# Strategy dynamics

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# Part II

# Adaptive Dynamics

# 4

# ON THE CONCEPT OF ATTRACTOR FOR COMMUNITY-DYNAMICAL PROCESSES: THE CASE OF UNSTRUCTURED POPULATIONS

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F. J. A. Jacobs and J. A. J. Metz, On the concept of attractor for community-dynamical processes I: The case of unstructured populations, Journal of Mathematical Biology 47, 222-234, 2003

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ABSTRACT

We introduce a notion of attractor adapted to dynamical processes as they are studied in community-ecological models and their computer simulations. This attractor concept is modeled after that of Ruelle as presented in [84] and [85]. It incorporates the fact that in an immigration-free community populations can go extinct at low values of their densities.

Keywords: Community dynamics, attractors, adaptive dynamics, chain recurrence, pseudo-orbits

MSC (2020): 37b20, 37c20, 37c70

## 4.1 INTRODUCTION

The aim of this paper is to introduce a modification of the attractor concept introduced by Ruelle ([84], [85]) and Hurley ([50]) (based on ideas of Conley ([13])), below referred to as chain attractors, that is adapted to the asymptotic behaviour of the dynamical systems studied in community ecology. The construction of chain attractors is based on the idea that any mathematical system is but an idealisation of reality and that neither physical nor numerical experiments produce the precise orbits of the theoretical system under consideration, but rather so-called pseudo-orbits that occur as a consequence of small disturbances or roundoff errors. We opted for the name chain attractor to bring out the close connection of this attractor concept with the notion of chain recurrence. Below we shall give a short review of Ruelle's construction and some of its properties (Section 2). In addition we introduce the useful terms chain repeller and chain saddle, and basin of chainability and of chain attraction, as it is sometimes convenient to refer to these concepts by name. Next we propose the modification (Section 3), followed by four examples (Section 4) and a discussion (Section 5). This modification is necessary in order to deal with the feature of extinction of a population as it may occur in community dynamics: a pseudo-orbit that reaches a boundary plane of the community state space spanned by the densities of the populations involved, will proceed in this boundary plane and cannot enter again into the interior of the community state space. This condition is not imposed in the construction of ordinary chain attractors, which in essence have their motivation in physics rather than community ecology.

## 4.2 CHAINING, CHAIN ATTRACTORS AND BASIN OF CHAIN ATTRACTION

No model of an empirical process in the form of a smooth deterministic dynamical system is ever exact. At best the empirical process matches its theoretical model up to some continual small perturbations of its states (due to externally imposed or internally generated noise in the case of physical, chemical or biological processes, or cut-off errors in the case of numerical processes). One way of formalising the ubiquitous presence of small perturbations is in terms of pseudo-orbits, to be defined below, leading to a characterisation of their asymptotic behaviour by means of chain attractors, which are constructed in terms of these pseudo-orbits. In this section we summarise this construction as presented in [84] and Section 8 of [85]. We concentrate on those results that are of importance with regard to the modification that we propose in the next section; for a more extensive exposition of the various concepts the reader is referred to [1].

Let $(M, d)$ be a compact metric space, and let $(\phi^t)_{t\geq 0}$ be a continuous semiflow on $M$. Furthermore, let $\varepsilon > 0$ and let $t_0, t_1 \in \mathbb{R}$, with $t_0 \leq t_1$. An $\varepsilon$-pseudo-orbit $\eta_{\varepsilon,[t_0,t_1]}$ of $(\phi^t)_{t\geq 0}$ is a (not necessarily continuous) function $\eta_{\varepsilon,[t_0,t_1]} : [t_0, t_1] \to M$ such that

$$d\left(\phi^{\beta}(\eta_{\varepsilon,[t_0,t_1]}(t+\alpha)), \phi^{\alpha+\beta}(\eta_{\varepsilon,[t_0,t_1]}(t))\right) < \varepsilon$$

whenever $\alpha, \beta \geq 0$, $\alpha + \beta \leq 1$, and $t, t+\alpha \in [t_0, t_1]$. Thus, during a unit time $\varepsilon$-pseudo-orbits are allowed to "accrue an amount of error of at most $\varepsilon$ relative to orbits", where the error measure takes into account how the error is transported along orbits (see Figure 1). (Another way of looking at $\varepsilon$-pseudo-orbits is by noting that in whatever way we sample the error within time steps $\leq 1$, the error per step relative to the unperturbed orbit will always be smaller than $\varepsilon$.)

