is a sufficiently small perturbation of A, $L_B = [B^{-1}u] \neq 0$ and L_B pierces $\mathring{\Delta}$ in a point e_B near e. Hence e_B is the required unique fixed point of φ_B in $\mathring{\Delta}$.

Case 2 : r(A) = n. Choose $x \in \mathbb{R}^{n+1}$, $x \neq 0$, such that Ax = 0. If x is not a multiple of e, let $x_t = tx + (1-t)e$. For t sufficiently small $[x_t]$ pierces $\mathring{\Delta}$ in a point, λx_t say, $\neq$ e. Furthermore λx_t is fixed under φ_A since $(A\lambda x_t)_i = \lambda(1-t)eAe$, which is independent of i. Therefore e is not isolated, since $\lambda x_t \to e$ as $t \to 0$, a contradiction. Therefore x is a multiple of e. Therefore Ae = 0.

Suppose (adjA)u = 0. Then the matrix obtained by replacing any one column of A by u has zero determinant. Since r(A) = n there are n linearly independent columns, and so u is dependent upon them. Therefore there exists $y \in \mathbb{R}^{n+1}$, $y \neq 0$, such that Ay = u. Therefore y is not a multiple of e since Ae = 0. For small t let $y_t = ty + (1-t)e$, and let $\lambda y_t = [y_t] \cap \mathring{\Delta}$. Then λy_t is fixed under φ_A since $(A\lambda y_t)_i = \lambda t$, which is independent of i. Therefore again e is not isolated, a contradiction. Therefore (adjA)u $\neq$ 0.

Furthermore (adjA)u is a multiple of e because all columns of adjA are multiples of e, since r(A) = n and Ae = 0. Let $L_A = [(\text{adj}A)u]$. Then $L_A \neq 0$ and L_A pierces $\mathring{\Delta}$ in e. Therefore if B is a sufficiently small perturbation of A, then $L_B = [(\text{adj}B)u] \neq 0$ and L_B pierces $\mathring{\Delta}$ in a point e_B near e. Furthermore e_B is fixed under φ_B since Be_B = multiple of B(adjB)u = (detB)u.

There remains to verify that e_B is isolated, and so suppose $x \in \mathring{\Delta}$ is any fixed point of φ_B. For sufficiently small perturbations, r(B) ≥ r(A) = n. If r(B) = n+1 then x = multiple of $B^{-1}u$ = multiple of (adjB)u, and so $x = e_B$. If r(B) = n, then

$$(xBx)(\text{adj}B)u = (\text{adj}B)(xBx)u = (\text{adj}B)Bx = (\det B)x = 0.$$

$$\therefore xBx = 0, \text{ since } (\text{adj}B)u \neq 0.$$

$$\therefore Bx = (xBx)u = 0 .$$

But Be_B = multiple of (detB)u = 0.

$\therefore$ x = multiple of e_B, since r(B) = n.

$\therefore x = e_B$; so we have shown that e_B is the unique fixed point of φ_B in $\mathring{\Delta}$, and therefore isolated.

Case 3 : rA < n. Since the eigenspace of 0 has dimension ≥ 2, we can choose $x \in \mathbb{R}^{n+1}$, $x \neq$ multiple of e, such that Ax = 0. Then, as in case 2, this implies that e is not isolated, a contradiction.

Proof of Theorem 4(ii). Let $L_A = [(\text{adj}A)u]$. Then $L_A \neq 0$ and L_A does not meet Δ, since by the hypothesis L_A meets the positive quadrant only in the origin. If B is a sufficiently small perturbation then $L_B = [(\text{adj}B)u] \neq 0$ and L_B does not meet Δ, since Δ is compact. Also rB ≥ rA ≥ n, since adjA $\neq$ 0. Therefore by the arguments in Cases 1 and 2 above, any fixed point of φ_B in $\mathring{\Delta}$ must lie in $L_B \cap \mathring{\Delta}$, which is empty. Therefore neither φ_A nor φ_B has any fixed points in $\mathring{\Delta}$.

To show that no fixed points in $\mathring{\Delta}$ implies no periodic orbits in $\mathring{\Delta}$, we use an argument of Sigmund et al. [11]. For suppose that was an orbit of period T. Let x(t), $0 \le t \le T$ denote the flow round the orbit, and let

$$e = \int_0^T x dt, \quad \lambda = \int_0^T xAx dt.$$

Then $e \in \mathring{\Delta}$, since each $e_i > 0$, and

$$(Ae)_i - \lambda = \int((Ae)_i - xAx)dt = \int \frac{\dot{x}_i}{x_i} dt = [\log x_i]_0^T = 0$$

Therefore $(Ae)_i = \lambda$, independent of i, and so e is fixed, a contradiction. This completes the proof of Theorem 4.

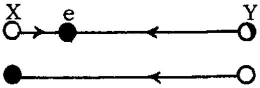
Bifurcations. We now examine the types of bifurcation that can occur in parametrised games. First we use Theorem 4 to show that there are no elementary catastrophes, the typical bifurcations of gradient systems [15]. Then we shall give some examples to show that classical Hopf bifurcations [5] and exchanges of stability can occur.

Corollary to Theorem 4. Elementary catastrophes cannot occur.

Proof. If an elementary catastrophe occured in $\mathring{\Delta}$ then some perturbation would have more than one isolated fixed point in $\mathring{\Delta}$, which is impossible by Lemma 2. If an elementary catastrophe occured in $\partial\Delta$, then some perturbation would contain a fold catastrophe, where the variation of a parameter causes two isolated fixed points to coalesce and disappear. Now it is quite possible to make an isolated point in $\mathring{\Delta}$ run into another one in the boundary, in $\mathring{\Gamma}$ say, $\Gamma < \Delta$, so that at the critical parameter value they coalesce to form an isolated fixed point in $\mathring{\Gamma}$, but it is then impossible to make the latter disappear because it is robust by Theorem 4(i) applied to $\mathring{\Gamma}$. Therefore elementary catastrophes cannot occur.

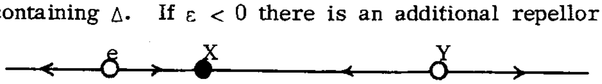
Example 3. Exchange of stabilities bifurcation.

Let $A_\varepsilon = \begin{pmatrix} 0 & 1 \\ \varepsilon & 0 \end{pmatrix}$



and let φ_ε denote the induced flow. It is easy to verify there are two cases according to the sign of the parameter ε. If $\varepsilon > 0$ then φ_ε has an attractor at $e = \left(\frac{1}{1+\varepsilon}, \frac{\varepsilon}{1+\varepsilon}\right)$, and repellors at the two vertices of the 1-simplex. If $\varepsilon \le 0$ then φ_ε has an attractor at $X = (1,0)$ and a repellor at $Y = (0,1)$. Therefore A_0 is unstable at the critical parameter value $\varepsilon = 0$. It is easy to verify A_ε is stable if $\varepsilon \ne 0$ (see Section 3 below). As $\varepsilon \to 0_+$ the attractor e runs into X and donates its attractiveness to X.

Mathematically the bifurcation is best understood by considering the induced flow on the line $\mathbb{R}$ containing Δ. If $\varepsilon < 0$ there is an additional repellor $e \in \mathbb{R}$ outside Δ.



