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HETEROCLINIC CYCLES IN ECOLOGICAL DIFFERENTIAL EQUATIONS

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ABSTRACT. Differential equations on \mathbb{R}^n that leave certain hyperplanes invariant, arise as models in mathematical biology and in systems with symmetry. In such systems heteroclinic cycles occur in a robust way. We survey examples from the literature and propose a classification into "planar", simple, and multiple heteroclinic cycles (or heteroclinic networks). We associate a *characteristic matrix* to such objects, consisting of certain eigenvalues at the fixed points, and show how to read off stability properties from this matrix. Instead of Poincaré sections we use average Lyapunov functions to obtain stability results.

1. Motivation

In mathematical biology ODE models often take one of the following forms. Ecological differential equations

$$\dot{x}_i = x_i f_i(x_1, \dots, x_n), \quad i = 1, \dots, n, \qquad (1)$$

are defined on the nonnegative orthant \mathbb{R}^n_+ . Such equations are used to model ecological interactions of species. The x_i are interpreted as densities of species. The most prominent and important special case are the Lotka-Volterra equations

$$\dot{x}_i = x_i \left(r_i + (\mathbf{A}x)_i \right). \tag{1'}$$

If the independent variables x_i are frequencies or there is a conservation of total mass, (1) is replaced by the *replicator equation*

$$\dot{x}_i = x_i (f_i(x) - \bar{f}(x)), \quad i = 1, \dots, n, \qquad \bar{f}(x) = \sum_{i=1}^n x_i f_i(x).$$
 (2)

Its state space is the simplex $S_n = \{x \in \mathbb{R}^n : x_i \ge 0, \sum x_i = 1\}$. Again a much studied particular case of (2) is the replicator equation with linear f_i which models the evolution of gene frequencies and game dynamics (see [HS]):

$$\dot{x}_i = x_i [(\mathbf{A}x)_i - x \cdot \mathbf{A}x]. \tag{2'}$$

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There are analogues of (2) and (2') where the state space is a product of simplices, e.g., for the dynamics of bimatrix games (see [HS]).

Mathematically, these classes of ODEs are characterized by the invariance of the boundary faces of the state space.

It should be noted that some of these equations occur also in other settings outside biomathematics. In particular, the Lotka–Volterra equation is quite ubiquitous (see, e.g., [PM]). It occurs as truncated normal form of the codimension n bifurcation with n pairs of purely imaginary eigenvalues. Generally, equations on \mathbb{R}^n which have a reflectional \mathbb{Z}_2^n symmetry must leave the coordinate planes invariant and hence take the form (1).



FIGURE 1. The May-Leonard system. The rock-scissors-paper game. The characteristic matrix.

Therefore, it is desirable to discuss the generic behaviour of such systems. One type of behaviour which is not possible in general dynamical systems is the occurrence of *robust* (= structurally stable within this class) attracting heteroclinic cycles on the boundary of the state space. The first example was given by May and Leonard [ML] and studied further by [C], [CPC], [S1], [HS]. It consists of three competing species, where 1 beats 2, 2 beats 3, 3 beats 1 (in the simplest case with LV dynamics and with cyclic symmetry). There is a robust heteroclinic cycle connecting the three one-species fixed points $F_1 \longrightarrow$ $F_2 \longrightarrow F_3 \longrightarrow F_1$ (see Fig. 1a). Whether this cycle is attracting or repelling, depends on the eigenvalues at the fixed points, see section 4. The same example, now in the setting of systems with symmetry, was presented again in [GH]. An equivalent dynamics occurs in the so-called "rock-scissors-paper" game (see [Z, p. 482, 490] or [HS, p. 130]), a replicator equation (2') on the triangle S_3 (see fig. 1b). Analogous cycles in higher dimensions were considered in [K2], [K3], [HS2], ...