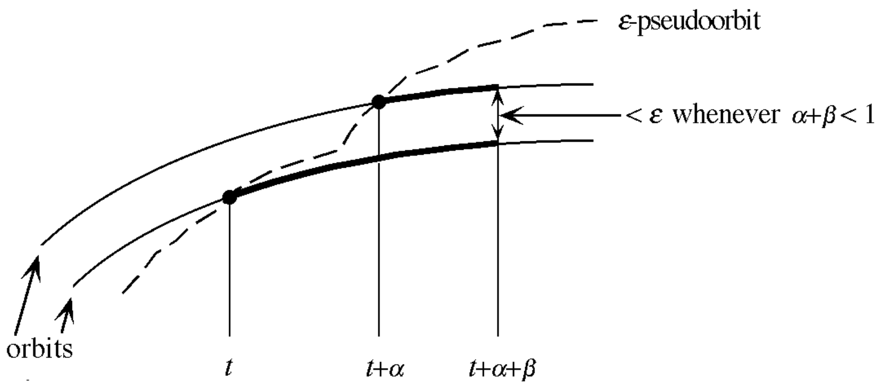


Figure 4.1: An illustration of an $\varepsilon$-pseudo-orbit

An $\varepsilon$-pseudo-orbit $\eta_{\varepsilon,[t_0,t_1]}$ is said to go from $\eta_{\varepsilon,[t_0,t_1]}(t_0)$ to $\eta_{\varepsilon,[t_0,t_1]}(t_1)$ (or to start in $\eta_{\varepsilon,[t_0,t_1]}(t_0)$ and to end in $\eta_{\varepsilon,[t_0,t_1]}(t_1)$), and to have length $t_1 - t_0$. (Note that the word "length" is used here in an unusual, but time honoured, manner for the time taken instead of the traversed distance.) By concatenation of two $\varepsilon$-pseudo-orbits, one going from $x$ to $y$ and of length $T$, the second one going from $y$ to $z$ and of length $T'$, we obtain a $2\varepsilon$-pseudo-orbit going from $x$ to $z$ and of length $T + T'$. The deviation from an unperturbed orbit allowed for in $\varepsilon$-pseudo-orbits is controlled in time by the bound imposed on the sum $\alpha + \beta$, and in state space by $\varepsilon$, where a change in one can be compensated by an appropriate change in the other.

For the applications of $\varepsilon$-pseudo-orbits we have in mind in this paper only arbitrarily small values of $\varepsilon$ are of importance.

Under the dynamical system $(\phi^t)_{t\geq 0}$ on $M$ the possible future states of an arbitrary $x \in M$ are well-determined by its forward orbit $\{\phi^t(x)\}_{t\geq 0}$. As indicated above, an $\varepsilon$-pseudo-orbit (more precisely, its image) through $x$ may deviate from this forward orbit. The intersection $C_+(x) = \bigcap\limits_{\varepsilon>0} N_{\varepsilon,+}(x)$, with $N_{\varepsilon,+}(x)$ the union of the images of all $\varepsilon$-pseudo-orbits of $(\phi^t)_{t\geq 0}$ starting at $x$, is called the *forward chain lineage through* $x$. The forward orbit through $x$ is contained in the forward chain lineage through $x$. However, where an orbit through $x$ 'ends' in the $\omega$-limit set of $x$, the forward chain lineage through $x$ may proceed beyond this $\omega$-limit set. For example, the forward chain lineage through an $x$ on the stable manifold of a saddle-point contains in addition to the orbit through $x$ at least also the full unstable manifold of that saddle-point. Analogously we can introduce the *backward chain lineage through* $x$, $C_-(x)$, as the union of the images of all $\varepsilon$-pseudo-orbits of $(\phi^t)_{t\geq 0}$ ending at $x$; the union $C(x) = C_+(x) \cup C_-(x)$ then is the *chain lineage through* $x$.

A point $x$ is chain recurrent if for every $\varepsilon > 0$ and every $T > 0$, there is an $\varepsilon$-pseudo-orbit of length $\geq T$ going from $x$ to $x$. Chain recurrence captures the notion of positive recurrence under arbitrarily small perturbations. (We recall that an element $x \in M$ is positively recurrent (in the ordinary sense) if for each $\delta > 0$ and each $T > 0$ there exists a $t > T$ such that $d\left(\phi^t(x), x\right) < \delta$.) The set of chain recurrent points is the chain recurrent set. Points that are not chain recurrent we shall refer to as *ephemeral*.