Thus as the parameter passes through the critical value the fixed points e, X cross and exchange stabilities. Taking coordinates (x, y) the dynamic is given by

$$\dot{x} = x(y-(1+\varepsilon)xy), \quad \dot{y} = y(\varepsilon x-(1+\varepsilon)xy) .$$

Putting $x = 1-y$, we can use y as a single variable for $\mathbb{R}$, with origin at X, and then the dynamic is equivalent to the single equation

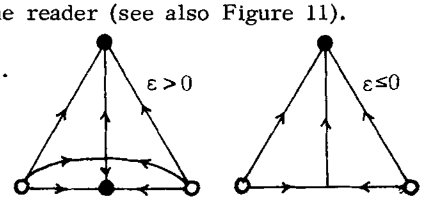
$$\dot{y} = -y^2+y^3 + \varepsilon(y-2y^2+y^3).$$

Within the constraint imposed by the games this is indeed a versal unfolding of the germ $\dot{y} = -y^2+y^3$ at $y = 0$, since the constraint requires that X be kept fixed, but if we were to allow arbitrary perturbations on $\mathbb{R}$ then a versal unfolding would include an additional constant term, thereby giving a catastrophe surface with a fold curve through the origin. Then our constraint would be the same as taking the tangential section of this surface at the origin, thereby recovering the above unfolding as the classical exchange of stabilities bifurcation.

The following example shows the same phenomenon in one higher dimension. Here a saddle in a 2-simplex runs into, and exchanges stabilities with, an attractor on an edge. The details of proof are left to the reader (see also Figure 11).

$$A_\varepsilon = \begin{pmatrix} 0 & 2+\varepsilon & -1 \\ 2+\varepsilon & 0 & -1 \\ 1 & 1 & 0 \end{pmatrix}$$

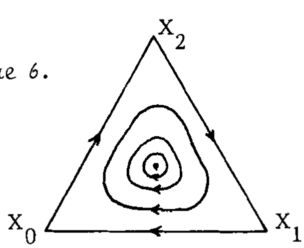
Figure 5.



Example 4. The rock-scissors-paper game.

$$A = \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix}$$

Figure 6.



The associated dynamic is given by permuting cyclically

$$\dot{x}_0 = x_0(x_1-x_2).$$

Let $V = x_0x_1x_2$. Then V has a maximum at the barycentre e, and no other stationary points in $\mathring{\Delta}$ (by an argument as in the proof of Theorem 1). Meanwhile

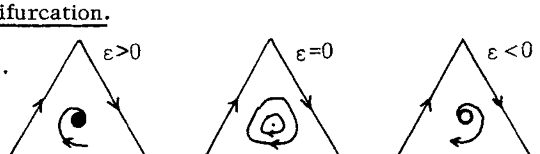
$$\dot{V} = \Sigma\frac{V}{x_i}\dot{x}_i = (x_1-x_2) + (x_2-x_0) + (x_0-x_1) = 0 .$$

Therefore the orbits of φ_A in $\mathring{\Delta}$-e are the level curves of V, which are smooth simple closed curves surrounding e. The following perturbation shows that A is unstable.

Example 5. Degenerate Hopf bifurcation.

$$A_\varepsilon = \begin{pmatrix} 0 & 1+\varepsilon & -1 \\ -1 & 0 & 1+\varepsilon \\ 1+\varepsilon & -1 & 0 \end{pmatrix}$$

Figure 7.



At the initial parameter value $\varepsilon = 0$ we have the previous example. When $\varepsilon \neq 0$ the same function V becomes a Lyapunov function for the flow, as we now show. The dynamic is given by permuting cyclically

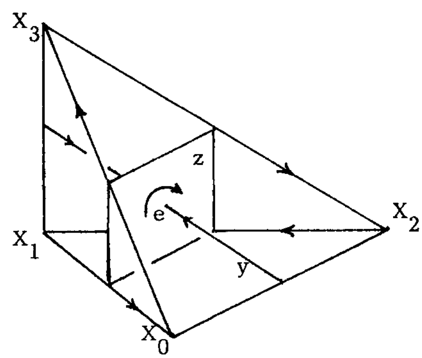
$$\dot{x}_0 = x_0(x_1-x_2+\varepsilon(x_1-\sigma)), \text{ where } \sigma = x_0x_1+x_1x_2+x_2x_0 .$$

Therefore $\dot{V} = \varepsilon(1-3\sigma)$. But σ has a maximum of $\frac{1}{3}$ at the barycentre e, and no other stationary points in Δ Therefore if $\varepsilon > 0$ then $\dot{V} > 0$ on $\mathring{\Delta} - e$, and so e is an *attractor with basin of attraction $\mathring{\Delta}$. Similarly if $\varepsilon < 0$ then $\dot{V} < 0$ on $\mathring{\Delta} - e$, and so e is a repellor with basin of repulsion $\mathring{\Delta}$. Therefore as the parameter passes through the critical value the flow exhibits a Hopf bifurcation as the fixed point switches from attractor to repellor [5].

Notice that this is a "degenerate" Hopf bifurcation in the sense that all the cycles occur at the critical value $\varepsilon = 0$, and so there are no small cycles before or after passing through the critical value. This type of Hopf bifurcation is called "degenerate" because it has codimension ∞ in the space of all 2-dimensional flows. However in our context it turns out to be typical rather exceptional, because in Theorem 6 below we show that it has codimension 1, and in Theorem 7 that all Hopf bifurcations on a 2-simplex are of this nautre. On the other hand if we raise the dimension by one then generic Hopf bifurcations do appear, as illustrated by the next example.

<ins>Example 6.</ins> <ins>Generic Hopf bifurcation.</ins>

Figure 8.



$$A = 4\begin{pmatrix} 0 & 1 & \varepsilon & 0 \\ 0 & 0 & 1 & \varepsilon \\ \varepsilon & 0 & 0 & 1 \\ 1 & \varepsilon & 0 & 0 \end{pmatrix}$$

This example is due to Sigmund and his coworkers [11 part (ii)], and they have generalised it to all $n \geq 3$. We first consider the critical case $\varepsilon = 0$, which they call the hypercycle, since it represents a cycle of 4 chemicals each catalyzing the next. We shall show the barycentre e of the tetrahedron Δ is an attractor with basin $\mathring{\Delta}$. It is convenient to choose coordinates $(y,z) \in \mathbb{R} \times \mathbb{C}$, centred at e, given by

$$y = (x_0+x_2) - (x_1+x_3)$$
$$z = z_1+iz_2 = (x_0-x_2) + i(x_1-x_3)$$

where, for this example only, the notation i means $\sqrt{-1}$. The dynamic is given by permuting cyclically

$$\dot{x}_0 = x_0(4x_1-1+y^2) \ .$$

Therefore in terms of y, z the dynamic can be rewritten

$$\dot{y} = -y+4z_1z_2+y^3$$
$$\dot{z} = -iz-(1-i)y\bar{z}+y^2z.$$

---

*Alternatively we could deduce this from Theorems 1 and 2, because e is an ESS, since $fx = 0$ and $gx = \varepsilon(\frac{1}{3}-\sigma) > 0$ on $\Delta - e$. However this argument fails to generalise when we need it for classification in Theorem 6 below.

The linear approximation at the fixed point is

$$\dot{y} = -y$$
$$\dot{z} = -iz \ .$$

Therefore the fixed point has eigenvalues -1, $\pm i$. Nevertheless e turns out to be an attractor, unlike the previous example. For consider the Lyapunov function $V = x_0x_1x_2x_3$, which has a maximum at e and no other stationary points in $\mathring{\Delta}$. Then $\dot{V} = 4Vy^2$, and so $\dot{V} > 0$ on $\mathring{\Delta}$ except on the plane $y = 0$. If $y = 0$ and $z_1z_2 \neq 0$ then $\dot{y} = 4z_1z_2 \neq 0$, and so the orbit crosses this plane transversally. If $y = z_1 = 0$ and $z_2 \neq 0$ then $\dot{z}_1 = z_2 \neq 0$, and so the orbit crosses the z_2-axis transversally. Similarly orbits cross the z_1-axis transversally. Therefore V decreases strictly along all orbits in $\mathring{\Delta}$-e. Hence e is an attractor with basin of attraction $\mathring{\Delta}$. The subtlety of this example compared with the previous one is that the orbits cannot linger in the eigenspace of the eigenvalues $\pm i$, and so they have to get sucked into e.