A biologically plausible example of a heteroclinic cycle was given by K i r l i n g e r [K1]. This is a two-prey two-predator system with Lotka-Volterra dynamics. The two prey species x_1 and x_2 live in severe competition, i.e., the dynamics of the x_1-x_2 plane is bistable: There are two stable one-species fixed points F_1 and F_2 . At F_1 predator y_1 , which is specialized on prey 1, is able to invade, leading to a coexistence equilibrium F_1^1 . At this equilibrium, the number x_1 of prey 1 is reduced due to predation so much, that it will be outcompeted by prey 2. There is a heteroclinic orbit in the $x_1 - x_2 - y_1$ subsystem which connects F_1^1 to F_2 . Assuming some symmetry between 1 and 2, there is a heteroclinic cycle on the boundary of \mathbb{R}^4_+ connecting the four equilibria $F_1 \longrightarrow F_1^1 \longrightarrow F_2 \longrightarrow F_2^2 \longrightarrow F_1$ (see Fig. 2). Similar cycles were considered in [K3], [HS2], [MR], [SR].



FIGURE 2. Kirlinger's heteroclinic cycle and its characteristic matrix.

2. The characteristic matrix of a heteroclinic cycle

Suppose the state space of our dynamical system is a polyhedron X in some \mathbb{R}^N , defined as the intersection of finitely many halfspaces $\{x \in \mathbb{R}^N : x_j \ge 0\}$, $j = 1, \ldots n$. Here x_j denotes a linear functional on \mathbb{R}^N which vanishes on one of the supporting hyperplanes of X. Let $\partial X = \bigcup_j \{x_j = 0\} \cap X$ denote the boundary of X and int $X = X \setminus \partial X$ the interior of the polyhedron. More

the boundary of X, and $\operatorname{int} X = X \setminus \partial X$ the interior of the polyhedron. More generally X could be a manifold with corners.

If ∂X is invariant under the smooth flow then we can write our differential equation in the form

$$\dot{x}_j = x_j f_j(x), \quad j = 1, \dots, n, \qquad (3)$$

(there will be some relations between the f_j if n > N). We can always assume that $n \ge N$ and that a point $x \in X$ is uniquely determined by its "coordinates" $x_j, j = 1, \ldots, n$. If not, we simply add some additional variables to achieve that.

Consider a fixed point \bar{x} of (3), and rearrange indices such that the zero coordinates come first. Then the Jacobian at \bar{x} takes the form $\begin{pmatrix} \mathbf{E} & \mathbf{O} \\ * & * \end{pmatrix}$, where **E** is a diagonal matrix whose entries are the *external eigenvalues* $\frac{\dot{x}_j}{x_j}|_{\bar{x}} = f_j(\bar{x})$. They describe the motion transverse to the hyperplane j.

Now let $\Gamma \subset \partial X$ be a heteroclinic cycle which consists of m fixed points F_k and heteroclinic orbits between them. Then we associate to Γ a rectangular

scheme of external eigenvalues: The entry in row k and column j is the external eigenvalue $f_j(F_k)$. (It is 0 if $x_j > 0$ at F_k .) We call this scheme the *characteristic matrix* **C** of Γ . E.g., in Fig. 1, at F_1 , there are two external eigenvalues, $f_2(F_1) > 0$ and $f_3(F_1) < 0$. Since $f_1(F_1) = 0$, these three numbers give the first row of the characteristic matrix in Figure 1c.

It seems that this matrix **C** contains the essential information about Γ . In particular the stability properties of Γ can be read off from **C** in all known cases, as shown in section 4. Apriori **C** is an $m \times n$ matrix (m = the number of fixed points, n = the number of boundary hyperplanes of the polyhedron X), but we can omit columns of zeroes, thus ignoring those hyperplanes which do not touch Γ . Each row of **C** contains at least one positive entry (under the generic assumption that the fixed points F_k are hyperbolic).

Classification of heteroclinic cycles. If each row and each column of C contains only one positive entry then we call Γ a simple heteroclinic cycle. Note that there are heteroclinic cycles where each row contains only one positive entry (one unstable transverse direction at each F_k), but m > n (e. g. on the cube (m = 8, n = 6) or on any polyhedron with more corners than faces) so that there are several positive entries in one column. We do not consider such heteroclinic cycles here, since we don't have general stability results for them.

If furthermore there is only one negative entry in each row and column (so that there are just two external directions at each F_k , one stable and one unstable) then we speak of a "planar" heteroclinic cycle. We will see below (Corollary 2) that they behave like heteroclinic cycles in the plane.

If some row of **C** contains at least two positive entries (so at least one F_k has an unstable manifold of dimension ≥ 2) then Γ is a multiple heteroclinic cycle or a heteroclinic network.