On $M$ the following relation $\succcurlyeq$, to be called *chaining*, is defined: $x \succcurlyeq y$ ('$x$ chains to $y$') if for every $\varepsilon > 0$ there exists an $\varepsilon$-pseudo-orbit going from $x$ to $y$. (Roughly stated $x \succcurlyeq y$ means that there is an orbit or an arbitrarily little perturbed orbit, or a sequence of arbitrarily little perturbed orbits, in $M$ going from $x$ to $y$.) Note that the forward chain lineage through $x$ corresponds to the image of $x$ under the relation $\succcurlyeq$. The relation $\succcurlyeq$ is reflexive ($x \succcurlyeq x$, trivially by means of an $\varepsilon$-pseudo-orbit of length 0) and transitive ($x \succcurlyeq y$ and $y \succcurlyeq z$ imply $x \succcurlyeq z$), and thus is a preorder on $M$. The relation $\succcurlyeq$ is also closed, in the sense that if $(x_i)$ and $(y_i)$ are two sequences in $M$ converging to $x$ and $y$ respectively and such that for all $i$: $x_i \succcurlyeq y_i$, then $x \succcurlyeq y$.

(For a proof of this statement see [1], Chapter 1 Proposition 8.) As a consequence, the chain recurrent set is closed. The following Proposition is straightforward (see also [1], Chapter 1 Proposition 11):

**Proposition 1.** Let $x, y \in M$. $x \succcurlyeq y$ if and only if either there is a $t \geq 0$ such that $\phi^t(x) = y$ or for all $t \geq 0$: $\phi^t(x) \succcurlyeq y$.

On $M$ the relation $\sim$, to be called *mutual chaining*, is defined in the following way: $x \sim y$ ('$x$ and $y$ chain to each other') if $x \succcurlyeq y$ and $y \succcurlyeq x$. Since $\succcurlyeq$ is a preorder, $\sim$ is an equivalence relation on $M$. The equivalence class of $x$ under $\sim$ is denoted by $[x]$. Clearly $\sim$ is a closed relation (in the sense indicated above), and therefore every equivalence class is closed.

An equivalence class $[x]$ is called a basic class if $x$ (and consequently every $y \in [x]$) is chain recurrent, and the chain recurrent set then is the union of all basic classes.

**Proposition 2.** The following three statement are equivalent:

1. $[x]$ is a basic class;
2. $x$ is a fixed point or $[x]$ contains more than one point;
3. for all $t \geq 0$: $\phi^t([x]) = [x]$.

The proof of this Proposition follows from Proposition 1.

A class that is not basic, as well as the corresponding state, will be called *chain ephemeral*.

Let $\mathcal{M} = \{[x] | x \in M\}$ denote the set of equivalence classes in $M$ under $\sim$. On $\mathcal{M}$ the relation $\geqslant$, to be called *connecting*, is defined by: $[x] \geqslant [y]$ ('$[x]$ connects to $[y]$') if $x \succcurlyeq y$. This relation is reflexive and transitive. In addition, $[x] \geqslant [y]$ and $[y] \geqslant [x]$ together imply that $[x] = [y]$. The relation $\geqslant$ thus imposes a partial ordering on $\mathcal{M}$.

**Definition 1.** A minimal element in $\mathcal{M}$ under $\geqslant$ is called a chain attractor.

An existence proof, through the use of Zorn's lemma, can be found in [84].

Ruelle in [84] and [85] does not introduce any special term to characterise his attractors; Buescu in [4] uses the term Conley-Ruelle attractor. Hurley, who independently introduced the same concept in [50] (though through a different, less physically interpretable, construction) refers to it as chain transitive quasi-attractor. Neither term seems to have caught on yet.

A chain attractor is a basic class, and, by Proposition 2, contains the $\omega$-limit sets of all its elements.

In addition to the above review of the idea of chain attractor, we introduce the terms chain repeller and chain saddle, and basin of chainability and basin of chain attraction.

**Definition 2.**

(i) A maximal basic class in $\mathcal{M}$ under $\geqslant$ is called a chain repeller.

(ii) Any basic class in $\mathcal{M}$ which is neither minimal nor maximal under $\geqslant$ is called a chain saddle.

(iii) Chain ephemeral classes, chain repellers and chain saddles, c.q. the states therein, shall be referred to as chain transient.

If $M$ is a manifold with boundary, any ephemeral maximal class in $\mathcal{M}$ under $\geqslant$ necessarily is contained in the boundary of $M$. This follows easily from the fact that an orbit through an ephemeral state in the interior of $M$ can be extended backward in time to another ephemeral state in the interior.