Now consider the perturbation $\varepsilon \neq 0$. The barycentre e is again the unique fixed point in $\mathring{\Delta}$, but this time the linearised equations at e are :

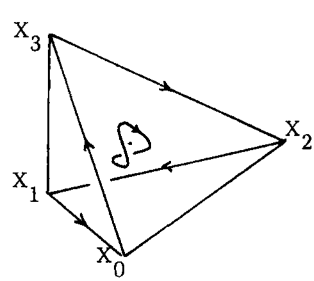
$$\dot{y} = (-1+\varepsilon)y$$
$$\dot{z} = -(\varepsilon+i)z \ .$$

This time the eigenvalues are $-1+\varepsilon$, $-\varepsilon \pm i$, and

$$\dot{V} = 4V[(1-\varepsilon)y^2 + 2\varepsilon|z|^2] \ .$$

Hence if $0 < \varepsilon < 1$ then e is an attractor (indeed an ESS) with basin $\mathring{\Delta}$. On the other hand if $\varepsilon < 0$ then e is a 1-saddle. For small $\varepsilon < 0$ there must be an attracting small closed cycle near e by the Hopf bifurcation theorem [5], since there are no small cycles for $\varepsilon \geq 0$. This attracting cycle is shaped like the seam on a tennis ball, and as ε decreases it expands out to the cycle $X_3X_2X_1X_0$ on the boundary.

Figure 9.



Chemically this example represents a mixture of 4 chemicals, and the Hopf bifurcation represents the continuous transition from a stable equilibrium into a little chemical clock - the precursor, perhaps, of the first biological clock? With only 3 chemicals this is impossible because by Theorem 7 below all Hopf bifurcations on a 2-simplex are degenerate as in the previous example, and so instead of getting a continuous transition from equilibrium to clock one would get a catastrophic breakdown of equilibrium, leading to the exclusion of two of the chemicals.

Section 3. Classification.

The eventual aim of classification is to list the equivalence classes, both the stable classes and their bordering relations with those of higher codimension, and to describe the qualitative nature of the resulting flows, bifurcations and catastrophes. In particular the classification would involve giving criteria for two matrices to be equivalent, in other words to induce topologically equivalent flows.

We begin very modestly in Lemma 3 by finding the condition for two matrices to induce the same flow. For instance if a constant is added to a column of A then the flow is unaltered. The interpretation of this in terms of game theory is as follows : if the pay-off to all strategies is increased equally then the relative advantage of each strategy is unaltered, and so the evolution is the same. Therefore given any matrix we can, without altering the flow, reduce its diagonal to zero by subtracting a suitable constant from each column. This simplifies the classification problem by reducing the dimension of the classifying space; it also explains why we have chosen zero diagonal in all our examples.

Notation. Let K_n, $\subset M_n$, be the set of nxn matrices all of whose columns are multiples of u. Let Z_n, $\subset M_n$, be the set of matrices with zero diagonal. Since $Z_n \cap K_n = 0$ we can write M_n as the direct sum or topological product

$$M_n = Z_n \times K_n .$$

Let Z_n^+ denote the dense subset of Z_n consisting of matrices with zero diagonal and non-zero off-diagonal terms.

Lemma 3. Given $A, B \in M_{n+1}$ then $\varphi_A = \varphi_B \Longleftrightarrow A - B \in K_{n+1}$.

Proof. Since $\dot{x}$ depends linearly upon A it suffices to prove $\varphi_A = 0$ if and only if $A \in K_n$.

$$\begin{aligned} \varphi_A = 0 &\Longrightarrow \dot{x} = 0, \ \forall x \in \Delta \\ &\Longrightarrow (Ax)_i \text{ independent of } i, \ \forall i, x, \text{ such that } x_i \neq 0 \\ &\Longrightarrow a_{ii}t + a_{ij}(1-t) = a_{ji}t + a_{jj}(1-t), \ \forall i,j,t, \text{ such that } \\ &\qquad 0 < t < 1 \text{ (putting } x_i = t, \ x_j = 1-t) \\ &\Longrightarrow a_{ij} = a_{jj}, \ \forall i,j \qquad \text{(comparing coefficients)} \\ &\Longrightarrow A \in K_n . \end{aligned}$$

$$\begin{aligned} \text{Conversely, } A \in K_n &\Longrightarrow a_{ij} \text{ independent of } i, \ \forall i,j \\ &\Longrightarrow (Ax)_i \text{ independent of } i, \ \forall i, x \\ &\Longrightarrow x \text{ fixed}, \ \forall x, \text{ and so } \varphi_A = 0 . \end{aligned}$$

Corollary. Every equivalence class in M_{n+1} is of the form $E \times K_{n+1}$, where E is an equivalence class of Z_{n+1}. Therefore stables are dense in M_{n+1} if and only if they are dense in Z_{n+1}, and to classify equivalence and stable classes in M_{n+1} it suffices to classify them in Z_{n+1}.

Classification for n = 1. The corollary enables us to dispose of this case at once. Here Δ is a 1-simplex, and Z_2 consists of games of the form $A = \begin{pmatrix} 0 & a \\ b & 0 \end{pmatrix}$. By examining the fixed points it is easy to verify there are 4 equivalence classes, as follows. In the first two classes there is a fixed point $e = \left(\frac{a}{a+b}, \frac{b}{a+b}\right) \in \mathring{\Delta}$, which is an attractor in the first class, and a repellor in the second. As usual, attractors are indicated by solid dots and repellors by open dots. In class (iv) all points are fixed. Equivalences can be constructed by mapping fixed points to fixed points and extending piecewise linearly. If one of the variables changes sign while the other remains non-zero there is an exchange of stabilities bifurcation as in Example 3 above.

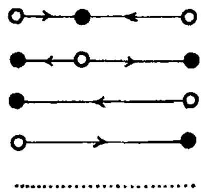
(i) $a, b > 0$

(ii) $a, b < 0$

(iii) $a \geq 0 \geq b$, not both zero

$a \leq 0 \leq b$, not both zero

(iv) $a = b = 0$.



Therefore A is stable $\Leftrightarrow A \in Z_2^+$. Therefore there are 3 stable classes (or 2 up to flow reversal since (i) is the reverse of (ii)), given by

(i) $a, b > 0$

(ii) $a, b < 0$

(iii) $a > 0 > b$ or $a < 0 < b$.

Lemma 4. $A \in Z_{n+1}$ and A stable $\Rightarrow A \in Z_{n+1}^+$.

Proof. Suppose not. Then $a_{ij} = 0$ for some $i \neq j$. Let Γ denote the edge ij. If $a_{ji} \neq 0$ then there are no fixed points in $\mathring{\Gamma}$, and a perturbation making a_{ij} the same sign as a_{ji} will introduce a fixed point in $\mathring{\Gamma}$, making an extra fixed point in the 1-skeleton of Δ, and hence an inequivalent flow. Therefore A is unstable. If $a_{ji} = 0$ then Γ is pointwise fixed, and a perturbation making a_{ij} non-zero will have no fixed point in $\mathring{\Gamma}$, making one fewer pointwise-fixed edge in the 1-skeleton, and hence an inequivalent flow. Therefore again A is unstable and the Lemma is proved.

Saddle points. Recall a fixed point is called hyperbolic if its eigenvalues have non-zero real part. It is called a saddle of index r, or more briefly an r-saddle, if the inset (= stable manifold) has dimension r and the outset (= unstable manifold) has dimension n - r. For instance an attractor is an n-saddle, and a repellor is a 0-saddle.

Lemma 5. If $A \in Z_{n+1}^+$ then all the vertices of Δ are hyperbolic. The index of X_j equals the number of negative terms in the jth column, and the inset, outset of X_j are open subsets of the faces $\{i; a_{ij} \leq 0\}$, $\{i; a_{ij} \geq 0\}$ respectively.