Since the numbering of the hyperplanes (or columns) and of the fixed points F_k (or rows of **C**) is arbitrary, the characteristic matrix is determined only up to permutations of rows and columns. Our stability criteria (Thm. 1 and 2) will therefore be independent against such permutations.

EXAMPLES. 1) The May–Leonard cycle is "planar". Its characteristic matrix is given in Figure 1c.

2) Kirlinger's cycle is not "planar" but still simple. See Figure 2c for its characteristic matrix.

3) The simplest robust heteroclinic cycle is probably the one shown in Figure 3. Two coordinate planes in \mathbb{R}^3 are supposed to be invariant, they contain the two connecting orbits. The two fixed points lie in the invariant line of intersection and are stable inthere. This is again a "planar" heteroclinic cycle. The third column in the characteristic matrix will be omitted before applying the stability criteria of section 4.

4) Heteroclinic cycles in the plane. X is essentially an n-gon in this case. The characteristic matrix can be arranged such that it contains the positive eigenvalues λ_k in the main diagonal and the negative eigenvalues $-\mu_k$ right next



FIGURE 3. The simplest robust heteroclinic cycle in \mathbb{R}^3_+ .

to it. Robust examples from biology are the rock-scissors-paper game (Figure 1b) and the "battle of the sexes" on the square $[0, 1]^2$ (see [HS]).

5) Heteroclinic cycles on the simplex. Let \mathbf{A} be an $n \times n$ matrix with $a_{ii} = 0$. If a_{ij} and a_{ji} have different sign for sufficiently many pairs (i, j), then \mathbf{A} will be the characteristic matrix of a heteroclinic cycle or network on S_n . The simplest dynamics (a "normal form" for the heteroclinic cycle?) is given by the replicator equation (2'). The cycle is simple if $a_{i,i+1} > 0$ and all other entries are ≤ 0 . This case was studied in [AH], [H2], [HS], etc. The classical "hypercycle" equation from prebiotic evolution [S2, H1, HS] is the prototype special or limiting case, for which the method of proof indicated in section 5 was originally developed. Networks were recently treated in [Br] and [KS].



FIGURE 4. Heteroclinic cycles and networks on the simplex

6) In the same way as the rock-scissors-paper game and the May-Leonard example (Figure 1) are essentially equivalent, all the above examples on the simplex S_n can be imbedded to heteroclinic cycles or networks in equations (1) or (1') on \mathbb{R}^n_+ . Thereby the *n* corners of the simplex are replaced by fixed points on the *n* coordinate axes. The dynamics on \mathbb{R}^n_+ could be chosen to be competitive in the sense of Hirsch.

7) Heteroclinic cycles on a cube and other polyhedra occur naturally in the

dynamics of n person games, whenever there is a cycle of best responses, see [GaH].

8) Another example can be found in [SR], again a two-prey two-predator system as in Ex. 2: It is a simple heteroclinic cycle of length three: $F_1 \longrightarrow F_1^1 \longrightarrow F_{12} \longrightarrow F_1$. The last connection is not in the $x_1 - x_2$ plane (the boundary face spanned by F_{12} and F_1), but in the $x_1 - x_2 - y_2$ subsystem. Therefore $y_2 > 0$ along this connection, but not at any of the equilibria, so that $y_2 = 0$ on the average along this cycle. Note also that the first column of **C** is zero (and hence can be ignored), since $x_1 > 0$ along the cycle. (See Figure 5).



FIGURE 5. The heteroclinic cycle of Sikder and Roy

There are also heteroclinic cycles whose minimal center of attraction consists of more complicated invariant sets than fixed points. See [S3] for a first example (of "planar" type), where one of the fixed points is replaced by a periodic orbit. In Kirlinger's two-prey two-predator systems it is easy to imagine the fixed points F_i^i being replaced by predator-prey limit cycles (if the restrictive class of Lotka–Volterra dynamics is left). For examples in the context of symmetry see [MCG].

9) A May-Leonard like system in \mathbb{R}^4_+ with three limit cycles in the $x_i x_4$ planes (i = 1, 2, 3). Such a "planar" heteroclinic cycle would still be robust even if one of the three limit cycles is internally unstable, since there may be transverse intersections of their stable and unstable manifolds.