**Definition 3.** Let $x \in M$.

(i) The basin of chainability of $x$, denoted $B_{\succcurlyeq}(x)$, is the collection of points $y \in M$ that chain to $x$: $B_{\succcurlyeq}(x) = \{y \in M | y \succcurlyeq x\}$.

(ii) The basin of chainability of the equivalence class $[x]$, denoted $B_{\succcurlyeq}([x])$, is: $B_{\succcurlyeq}([x]) = B_{\succcurlyeq}(x)$.

(iii) If $[x]$ is a chain attractor, we refer to its basin of chainability as its basin of chain attraction, and shall denote it as $Att([x])$.

Note that for each $x \in M$, $B_{\succcurlyeq}(x) \neq \emptyset$ since $x \in B_{\succcurlyeq}(x)$. An element of $M$ can belong to several basins of chainability, and each element of $M$ belongs to the basin of chain attraction of at least one chain attractor (again by Zorn's lemma, see [84]).

Therefore the different asymptotic regimes of a dynamical system, described by a semiflow on $M$ that is subject to (very) small perturbations, are captured by its chain attractors.

## 4.3 EXTINCTION PRESERVING CHAIN ATTRACTORS FOR IMMIGRATION-FREE COMMUNITIES

We now restrict our attention to point-dissipative community-dynamical processes for closed communities (i.e., communities without immigration). We recall that a dynamical system is point-dissipative if there exists a bounded set such that each orbit eventually enters this set and remains in it. The compact metric space $(M, d)$ of the previous section here is understood to be the community state space spanned by the densities of the populations involved in the community-dynamical process under consideration. For $k \geq 1$ populations $1, ..., k$, with respective densities $n_1, ..., n_k$, $M$ is the intersection of $\mathbb{R}^k_+ \subset \mathbb{R}^k$ with the closure of a simply connected neighbourhood of 0 in $\mathbb{R}^k$. $M$ is supposed to be provided with the standard (Euclidean) metric and topology.

For $l \in \mathbb{N}$, with $1 \leq l \leq k$, and for $i_1, ..., i_l \in \{1, ..., k\}$ such that $1 \leq i_1 < ... < i_l \leq k$, $\mathrm{bd}_{i_1,...,i_l}\left(\mathbb{R}^k_+\right)$ denotes the set

$$\left\{(n_1, ..., n_k) \in \mathbb{R}^k_+ | n_{i_1} = ... = n_{i_l} = 0\right\} \subset \mathrm{bd}\left(\mathbb{R}^k_+\right) = \left\{(n_1, ..., n_k) \in \mathbb{R}^k_+ | \exists i \in \{1, ..., k\} : n_i = 0\right\},$$

which is the boundary set of $\mathbb{R}^k_+$. Furthermore we write $\mathrm{bd}_{i_1,...,i_l}(M)$ for $M \cap \mathrm{bd}_{i_1,...,i_l}\left(\mathbb{R}^k_+\right)$, and call it the extinction boundary for the populations $i_1, ..., i_l$; $\mathrm{bd}_{\mathrm{e}}(M)$ denotes the intersection of $M$ with $\mathrm{bd}\left(\mathbb{R}^k_+\right)$. In addition, we write $\mathrm{bd}_{\mathrm{int}}(M)$ for the intersection of the boundary of $M$ with $\mathrm{int}\left(\mathbb{R}^k_+\right)$. The assumption of no immigration translates into the invariance of the extinction boundaries $\mathrm{bd}_{i_1,...,i_l}(M)$ under the semiflow $\left(\phi^t\right)_{t \geq 0}$.

For later use we mention here that $M$ is a normal space, i.e., it satisfies the following property: if $C_1$ and $C_2$ are two closed and disjoint subsets of $M$, then there exist open and disjoint subsets $O_1, O_2$ in $M$ such that $C_1 \subset O_1$ and $C_2 \subset O_2$.

The closure of a subset $U$ of $M$ will be denoted by $\overline{U}$.

For $n \in \mathrm{bd}_{i_1,\ldots,i_l}(M)$ the equivalence class generated by the relation of mutual chaining connected to the semiflow $\left(\phi^t|_{\mathrm{bd}_{i_1,\ldots,i_l}(M)}\right)_{t\geq 0}$ will be denoted as $[n]_{i_1,\ldots,i_l}$.