Proof. Taking $x_i, i \neq j$, as local coordinates at X_j, the linearization of the dynamic at X_j is $\dot{x}_i = a_{ij}x_i, i \neq j$. Hence the eigenvalues of X_j are $a_{ij}, i \neq j$, which are non-zero by the hypothesis $A \in Z_{n+1}^+$. Therefore X_j is hyperbolic with the required index. Since the faces of Δ are invariant X_j is an attractor, repellor of the induced flows on the two faces specified, and so its basins of attraction in them are open subsets of them, and these are the same as its inset, outset under φ_A.

Combinatorial equivalence. Given $A, B \in Z_{n+1}^+$ call them sign equivalent if corresponding off-diagonal elements have the same sign. Denote a sign class by the corresponding matrix of signs. Given a permutation σ of $\{0, 1, \ldots, n\}$ let σA denote the matrix obtained by permuting both rows and columns by σ. Call A, B combinatorially equivalent if $\sigma A, B$ are sign equivalent for some σ.

Lemma 6. Stable classes refine combinatorial classes.

Proof. By Lemma 4 stable classes in Z_{n+1} are contained in Z^+_{n+1}, and so it suffices to show that $A \sim B$ implies A is combinatorially equivalent to B. Let h be a face-preserving homeomorphism of Δ inducing $A \sim B$. In particular h permutes the vertices, by a permutation σ, say. If σ_* denotes the induced linear homeomorphism of Δ then σ_* gives an equivalence $A \sim \sigma A$. Therefore $h\sigma_*^{-1}$ gives an equivalence $\sigma A \sim B$, that fixes the vertices. But any equivalence maps insets to insets and outsets to outsets. Therefore σA is sign equivalent to B by Lemma 5, and so A is combinatorially equivalent to B, as required.

Therefore the problem of classifying stable classes can be split into two, firstly the listing of combinatorial classes, and then the decomposition of them. It is a straightforward combinatorial task to list them, since each is characterised by the fixed points in the 1-skeleton of Δ, although the list tends to get large as n increases. Meanwhile to decompose a combinatorial class it suffices to consider a single sign class (since all the other sign classes decompose isomorphically). In each sign class there seems to be relatively few equivalence classes, although to establish the actual decomposition in each case appears to be a non-trivial problem.

Theorem 5. The number of combinatorial class (up to sign reversal) is as follows:-

n	1	2	3	...
number of classes	2	10	114	

The case n = 1 has been already done above; we shall prove the case n = 2 and leave n = 3 to the reader. Figure 10 illustrates the 10 cases for n = 2 by giving in each case an example of the flow on the 1-skeleton. As abbreviated visual notation we only put an arrow on an edge if there is no fixed point in the interior of the edge, and otherwise indicate the fixed point by a solid, open dot according as to whether it is an attractor, repellor for that edge, although of course when the flow is extended over the interior it may in fact turn out to be a 1-saddle, depending upon the coefficients in A.

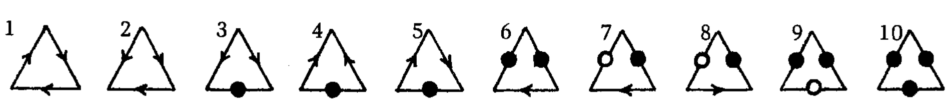


Figure 10.

Proof. We compute the number N_r of classes having fixed points inside r edges by listing the inequivalent ways of putting arrows on the other edges. $N_0 = 2$ because the arrows can be cyclic or not, giving classes 1,2. $N_1 = 3$ because up to flow reversal we can choose the fixed point to be an attractor, and then the opposite vertex can be a repellor, attractor or saddle, giving classes 3,4,5. $N_2 = 3$ because if the two fixed points are similar the direction of the arrow does not matter, giving class 6, but if they differ it does, giving classes 7,8. Finally $N_3 = 2$ because the three fixed points can be similar or not, giving classes 9,10.

Now comes the more difficult business of decomposing combinatorial classes into stable classes. We only attempt this for n = 2, because this dimension seems to have the following convenient property.

Conjecture 3. If $n = 2$ the fixed points determine the stable classes. The conjecture looks harmless, but is surprising because it implies there are no periodic orbits in the stable classes. This in turn implies that there are no generic Hopf bifurcations, but we prove this result separately in Theorem 7 below. (For $n \geq 3$ there are generic Hopf bifurcations by Example 6 above). The conjecture also implies the classification :

Corollary to Conjecture 3. If $n = 2$ there are 19 stable classes (up to flow reversal) as shown in Figure 11. Taylor and Jonker [14] and Schuster et al. [11, Part (iv)] have published computer drawings of some, but not all, of these 19 classes. We have arranged them in Figure 11 so that the first 5 classes are those with an attractor in the interior, the next 4 are those with a saddle, and the last 10 are those without a fixed point in the interior;of the latter the first 4 have one attractor on the boundary, the next 5 have two attractors, and the last has three attractors. In each class we have chosen a representative matrix such that, if there is a fixed point in the interior, it is the barycentre, and, if not, the fixed points on the edges are at their barycentres. We have labelled each class by the combinatorial class containing it (see Figure 10), with a suffix if necessary, and a minus sign in those cases without a fixed point in the interior where the reverse flow has been chosen in order to maximise the number of attractors on the boundary. The three combinatorial classes 2, 3 and 8 are in fact equal to stables classes, but the other seven combinatorial classes each contain more than one stable class. In particular class 1 contains both the class shown and its reversal. It can be shown that the 19 cases are the only possible stable configurations of fixed points, and that these configurations are dense. In the last 14 cases it is easy to verify by Poincaré-Bendixson theory [3] that the fixed points determine the topology of the phase portrait, but in the first 5 cases this is not so obvious because it is necessary to prove the non-existence of periodic orbits surrounding the attractor. We prove this for class 1 in Theorem 6 below, but my proof for the other 4 classes is incomplete. Before we prove this we simplify the problem by showing how to move a fixed point in the interior to the barycentre.

Let P be a positive diagonal matrix $P = \begin{pmatrix} p_0 & & 0 \\ & \ddots & \\ 0 & & p_n \end{pmatrix}$, where $p_i > 0$, $i = 0, 1, \ldots, n$.

Let $p: \Delta \to \Delta$ be the induced projective map given by $(px)_i = \pi^{-1} p_i x_i$, where $\pi = \Sigma p_i x_i$.

Lemma 7. p induces an equivalence $AP \sim A$.

Proof. Let v, w be the vector fields on Δ induced by A, AP respectively. Then

$$(vx)_i = x_i((Ax)_i - xAx), \qquad (wx)_i = x_i((APx)_i - xAPx).$$

The derivative maps $((Dp)w)_i = \sum_j \frac{\partial}{\partial x_j} (px)_i w_j = \pi^{-1} p_i w_i - \pi^{-2} p_i x_i \sum_j p_j w_j$

$$\therefore\ ((Dp)wx)_i = \pi^{-1} p_i x_i (APx)_i - \pi^{-2} p_i x_i \Sigma p_j x_j (APx)_j$$

(since the other two terms cancel)

$$= p_i x_i ((A\pi^{-1}Px)_i - xP\pi^{-1}A\pi^{-1}Px)$$

$$= \pi (v(px))_i$$

Therefore Dp maps w onto v multiplied by the scalar π, and so p maps φ_{AP}-orbits to φ_A-orbits as required.

Call a matrix central if it has an isolated fixed point at the barycentre of Δ. Suppose we are now given A with an isolated fixed point $e \in \mathring{\Delta}$ (which is then the unique fixed point in $\mathring{\Delta}$ by Lemma 1). Let E denote the diagonal matrix with e along the diagonal. Define the centralisation of A to be the matrix $\overline{A} = (n+1)AE$.