Our approach applies also to such heteroclinic cycles, as long as the components Λ_k of the minimal center of attraction are uniquely ergodic invariant sets. The entries of the characteristic matrix are then given as the external Lyapunov exponents

$$\lambda_i(\Lambda_k) = \lim_{T \to \infty} \frac{1}{T} \int_0^T f_i(x(t)) dt = \int_{\Lambda_k} f_i(x) d\mu_k(x)$$
(4)

with respect to the unique invariant measure μ_k on the invariant set Λ_k .

3. Permanence and repelling sets

In all these examples it is of interest to know the stability properties of this heteroclinic cycle. In particular, one would like to know whether Γ does attract interior orbits or repels them all. This is closely related to the question of persistence or permanence of ecological systems ([HS], [HuS]). A system (1), (2) or (3) is called *permanent* if the boundary of the state space X is a repeller in the sense that there is a $\delta > 0$ such that $\liminf_{t\to\infty} x_i(t) > \delta > 0$ holds for each solution x(t) > 0 of (1), (2) or (3). If X is unbounded (e.g. \mathbb{R}^n_+) we also assume that the (semi)flow is dissipative.

We call a compact invariant subset Λ of ∂X repelling (a better terminology might be: ∂X is repelling near Λ), whenever both of the following two conditions are satisfied:

- (i) there is no $x \in \operatorname{int} X$ with $\omega(x) \subset \Lambda$, and
- (ii) there is a neighbourhood U of Λ in X such that for each $x \in U \setminus \partial X$ $\exists t \in \mathbb{R}: x(t) \notin U. \ (\partial X \text{ is isolated near } \Lambda.)$

The following characterization of permanence follows from classical stability results in [BS].

A system on X is permanent iff ∂X is repelling in the above sense.

This can be sharpened to (see [G, H3]):

A system on X is permanent iff every chain-recurrent invariant subset $\Lambda \subset \partial X$ is repelling in the above sense.

Heteroclinic cycles are such chain-recurrent subsets and it is therefore of importance to characterize when they are repelling.

4. Stability conditions for heteroclinic cycles

Let $\Lambda \subset \partial X$ be a compact invariant subset of the boundary and $\Lambda_k \subset \Lambda$ $(k = 1, \ldots, m)$ be such that for each $x \in \Lambda$ there is a k with $\omega(x) \subset \Lambda_k$. We assume further that each set Λ_k is a compact invariant, uniquely ergodic subset of a single boundary face. Then the external eigenvalues are uniquely defined at Λ_k by (4) and can be arranged in the characteristic matrix **C** of the set Λ . We omit those columns which consist of zero entries only, thus ignoring those hyperplanes which do not touch Λ , as in Examples 3 and 8. We need not assume for the following that Λ is a heteroclinic cycle or network in the sense that each Λ_k can be reached by a sequence of heteroclinic connections from any other Λ_l .

THEOREM 1. a) If there is a vector $\mathbf{p} \in \mathbb{R}^n$ such that $\mathbf{p} > 0$ and $\mathbf{C}\mathbf{p} > 0$ then Λ is repelling.

b) If Λ is asymptotically stable within ∂X and there is a $\mathbf{p} < 0$ such that $\mathbf{C}\mathbf{p} > 0$ then Λ is asymptotically stable in X.

c) If Λ is asymptotically stable within ∂X and there is a $\mathbf{p} \in \mathbb{R}^n$ such that $p_i < 0$ for at least one *i* and $\mathbf{C}\mathbf{p} > 0$ then Λ attracts at least one (actually an open set of) interior orbit(s) from X.

The proof is deferred to Section 5. A consequence is

THEOREM 2. Let Λ be asymptotically stable within ∂X ; m = n' (= number of nonzero columns) so that the (reduced) characteristic matrix **C** is a square matrix, and let det $\mathbf{C} \neq 0$. Then Λ is repelling iff $\mathbf{C}^{-1} \geq 0$, i.e., the inverse of **C** has only nonnegative entries.

Proof. If Λ is repelling then case c) of Theorem 1 must not apply and hence for any positive vector $\boldsymbol{q} > 0$ in \mathbb{R}^n , we must have $\boldsymbol{p} = \mathbf{C}^{-1} \boldsymbol{q} \ge 0$. This implies $\mathbf{C}^{-1} \ge 0$. The converse follows immediately from case a).