In the theory reviewed in Section 2, an $\varepsilon$-pseudo-orbit which has a point in common with (or, more generally, comes arbitrarily close to) an extinction boundary of $M$, may again get away from this extinction boundary and proceed in $M \setminus \mathrm{bd_e}(M)$. This is unrealistic in the case of community-dynamical processes, in which populations that attain densities arbitrarily close to zero are bound to go irreversibly extinct due to the discreteness of individuals. To incorporate this restriction into our considerations we introduce the notion of extinction preserving $\varepsilon$-pseudo-orbits.

**Definition 4.** Let $\eta_{\varepsilon,[t_0,t_1]}$ be an $\varepsilon$-pseudo-orbit in $M$. For $t_\alpha \in [t_0, t_1]$, $\mathrm{ext}(t_\alpha)$ denotes the collection of the minimal (with regard to the partial ordering by $\subseteq$) extinction boundaries that have a non-empty intersection with the set of accumulation points $\lim\limits_{t\to t_\alpha} \eta_{\varepsilon,[t_0,t_1]}(t)$.

Note that if $\eta_{\varepsilon,[t_0,t_1]}$ is (left-)continuous in $t = t_\alpha$, then $ext(t_\alpha)$ contains only the unique minimal extinction boundary containing $\eta_{\varepsilon,[t_0,t_1]}(t_\alpha)$.

**Definition 5.** An $\varepsilon$-pseudo-orbit $\eta_{\varepsilon,[t_0,t_1]}$ in $M$ is extinction preserving (abbreviated as ep) if the following property holds: if $t_\alpha \in [t_0, t_1]$ is such that $\mathrm{ext}(t_\alpha) \neq \emptyset$, then there is a $\mathrm{bd}_{i_1,\ldots,i_l}(M) \in \mathrm{ext}(t_\alpha)$ such that for all $t \in [t_\alpha, t_1]$: $\eta_{\varepsilon,[t_0,t_1]}(t) \in \mathrm{bd}_{i_1,\ldots,i_l}(M)$.

In addition we define:

**Definition 6.** A point $n$ is ep-chain recurrent if for every $\varepsilon > 0$ and every $T > 0$ there is an ep $\varepsilon$-pseudo-orbit of length $\geq T$ going from $n$ to $n$. The set of ep-chain recurrent points is called the ep-chain recurrent set.

Note that an ep-chain recurrent point satisfies either one of the following two mutually exclusive conditions:

1. $n$ as well as every ep $\varepsilon$-pseudo-orbit going from $n$ to $n$ belongs to $M \cap \mathrm{int}\left(\mathbb{R}^k_+\right)$;
2. $n$ as well as every ep $\varepsilon$-pseudo-orbit going from $n$ to $n$ belongs to $M \cap \mathrm{int}\left(\mathrm{bd}_{i_1,\ldots,i_l}\left(\mathbb{R}^k_+\right)\right)$, for a unique $\mathrm{bd}_{i_1,\ldots,i_l}\left(\mathbb{R}^k_+\right)$.

Furthermore, the ep-chain recurrent set is a subset of the chain recurrent set.

In accordance with the previous section we define an equivalence relation on $M$ and a partial ordering on the corresponding equivalence classes, now however in terms of ep $\varepsilon$-pseudo-orbits.

**Definition 7.** For $a, b \in M$ we define $a \succcurlyeq_{ep} b$ ('$a$ ep-chains to $b$') if for every $\varepsilon > 0$ there exists an ep $\varepsilon$-pseudo-orbit going from $a$ to $b$.

The relation $\succcurlyeq_{ep}$ (to be called *ep-chaining*) is a preorder on $M$. Ep-chaining is not necessarily a closed relation: if $(a_i)$ and $(b_i)$ are two sequences in $M$ that converge to $a$ and $b$ respectively and are such that for all $i$: $a_i \succcurlyeq_{ep} b_i$, then not necessarily $a \succcurlyeq_{ep} b$ (take e.g. $a$ and $b$ in different extinction boundaries of $M$ and not in their intersection).

We shall refer to the image of $a$ under $\succcurlyeq_{ep}$ as the forward ep-chain lineage through $a$, denoted as $C_{ep,+}(a)$. The backward ep-chain lineage through $a$, denoted as $C_{ep,-}(a)$, is defined as the inverse image of $a$ under $\succcurlyeq_{ep}$; the ep-chain lineage through $a$ is the union $C_{ep,-}(a) \cup C_{ep,+}(a)$ and is denoted by $C_{ep}(a)$.

**Definition 8.** For elements $a, b \in M$ the relation $\sim_{ep}$ is defined by: $a \sim_{ep} b$ if $a \succcurlyeq_{ep} b$ and $b \succcurlyeq_{ep} a$.