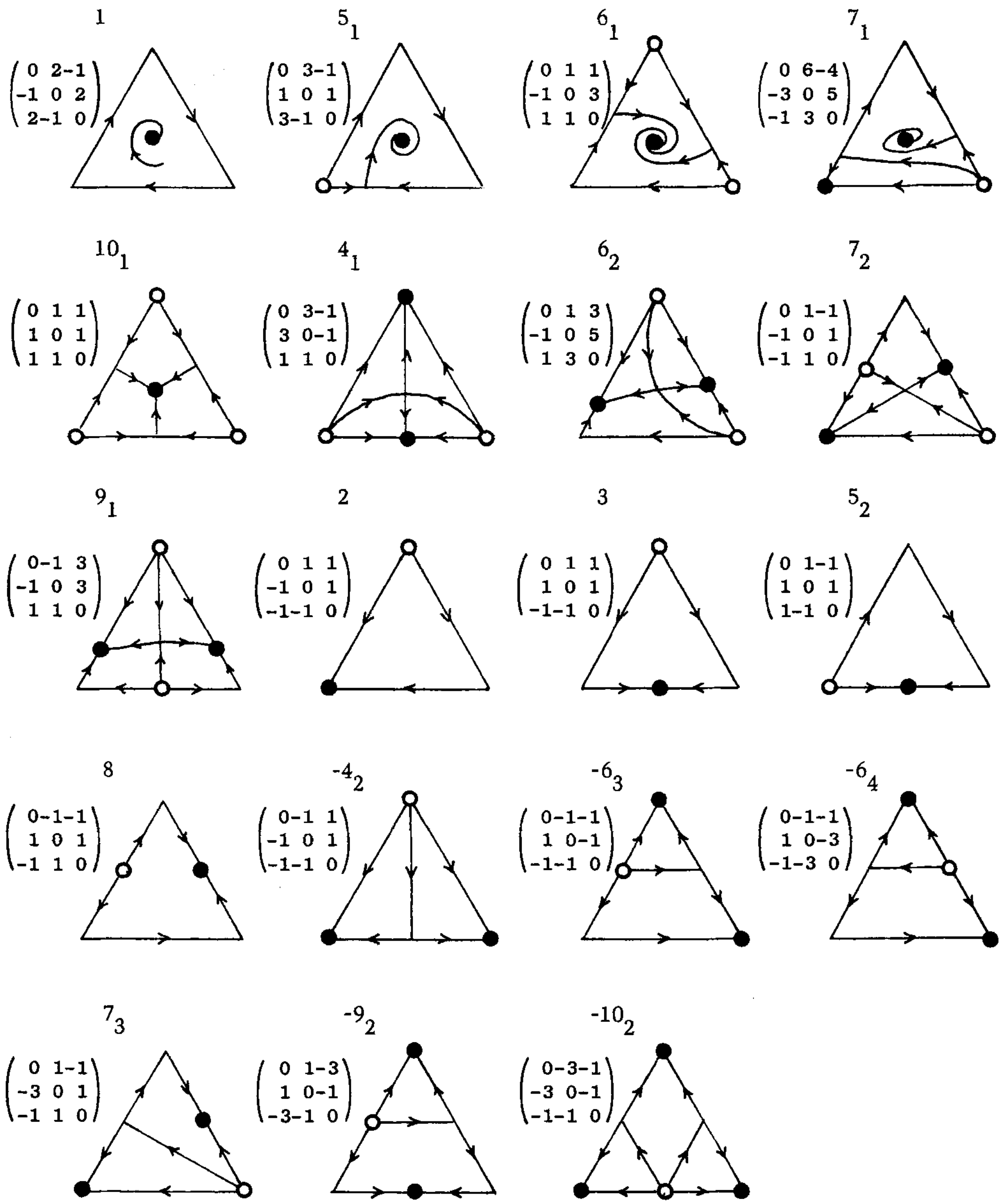


Figure 11. *The conjectured list of 19 stable classes for $n=2$ (up to flow reversal). Attractors are marked with a solid dot, repellors by an open dot, and saddles by their insets and outsets. All other orbits flow from a repellor to an attractor, except in class 1, where the α-limit is the boundary. The numbers refer to the combinatorial class in Figure 10, and a minus sign indicates flow reversal. A representative matrix is given for each class.*

Lemma 8. $\bar{A}$ is central and $\bar{A} \sim A$. If A central then $\bar{A} = A$.

Proof. Let $P = (n+1)E$. Then $\bar{A} = AP$ and so $p: \bar{A} \sim A$ by Lemma 7. Meanwhile p maps the barycentre to e, and so $\bar{A}$ is central. If A is already central then $P = I$, and so $\bar{A} = A$.

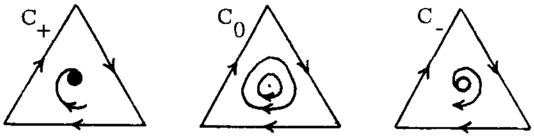
Let C = combinatorial class 1, which consists of the two sign classes

$$S = \begin{pmatrix} 0 & + & - \\ - & 0 & + \\ + & - & 0 \end{pmatrix}, \qquad -S = \begin{pmatrix} 0 & - & + \\ + & 0 & - \\ - & + & 0 \end{pmatrix}$$

Let C_+, C_0, C_- denote the subsets of C given by det $A \gtreqless 0$. (Note that each subset meets each sign class.)

Theorem 6. Two matrices in C are equivalent if and only if their determinants have the same sign. Therefore C contains three equivalence classes, of which C_+, C_- are stable classes and flow reversals of each other, while C_0 is unstable, being a submanifold of codimension 1 separating the stable classes. If $A \in C_+, C_-$ then φ_A has an attractor, repellor in $\mathring{\Delta}$ with basin of attraction, repulsion equal to $\mathring{\Delta}$. If $A \in C_0$ then φ_A has a focus in $\mathring{\Delta}$, and all other orbits in $\mathring{\Delta}$ are cycles. The phase portraits are :

Figure 12.



Therefore any path in C crossing C_0 transversally induces a degenerate Hopf bifurcation, as in Example 5 above.

Example 7. Before we prove Theorem 6 we use it to correct a mistake of Taylor and Jonker [14, p.151]. They give a (computer inspired) example

$$A = \begin{pmatrix} 2 & 1 & 5 \\ 5 & \alpha & 0 \\ 1 & 4 & 3 \end{pmatrix}$$

which they claim has an attractor in $\mathring{\Delta}$ when $\alpha = 3$, undergoes a generic Hopf bifurcation when α passes 3, and has a small attracting cycle with $\alpha = 3 + \varepsilon$, $\varepsilon > 0$, provided ε sufficiently small. However, by Lemma 3, A gives the same flow as

$$B = \begin{pmatrix} 0 & 1-\alpha & 2 \\ 3 & 0 & -3 \\ -1 & 4-\alpha & 0 \end{pmatrix}$$

and $\det B = 9(3-\alpha) = -9\varepsilon$. Therefore by Theorem 6 when $\alpha = 3$ the fixed point is a focus rather than an attractor, as α passes 3 the Hopf bifurcation is degenerate rather than generic, and when $0 < \varepsilon < 1$ the fixed point is a repellor with basin of repulsion $\mathring{\Delta}$, so there are no cycles.

Proof of Theorem 6. Up to equivalence it suffices to confine attention to the sign class S, because if $B \in -S$, and σ is any odd permutation, then $\sigma B \in S$, $\sigma B \sim B$ and $\det \sigma B = \det B$. Therefore suppose $A \in S$. Then all the coefficients of adjA are positive, and hence so are those of (adjA)u. Therefore the vector subspace generated by (adjA)u meets $\mathring{\Delta}$ is a point e, which is therefore the unique fixed point of φ_A in $\mathring{\Delta}$. By Lemma 8, A is equivalent to its centralisation. Therefore up to equivalence it suffices to assume A is central, in other words e is the barycentre. Therefore, since $(Ae)_i$ is independent of i, the sum of the columns of A is a multiple of u, $= 2\theta u$ say. Therefore we can write

$$A = \begin{pmatrix} 0 & \theta+a_0 & \theta-a_0 \\ \theta-a_1 & 0 & \theta+a_1 \\ \theta+a_2 & \theta-a_2 & 0 \end{pmatrix}, \quad 0 \le |\theta| < a_i .$$

Then $\det A = 2\theta(\theta^2+\rho)$, where $\rho = a_0a_1 + a_1a_2 + a_2a_0 > 0$. Therefore $\det A \gtreqless$ as $\theta \gtreqless 0$.