Matrices **C** satisfying condition a) of Thm. 1 are called *semipositive*. The step from Theorem 1 to Theorem 2 is closely related to a result of [FP] on irreducibly semipositive matrices. The case where **C** is not square $(n' \neq m)$ is largely unresolved. Thm. 1 gives only a partial result in this case. Also the stability assumption within the boundary should be relaxed. Sometimes it can be replaced by assuming Λ to have nontrivial index within ∂X , as in [CG].

Note that this property of **C** is invariant under interchanges of rows or columns of the characteristic matrix **C**. If one entry of \mathbf{C}^{-1} is negative then some interior orbit will converge to (some subset of) Λ . If Λ is a heteroclinic network, a more detailed analysis is necessary to decide which parts of it can attract interior orbits. See [Br] for some interesting results in this direction: He identifies (for a 4×4 matrix **C**) those 3×3 minors which determine the stability of the cycles of length 3.

For simple heteroclinic cycles the situation is considerably simpler because case c) can be ignored: We can apply the theory of M-matrices to solve the arising linear inequalities.

COROLLARY 1. Let Λ be a simple heteroclinic cycle, which is asymptotically stable within ∂X . (This is automatically satisfied if the cycle is robust and all Λ_k are fixed points.) Then **C** is a square matrix (after elimination of superfluous columns) with positive entries occurring only in the main diagonal (after a suitable rearrangement of the rows or columns). Let det $\mathbf{C} \neq 0$.

If **C** is an *M*-matrix (all leading principal minors of **C** are positive) then Λ is repelling.

If **C** is not an *M*-matrix (at least one leading principal minor is negative) then Λ is asymptotically stable.

COROLLARY 2. Let Λ be a "planar" heteroclinic cycle, which is asymptotically stable within ∂X . Let $\lambda_k > 0$ and $-\mu_k < 0$ be the two external eigenvalues at Λ_k . If $\prod \lambda_k > \prod \mu_k$ then Λ is repelling. If $\prod \lambda_k < \prod \mu_k$ then Λ is asymptotically stable.

Corollary 2 was known for heteroclinic cycles in the plane (Ex. 4) to Dulac, and rediscovered by [R], [H1], and others. It applies to our Examples 1, 3 and

9. Corollary 1 covers most of the examples of robust heteroclinic cycles, forced by invariance of hyperplanes, considered in the literature so far. In particular it applies to Examples 1-4, 7-9 above. The essential special case of Example 5 was treated in [AH, Thm. 5] and [HS, ch. 20.5]. The stability of simple heteroclinic cycles was analyzed again with Poincaré sections in [H2], [HS, ch. 29.3], [FS], [KM, Thm. 7.1]. For the behaviour of time-averages near (planar and simple) attracting heteroclinic cycles see [A], [Gau], [GaH] and [T].

The method of Poincaré sections is more involved (if done rigorously). First it requires the existence of a smooth linearization near the fixed points in order to compute the Poincaré map. This point was ignored in most of the above papers. According to Sternberg, smooth linearizations exist if sufficiently many non-resonance conditions are satisfied. However, the existence of n invariant hyperplanes near a hyperbolic fixed point in \mathbb{R}^n already implies the existence of a \mathbb{C}^1 -linearization, even if there are resonances between the n real eigenvalues. This follows from the work of [Be] and [Sa].

Also the conditions obtained by Poincaré maps are far less explicit (in higher dimensions at least, in terms of a spectral radius) and it is not obvious how to derive our explicit characterization on **C** from them. Moreover Poincaré sections would be more difficult to apply if the Λ_k are not fixed points but more complicated invariant sets. In this respect our method seems superior. On the other hand, the Poincaré map contains more information on the dynamics and one can treat also the induced bifurcations.

5. Appendix: Proof of Theorem 1

Part a) is essentially contained (although not explicitly stated in this form) in [H1], [Hu], [H3]. The basic idea is to use $P(x) = \prod x_k^{p_k}$ as an average Ljapunov function: The assumption $\mathbf{Cp} > 0$ means that P increases most of the time along orbits as long as they are close to Λ . Hence they finally have to move away from Λ .