Since $\succcurlyeq_{ep}$ is a preorder, $\sim_{ep}$ is an equivalence relation on $M$, to be called *mutual ep-chaining*. The expression $a \sim_{ep} b$ ('$a$ and $b$ ep-chain to each other') implies that either both $a$ and $b$ belong to $M \cap \operatorname{int}\left(\mathbb{R}^k_+\right)$, or that $a$ and $b$ both belong to $M \cap \operatorname{int}\left(\mathrm{bd}_{i_1,\ldots i_l}\left(\mathbb{R}^k_+\right)\right)$, for one and the same $\mathrm{bd}_{i_1,\ldots,i_l}\left(\mathbb{R}^k_+\right)$. The equivalence class of $a$ under $\sim_{ep}$ is denoted as $[a]_{ep}$, and $\mathcal{M}_{ep}$ denotes the set of equivalence classes in $M$ under $\sim_{ep}$. Note that the relation $\sim_{ep}$ is not closed (in the sense indicated above).

**Proposition 3.** If $\overline{[a]_{ep}} \subset M \cap \operatorname{int}\left(\mathbb{R}^k_+\right)$, then $[a]_{ep} = [a]$; if $\overline{[a]_{ep}} \subset M \cap \operatorname{int}\left(\mathrm{bd}_{i_1,\ldots,i_l}\left(\mathbb{R}^k_+\right)\right)$, then $[a]_{ep} = [a]_{i_1,\ldots,i_l}$. Consequently, in both cases $[a]_{ep}$ is closed.

**Proof** $M$ is a normal space, and so are the $\mathrm{bd}_{i_1,\ldots,i_l}(M)$. Therefore, under the constraints of the Proposition, if $b \in [a]_{ep}$ there exists a $\delta > 0$ such that for every $\varepsilon < \delta$ there exists at least one $\varepsilon$-pseudo-orbit going from $a$ to $b$ (and also at least one going from $b$ to $a$) that is confined to $M \cap \operatorname{int}\left(\mathbb{R}^k_+\right)$ or to $M \cap \operatorname{int}\left(\mathrm{bd}_{i_1,\ldots,i_l}\left(\mathbb{R}^k_+\right)\right)$. Any of these $\varepsilon$-pseudo-orbits then are ep $\varepsilon$-pseudo-orbits.

**Definition 9.** $[a]_{ep}$ is called an ep-basic class if $a$ (and consequently every $x \in [a]_{ep}$) is ep-chain recurrent.

The ep-chain recurrent set is the union of all ep-basic classes. Three equivalent statements similar to the characterisation of basic classes in Proposition 2 can be made for ep-basic classes:

**Proposition 4.** The following three statements are equivalent:

1. $[a]_{ep}$ is an ep-basic class;
2. $a$ is a fixed point or $[a]_{ep}$ contains more than one point;
3. for all $t \geq 0$: $\phi^t([a]_{ep}) = [a]_{ep}$.

A class that is not ep-basic, as well as the corresponding state, will be called *ep-chain ephemeral*. As the term ephemeral is tied in the negative to the notion of recurrence, we have from the implications:

$$a \text{ is positively recurrent} \Rightarrow a \text{ is ep-chain recurrent} \Rightarrow a \text{ is chain recurrent}$$

that:

$$a \text{ is chain ephemeral} \Rightarrow a \text{ is ep-chain ephemeral} \Rightarrow a \text{ is ephemeral.}$$

**Definition 10.** For elements $[a]_{ep}, [b]_{ep} \in \mathcal{M}_{ep}$ the relation $\geqslant_{ep}$ is defined by: $[a]_{ep} \geqslant_{ep} [b]_{ep}$ if $a \succcurlyeq_{ep} b$.

The relation $\geqslant_{ep}$ (to be called *ep-connecting*) is a partial ordering on the set of equivalence classes of $\sim_{ep}$. By means of $\geqslant_{ep}$ we adapt the definitions of chain attractors, -repellers and -saddles to community-dynamical processes.

**Definition 11.**

(i) $[a]_{ep}$ is an ep-chain attractor if it is a minimal element of the partial ordering $\geqslant_{ep}$.

(ii) $[a]_{ep}$ is an ep-chain repeller if it is a maximal ep-basic class of the partial ordering $\geqslant_{ep}$.

(iii) $[a]_{ep}$ is an ep-chain saddle if it is an ep-basic class that is neither minimal nor maximal under $\succcurlyeq_{ep}$.