We now construct a Lyapunov function V for φ_A in $\mathring{\Delta}$ as follows. For $i = 0,1,2$ let $b_i = \frac{b}{a_i}$, where $b = (\Sigma \frac{1}{a_i})^{-1}$. Then $b_i > 0$ and $\Sigma b_i = 1$. Given $x \in \mathring{\Delta}$, let

$$V = PQ, \text{ where } P = \prod x_i^{-b_i},\ Q = \Sigma b_i x_i .$$

Then $V_i \equiv \frac{\partial V}{\partial x_i} = PQ_i + P_iQ = Pb_i - \frac{Pb_iQ}{x_i}$. By Lagrange's method V has a stationary point at x provided $V - \lambda(\Sigma x_i - 1)$ is stationary. $\therefore V_i - \lambda = 0$

$$\therefore Pb_ix_i - Pb_iQ - \lambda x_i = 0.$$

Summing over i, $\lambda = 0$. $\therefore x_i = Q$. $\therefore x = e$. Therefore e is the only stationary point of V in $\mathring{\Delta}$, and is a minimum because $V \to \infty$ as $x \to \partial\Delta$.

$$\begin{aligned} \dot{V} = \Sigma V_i \dot{x}_i &= \Sigma Pb_i(1-\tfrac{Q}{x_i})x_i[(Ax)_i - xAx] \\ &= P\Sigma b_i(x_i-Q)[(Ax)_i - xAx] \\ &= P[\Sigma b_ix_i(Ax)_i - QbAx], \text{ since the other two terms cancel.} \end{aligned}$$

$$\begin{aligned} \text{Now } b_0x_0(Ax)_0 &= b_0x_0[(\theta+a_0)x_1 + (\theta-a_0)x_2] \\ &= \theta b_0(x_0x_1+x_0x_2) + b(x_0x_1-x_0x_2) \\ \therefore \Sigma b_ix_i(Ax)_i &= \theta \sum_{i<j}(b_i+b_j)x_ix_j . \\ b_0(Ax)_0 &= b_0[(\theta+a_0)x_1 + (\theta-a_0)x_2] \\ &= \theta b_0(x_1+x_2) + b(x_1-x_2) \\ \therefore bAx &= \theta \sum_{i\neq j} b_ix_j = \theta\Sigma(1-b_j)x_j , \quad \text{since } \Sigma b_i = 1 \\ \therefore QbAx &= \theta\Sigma b_ix_i\Sigma(1-b_j)x_j = \theta[\Sigma b_i(1-b_i)x_i^2 + \sum_{i\neq j} b_i(1-b_j)x_ix_j] \\ &= \theta\sum_{i<j}[b_ib_j(x_i^2+x_j^2) + (b_i+b_j-2b_ib_j)x_ix_j] \\ &= \theta\sum_{i<j}[b_ib_j(x_i-x_j)^2 + (b_i+b_j)x_ix_j] . \\ \therefore \dot{V} &= -\theta P\sum_{i<j} b_ib_j(x_i-x_j)^2 \end{aligned}$$

If $x \in \mathring{\Delta} - e$ then $x_i \neq x_j$ for some $i \neq j$, and so

$$\dot{V} \lesseqgtr 0 \text{ as } \theta \gtreqless 0, \text{ hence as } \det A \gtreqless 0.$$

If $\det A > 0$ all orbits in $\mathring{\Delta} - e$ flow towards the minimum e of V, which is therefore an attractor with basin $\mathring{\Delta}$. Similarly if $\det A < 0$ then e is a repellor with basin $\mathring{\Delta}$. If $\det A = 0$ then $\dot{V} = 0$ and the orbits of φ_A in $\mathring{\Delta} - e$ are the level curves of V, which are all simple closed curves surrounding e. We have established the phase portraits. Given two central matrices A, B whose determinants have the same sign we need to show they are equivalent, and in order to construct the required homeomorphism the following lemma is convenient.

Lemma 9. The orbits in $\mathring{\Delta} - e$ cross the rays through e transversally, going clockwise around e.

Proof. $\dot{x} \wedge (x-e)$ = multiple of u, $= \frac{1}{3}\delta u$ say. We need to show that $\delta > 0$ on $\mathring{\Delta} - e$. Throughout this proof let Σ denote the sum of the three terms obtained by permuting the suffices 012 cyclically. Adding the components of $\dot{x} \wedge (x-e)$ gives

$$\delta = \Sigma \dot{x}_0(x_1 - x_2) = \Sigma x_0 (Ax)_0 (x_1 - x_2).$$

When $\theta = 0$, $(Ax)_0 = a_0(x_1 - x_2)$, and so

$$\delta = \Sigma a_0 x_0 (x_1 - x_2)^2 > 0, \text{ since } x_i \neq 0, \text{ some } x_i \neq x_j .$$

When $\theta > 0$, $(Ax)_0 = (a_0 - \theta)(x_1 - x_2) + 2\theta x_1$, and so

$$\delta = \Sigma(a_0 - \theta) x_0 (x_1 - x_2)^2 + 2\theta\alpha, \text{ where } \alpha = \Sigma x_0 x_1 (x_1 - x_2) .$$

Since $|\theta| < a_i$ the first term > 0, and so it suffices to show $\alpha \geq 0$ in Δ. Let $\beta = \Sigma x_0(x_0 - x_1)$. Now $\alpha, \beta \geq 0$ on $\partial\Delta$, because if $x = (s, 1-s, 0)$, $0 \leq s \leq 1$, or cyclically for the other sides, then

$$\alpha x = s(1-s)^2 \geq 0, \quad \beta x = 3s^2 - 3s + 1 > 0 .$$

Therefore if $x_t = tx + (1-t)e$, $x \in \partial\Delta$, $0 \leq t \leq 1$,

$$\alpha(x_t) = t^3 \alpha x + \tfrac{1}{3} t^2 (1-t) \beta x \geq 0 .$$

Finally the case $\theta < 0$ is obtained by reversing the flow and permuting 01.

Returning to the proof of Theorem 6, we can construct a radial homeomorphism of Δ keeping e and $\partial\Delta$ fixed, and throwing φ_A-orbits to φ_B-orbits by the standard technique of structural stability [10] of using the two Poincaré return maps on one particular ray, and extending orbitwise to the other rays. Hence $A \sim B$.

Finally C_0 is a submanifold of codimension 1 separating $C_{\pm}$ necause we can parametrise any matrix in C by the parameters (e, θ, a_i) where e denotes its fixed point and θ, a_i denote the parameters of its centralisation . This completes the proof of Theorem 6.

Remark. If we allow the parameters a_i to be negative, then we can use the same Lyapunov function V to determine the phase portraits of the four other stable classes in Figure 11 with an attractor (or repellor) in $\mathring{\Delta}$ provided $\rho > 0$. However, if $\rho < 0$ then V is no good because its stationary point becomes a saddle rather than a maximum or minimum, and so what is needed to complete the proof of Conjecture 3 is to find another Lyapunov function to cover the case $\rho < 0$. On the other hand we shall show that Hopf bifurcations can only occur when $\rho > 0$, and so we can at least classify those.

Suppose A has an isolated fixed point $e \in \mathring{\Delta}$, and centralisation

$$\bar{A} = 3AE = \begin{pmatrix} 0 & \theta+a_0 & \theta-a_0 \\ \theta-a_1 & 0 & \theta+a_1 \\ \theta+a_2 & \theta-a_2 & 0 \end{pmatrix}, \quad \theta, a_i \in \mathbb{R}$$

We call θ, a_i the central parameters of A. As before let $\rho = a_0a_1+a_1a_2+a_2a_0$.