Part b) generalizes Thm. 3 in [AH]. The idea to consider $\boldsymbol{p} \in \mathbb{R}^n$ with both positive and negative entries as in case c) was first exploited by [J].

For the proof of b) and c) let $P(x) = \prod x_i^{-p_i}$. Let $I = \{i : p_i < 0\}$ and $X_0 = \{x \in X : x_i = 0 \text{ for some } i \in I\}$ be the part of ∂X where P vanishes. Now $\frac{\dot{P}}{P} = -\sum_j p_j \frac{\dot{x}_j}{x_j}$ extends continuously to ∂X and takes the (average) value $-\sum_j p_j \lambda_j(\Lambda_k) = -(\mathbf{C}\mathbf{p})_k < 0$ at the fixed point (resp. along the uniquely ergodic set) Λ_k . Intuitively this means that P decreases exponentially (in the average) near Λ and we expect that orbits close to Λ will converge to X_0 . More precisely, with $\Lambda_0 = \Lambda \cap X_0$ we have the following LEMMA. Suppose there is a $\mathbf{p} \in \mathbb{R}^n$ such that $p_i < 0$ for at least one i and

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 $\mathbf{Cp} > 0$ and that Λ_0 is asymptotically stable within X_0 . Then all orbits starting in a set $\{x \in \text{int } X : P(x) < \delta\}$ and close enough to Λ_0 will converge to Λ_0 .

If all $p_i < 0$ then $X_0 = \partial X$ and the Lemma implies that Λ is asymptotically stable in X. This shows part b) of Theorem 1. If \boldsymbol{p} has positive and negative components then the Lemma isolates a partially attracting part Λ_0 of Λ . (It is easy to see that $\Lambda_0 \neq \emptyset$.) The situation in the Lemma and its proof can be illustrated by the behaviour of the planar system in Fig. 6 which has an elliptic sector at 0: X_0 corresponds to the x-axis, Λ to the y-axis, Λ_0 to the origin, and the assumptions on **C** are replaced by the fact that P = y/x decreases in the positive quadrant. It may be interesting to remark that the return map near a heteroclinic network may have such elliptic sectors for an open set in parameter space, see [Br].



FIGURE 6. An elliptic sector

Proof. Since Λ_0 is asymptotically stable within the invariant subset X_0 one can find a neighbourhood $U \subset X_0$ of Λ_0 in X_0 which is forward invariant and its smooth boundary is transverse to the vector field in X_0 . (If $\Lambda_0 = X_0$, then we set $U = X_0$.) For small enough ε , the cylinder $U_{\varepsilon} = \bigcup_{i \in I} \{x \in X : 0 \leq x_i < \varepsilon$ and $\pi_i(x) \in U\}$ (where π_i is a suitable projection onto the face $\{x_i = 0\}$), with base set U and height ε , is then still forward invariant along its side surface (but not necessarily at its top). Let $U_{\varepsilon}^{\delta} = U_{\varepsilon} \cap \{x \in X : P(x) < \delta\}$, with δ so small that $\min\{x_i : i \in I\} < \varepsilon$ holds for all x with $P(x) \leq \delta$. As in [H1] or [Hu] we can find constants $\overline{T} > 1$, k < 1 and K > 0 such that for all $x \in X$ close to Λ there is a time T with $1 < T < \overline{T}$ such that P(x(T)) < kP(x) and P(x(t)) < KP(x) for all $0 < t < \overline{T}$. So for $x \in U_{\varepsilon}^{\delta/K}$ and $0 < t < \overline{T}$, $x(t) \in U_{\varepsilon}^{\delta}$ while $x(T) \in U_{\varepsilon}^{k\delta/K}$. Iterating this argument we see that the forward orbit of x cannot leave U_{ε}^{δ} and P(x(t)) will converge exponentially to 0, as $t \to \infty$. Hence $\omega(x) \subset \Lambda_0$ (the maximal compact invariant subset of U_{ε}^{δ}) and Λ_0 is stable for the semiflow restricted to $U_{\varepsilon}^{\delta/K}$.

An alternative way to prove the Lemma is to apply the approach of [G, H3] for backward time and show that there is no negative orbit in the set U_{ε}^{δ} .

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