(iv) Ep-chain ephemeral classes, ep-chain repellers and ep-chain saddles, c.q. the states therein, shall be referred to as ep-chain transient.

An ep-chain attractor is an ep-basic class, and, by Proposition 4, contains the $\omega$-limit sets of all its elements.

Existence of ep-chain attractors follows along the same line of reasoning that guarantees the existence of chain attractors: since $M$ is a normal space, under the restriction of ep $\varepsilon$-pseudo-orbits any forward ep-chain lineage necessarily ends up in either some compact set in the interior of the community state space, or in a compact set in the interior of one of the extinction boundaries, of which there are only finitely many. Since on such a compact set the restriction of $\succsim_{ep}$ coincides with $\succsim$, we can fall back on Ruelle's result in [84] for chain attractors.

Any ephemeral maximal class in $\mathcal{M}_{ep}$ under $\succcurlyeq_{ep}$ belongs to $\overline{\mathrm{bd}_{\mathrm{int}}(M)}$.

**Proposition 5.** Any ep-chain attractor is closed.

**Proof** If not($\overline{[a]_{ep}} \subset M \cap \mathrm{int}\left(\mathbb{R}_+^k\right)$ or $\overline{[a]_{ep}} \subset M \cap \mathrm{int}\left(\mathrm{bd}_{i_1,\ldots,i_l}\left(\mathbb{R}_+^k\right)\right)$ for some $i_1, \ldots, i_l$), then $[a]_{ep}$ is not a minimal element of $\succcurlyeq_{ep}$. The result now follows from Proposition 3.

In addition we adapt the definition of the basin of chainability.

**Definition 12.** Let $a \in M$.

(i) The basin of ep-chainability of $a$, denoted $B_{\succsim_{ep}}(a)$, is the collection of points $b \in M$ that ep-chain to a: $B_{\succsim_{ep}}(a) = \{b \in M | b \succsim_{ep} a\}$.

(ii) The basin of ep-chainability of the equivalence class $[a]_{ep}$, denoted $B_{\succsim_{ep}}([a]_{ep})$, is: $B_{\succsim_{ep}}([a]_{ep}) = B_{\succsim_{ep}}(a)$.

(iii) If $[a]_{ep}$ is an ep-chain attractor, we refer to its basin of ep-chainability as its basin of ep-chain attraction, and shall denote it as $Att_{ep}([a]_{ep})$.

The basins of ep-chainability have properties similar to the ones for the basins of chainability: for each $a \in M$, $B_{\succsim_{ep}}(a) \neq \emptyset$; also, an element of $M$ can belong to several basins of ep-chainability, and each element of $M$ belongs to the basin of ep-chain attraction of at least one ep-chain attractor (by the same argument as used to show the existence of ep-chain attractors).

**Proposition 6.** Every chain attractor contains an ep-chain attractor.

**Proof** Let $[a]$ denote a chain attractor. If $[a] \subset M \cap \operatorname{int}\left(\mathbb{R}_+^k\right)$ or $[a] \subset M \cap \operatorname{int}\left(\operatorname{bd}_{i_1,\dots,i_l}\left(\mathbb{R}_+^k\right)\right)$, then $[a] = [a]_{ep}$ and the validity of the statement follows immediately. In general, choose $b \in [a]$. $b$ belongs to the basin of ep-chain attraction of at least one ep-chain attractor $[c]_{ep}$. Since any ep $\varepsilon$-pseudo-orbit through $b$ also is an $\varepsilon$-pseudo-orbit through $b$, it follows that $[c]_{ep} \subset [a]$.

## 4.4 FOUR EXAMPLES

*Example 1*

Figure 4.2 depicts a dynamical system consisting of two populations that are population-dynamically equivalent, e.g. since their members differ only in some neutral marker. The dynamics is degenerate, in the sense that there exists a line AB of neutrally stable equilibria. Each equilibrium on this line attracts all points on the straight line through it and the origin, except for the origin itself (which is an unstable equilibrium on each line). In particular, A and B are globally stable equilibria for the two single populations.

For each pair $E_1$, $E_2$ of neutrally stable equilibria on AB we have that $E_1 \sim E_2$, as $E_1$ and $E_2$ are connected for all $\varepsilon > 0$ by back and forth $\varepsilon$-pseudo-orbits consisting of movement at a fixed speed $\varepsilon/2$ along the line AB. Consequently, the line AB is the (unique) chain attractor for the dynamics depicted in Figure 4.2. The ep-chain attractors are given by equilibria A and B and the origin. The origin is a degenerate ep-chain attractor, since its basin of ep-chain attraction contains only one point (and it is at the same time an ep-chain repeller).