Lemma 10. The eigenvalues of φ_A at e are $\frac{1}{3}(-\theta \pm \sqrt{-\rho})$. Therefore they depend only on the central parameters and not on e.

Proof. Let $x = e+y$. Then $yu = 0$ and so $yAe = 0$.

$$\therefore \dot{y}_i = (e_i+y_i)[(Ae)_i + (Ay)_i - eAe - eAy - yAe - yAy]$$
$$= e_i[(Ay)_i - eAy] + \text{higher order terms in } y.$$

Therefore the linearisation et e is

$$\dot{y} = EAy - e(eAy) = (E-ee)Ay.$$

The eigenvalues are the same as those of the matrix

$$M = A(E-ee) = AE - (Ae)e = AE - (\tfrac{2}{3}\theta u)e, \text{ since } Ae = AEu = \tfrac{2}{3}\theta u,$$

$$= \frac{1}{3}\begin{pmatrix} -2\theta e_0 & \theta+a_0-2\theta e_1 & \theta-a_0-2\theta e_2 \\ \theta-a_1-2\theta e_0 & -2\theta e_1 & \theta+a_1-2\theta e_2 \\ \theta+a_2-2\theta e_0 & \theta-a_2-2\theta e_1 & -2\theta e_2 \end{pmatrix}$$

Now $\det M = 0$ because $(E-ee)u = 0$. Therefore the eigenvalues are given by $\lambda^3-2\alpha\lambda^2+\beta\lambda = 0$, where

$$2\alpha = \text{trace } M = -\frac{2\theta}{3}. \quad \therefore \alpha = -\frac{\theta}{3}.$$
$$\beta = \text{trace}(\text{adj}M) = \frac{1}{9}\Sigma[-(\theta+a_0)(\theta-a_1) + 2\theta e_0(\theta+a_0) + 2\theta e_1(\theta-a_1)]$$
$$= \frac{1}{9}(\theta^2+\rho).$$

The eigenspace corresponding to $\lambda = 0$ is transverse to Δ, and so the eigenvalues for φ_A are $\lambda = \alpha \pm \sqrt{\alpha^2-\beta} = \frac{1}{3}(-\theta \pm \sqrt{-\rho})$.

Theorem 7. When n = 2 all Hopf bifurcations are degenerate.

Proof. For a Hopf bifurcation to occur at a matrix A_0, it is necessary for it to have an isolated fixed point $e \in \mathring{\Delta}$ with pure imaginary eigenvalues. Therefore if θ, a_i denote the central parameters of A_0 then $\theta = 0$ and $\rho > 0$ by Lemma 10. Up to equivalence it suffices to assume A_0 central, by Lemma 8, since this does not affect the eigenvalues, by Lemma 10. There are three cases :-

(1) All a_i non-zero and the same sign.

(2) All a_i non-zero, but not all the same sign.

(3) Some $a_i = 0$.

Case (1) is covered by Theorem 6. In case (2), by permuting and reversing sign if necessary, we can assume

$$a_0, a_1 > 0, \quad a_2 < 0.$$

As before let $b = (\Sigma \frac{1}{a_i})^{-1} = \frac{a_0 a_1 a_2}{\rho}$, $b_i = \frac{b}{a_i}$. Then $\Sigma b_i = 1$ and $b_2 > 0$. but $b, b_0, b_1 < 0$. We use the same Lyapunov function V as in Theorem 6, and again the only stationary point of V in $\mathring{\Delta}$ is the barycentre e. However, this time V = 0 on the edges X_0X_2, X_1X_2 and on the line Q = 0, which meets those edges in points

$$Y = \left(\frac{a_0}{a_0-a_2}, \ 0 \ , \frac{-a_2}{a_0-a_2}\right), \ Z = \left(0, \frac{a_1}{a_1-a_2}, \frac{-a_2}{a_1-a_2}\right) \ .$$

Also $V \to -\infty$ as $x \to$ interior (edge X_0X_1). The level curves of V are illustrated in the middle picture of Figure 13 below. The condition $\rho > 0$ implies that e lies inside the triangle X_2YZ, in which $V > 0$, and so e is a maximum, and the level curves inside the triangle are simple closed curves surrounding e. Meanwhile inside the complementary trapezium $V < 0$ and the level curves are arcs joining X_0, X_1. As before $\dot{V} = 0$ in $\mathring{\Delta}$ because $\theta = 0$. Therefore the orbits of φ_{A_0} are the level curves of V, with a focus at e, an attractor at X_0, a repellor at X_1, saddles at X_2, Y, Z, and a saddle-connection ZY, as shown in Figure 13.

Now consider a perturbation A of A_0. We can assume A has an isolated fixed point in $\mathring{\Delta}$, since this is a robust property by Theorem 4, and so up to equivalence we can centralise A. Therefore we can write A in the same form as in the proof of Theorem 6, with fixed point at the barycentre e, and central parameters θ, a_i satisfying

$$a_0, a_1 > 0, \quad a_2 < 0, \quad |\theta| < |a_2|, \ \rho > 0.$$

As before

$$\dot{V} = -\theta P \sum_{i<j} b_i b_j (x_i - x_j)^2 = K\psi \text{ say, where}$$

$$K = -\frac{6Pb^2}{a_0 a_1 a_2} \gtrless 0 \text{ as } \theta \gtrless 0, \text{ since } a_2 < 0, \text{ and}$$

$$\psi = \text{cyclic sum } \Sigma a_i (x_j - x_k)^2 \ .$$

Lemma 11. $\psi > 0$ on $\Delta - e$.

Proof. Notice that the sum of any pair of a_i's is positive, for :

$$\begin{aligned} a_0 + a_1 &> 0 &&, \quad \text{since } a_0, a_1 > 0 \\ a_0(a_1+a_2) &> -a_1 a_2 &&, \quad \text{since } \rho > 0 \\ &> 0 &&, \quad \text{since } a_1 > 0 > a_2 \\ \therefore a_1 + a_2 &> 0 &&, \quad \text{since } a_0 > 0 \ . \\ a_0 + a_2 &> 0 &&, \quad \text{similarly.} \end{aligned}$$

It suffices to prove the lemma for $x \in \partial\Delta$, because if $x_t = tx + (1-t)e$ then $\psi(x_t) = t^2\psi x > 0$, $\forall t$, $0 < t \le 1$. If $x = (s, 1-s, 0)$ then

$$\begin{aligned}\psi x &= a_0(1-s)^2 + a_1 s^2 + a_2(2s-1)^2 \\ &= (a_0+a_1+4a_2)s^2 - 2(a_0+2a_2)s + (a_0+a_2) \\ &> 0, \ \forall s, \text{ since}\end{aligned}$$

$a_0 + a_2 > 0$, and $(a_0+a_1+4a_2)(a_0+a_2) - (a_0+2a_2)^2 = \rho > 0$. Therefore $\psi > 0$ on X_0X_1, and similarly on the other edges. This completes the proof of Lemma 11.

Continuing with the proof of Theorem 7 we have shown $\dot{V} \gtreqless 0$ as $\theta \gtreqless 0$ on $\mathring{\Delta} - e$. Therefore if $\theta > 0$ then φ_A has an attractor at e. It also has another attractor at X_0, a repellor at X_1, and saddles at X_2, Y_θ, Z_θ, where

$$Y_\theta = \left(\frac{a_0-\theta}{a_0-a_2-2\theta}, \ 0 \ , \ \frac{-a_2-\theta}{a_0-a_2-2\theta}\right) \in YX_0$$

$$Z_\theta = \left(0, \frac{a_1+\theta}{a_1-a_2+2\theta}, \ \frac{-a_2+\theta}{a_1-a_2+2\theta}\right) \in ZX_2$$

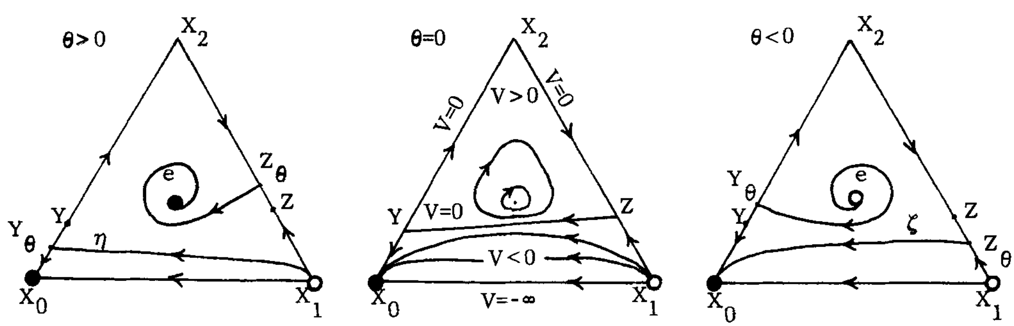


Figure 13.

Therefore, since $\dot{V} > 0$, the inset η of Y_θ must come from the repellor X_1, and the outset of Z_θ must go to the attractor e. Since $\dot{V} > 0$ there are no closed cycles in $\mathring{\Delta} - e$, and so all orbits in $\mathring{\Delta} - e$ must come from X_1, and, except for η, must go to X_0 or e. Therefore η separates the basins of attraction of X_0 and e, and the phase portrait is as in Figure 13. The numerical Example 1 in Section 1 above was obtained by putting $a_0 = 5$, $a_1 = 4$, $a_2 = -2$, $\theta = 1$.

If $\theta < 0$ then the reverse situation occurs, with X_0 the only attractor, e a repellor, and the outset ζ of Z_θ separating the basins of repulsion of e and X_1.

Let J denote the open subset of the sign class $\begin{pmatrix} 0 & + & - \\ - & 0 & + \\ - & + & 0 \end{pmatrix}$ consisting of matrices having an isolated fixed point in $\mathring{\Delta}$, and central parameters θ, a_i such that $a_1, a_2 > 0$, $a_2 < 0$, $|\theta| < |a_2|$, $\rho > 0$. We have shown that the subsets J_+, J_0, J_- of J given by $\theta \gtreqless 0$ have phase portraits as in Figure 13. Given two matrices in the same subset we show equivalence by constructing a homeomorphism of Δ throwing orbits to orbits, as follows. When $\theta \neq 0$

the flows are gradient-like, so the construction uses the standard techniques of structural stability [9], mapping fixed points to fixed points, and extending inductively to tubular neighbourhoods of their insets, starting with repellors and finishing with attractors. When $\theta = 0$ again map fixed points to fixed points and extend piecewise linearly to $\partial\Delta \cup YZ$; then map the inside of the triangle radially from e so as to preserve orbits, and use the structural stability technique inside the trapezium.

Therefore $J_{\pm}, J_0$ are the intersections of J with 3 equivalence classes. Since $J_{\pm}$ are open, they are contained in stable classes; J_+ is contained in class 7_1 of Figure 11, and J_- in the reversal. However they are not connected components of the stable classes, because the latter also contain matrices for which $\rho \leq 0$. On the other hand J_0 is a connected component of its equivalence class because by Lemma 9 a focus implies $\rho > 0$; the other 5 components are obtained by the action on the triangle of the symmetry group of order 6. Now J is a neighbourhood of J_0, and J_0 is a submanifold of codimension 1 separating $J_{\pm}$. Therefore to obtain a Hopf bifurcation we must take a path in J crossing J_0 transversally from J_+ to J_-. As this path crosses J_0 there occur simultaneously the degenerate Hopf bifurcation at e and the crossing of the saddle-connection ZY. The latter is really part of the former, and that explains why the simultaneity can be a codimension 1 phenomenon.

There remains case (3), where the matrix A_0 has one of its central parameters $a_i = 0$. Since $\rho > 0$ the other two a's must be non-zero and the same sign, and so without loss of generality suppose $a_0, a_1 > 0$, $a_2 = 0$, $\theta = 0$. Consider the perturbation A of A_0 given by putting $a_2 = 2\theta \neq 0$.

$$A = \begin{pmatrix} 0 & \theta+a_0 & \theta-a_0 \\ \theta-a_1 & 0 & \theta+a_1 \\ 3\theta & -\theta & 0 \end{pmatrix}, \quad |\theta| < a_0, a_1.$$

When $\theta > 0$ the phase portrait of φ_A is as in case (1), the left-hand picture in Figure 12, and when $\theta < 0$ it is as in case (2), the right-hand picture in Figure 13. Therefore there are no small cycles when $\theta \neq 0$, and so by the Hopf bifurcation theorem [5] there is a 1-parameter family of cycles surrounding e in the phase portrait of φ_{A_0}. Therefore any path through A_0 transverse to $\theta = 0$ induces a degenerate Hopf bifurcation. This completes the proof of Theorem 7.

References.

1. M. Eigen & P. Schuster, The Hypercycle, a principal of natural self organisation. (A) Emergence of the hypercycle *Naturwissenschaften* 64 (1977) 541-565; (B) The abstract hypercycle 65 (1978), 7-41; (C) The realistic hypercycle 65 (1978) 341-369.

2. W.G.S. Hines, Strategy stability in complex populations, Preprint, Guelph, Ontario, 1979.

3. M.W. Hirsch & S. Smale, *Differential equations, dynamical systems and linear algebra,* Academic, New York, London, 1974.

4. J. Hofbauer, P. Schuster & K. Sigmund, A note on evolutionary stable strategies and game dynamics, *J. theor. Biol,* (to appear).

5. J. Marsden & M. McCracken, *The Hopf bifurcation and its applications,* Appl. Math. Sc. 19 Springer, New York, 1976.

6. J. Maynard Smith & G.R. Price, The logic of animal conflicts, *Nature* 246 (1973) 5427, 15-18.

7. J. Maynard Smith, The theory of games and the evolution of animal conflicts, *J. theor. Biol.* 47 (1974) 209-221.

8. J. Maynard Smith, Evolution and the theory of games, *Am. Scientist,* 64 (1976) 41-45.

9. J. Palis & S. Smale, Structural stability theorems, *Global Analysis, Proc. Symp. Pure Math.* 14, Am. Math. Soc. (1970) 223-231.

10. M.M. Peixoto, Structural stability on two-dimensional manifolds, *Topology* 1 (1962) 101-120.

11. P. Schuster, K. Sigmund & R. Wolff, Dynamical systems under constant organisation. I : Topological analysis of a family of non-linear differential equations, *Bull. Math. Biophys.* 40 (1978), 743-769. II (with J. Hofbauer) : Homogeneous growth of functions of degree p = 2, *SIAM J. Appl. Math.* (to appear). III : Cooperative and competitive behaviour of hypercycles, *J. Diff. Eq.* 32 (1979), 357-368. IV : Second order growth terms for mass action kinetics, Preprint, Vienna, 1979.

12. P. Schuster, K. Sigmund & R. Wolff, A mathematical model of the hypercycle, Preprint, Vienna, 1979.

13. P. Schuster & K. Sigmund, Coyness, philandering and stable strategies, Preprint, Vienna, 1979.

14. P.D. Taylor & L.B. Jonker, Evolutionarily stable strategies and game dynamics, *Math. Biosc.* 40 (1978) 145-156.

15. R. Thom, *Structural stability and morphogenesis,* (Trans. D.H. Fowler), Benjamin, Reading, Massachusetts, 1975.

16. E.C. Zeeman, Dynamics of the evolution of animal conflicts, Preprint, Warwick, 1979.

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