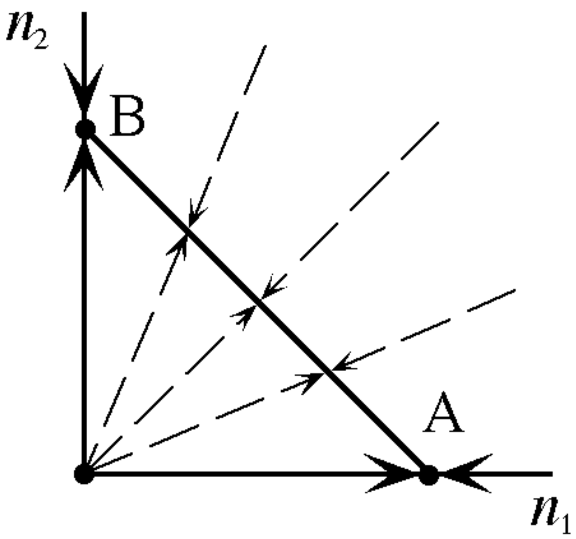


Figure 4.2: A degenerate dynamical system, which has the line AB as its unique chain attractor and A, B and the origin as its ep-chain attractors

*Example 2*

The dynamical system depicted in Figure 4.3 results as the simplest perturbation of the degenerate case shown in Figure 4.2. The neutrally stable equilibria on AB in Figure 4.2 have turned ephemeral, but for the two single species and the one two-species equilibria. These three equilibria together with the origin are the ep-chain attractors.

*Example 3*

In the May-Leonard system as described in [68], the community state moves towards a chain attractor in the form of a heteroclinic cycle in bd $\left(\mathbb{R}^3_+\right)$, connecting three single species equilibria; see Figure 4.4. These three equilibria and the origin are the ep-chain attractors of the system.

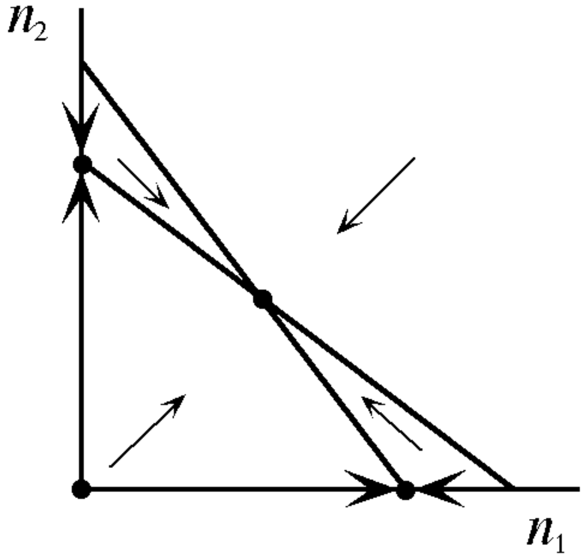


Figure 4.3: The simplest perturbation of the dynamical system from Example 1. The four ep-chain attractors are: the two-species equilibrium, the two non-trivial single species equilibria, and the origin

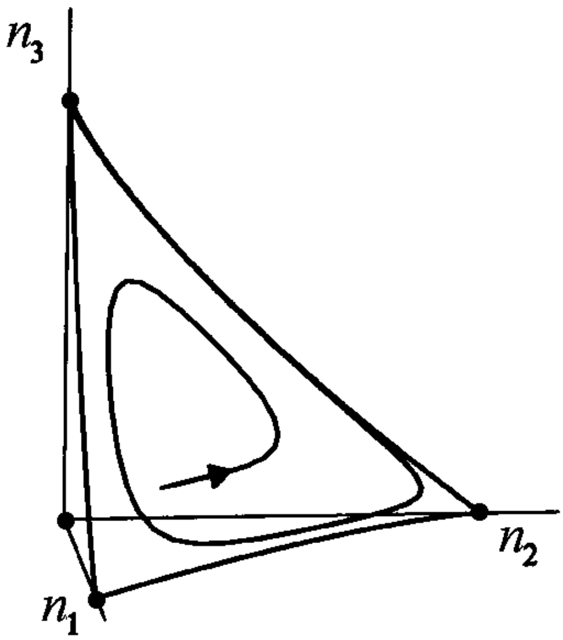


Figure 4.4: The May-Leonard dynamical system, with a heteroclinic cycle as its chain attractor and three non-trivial single species equilibria together with the origin as its ep-chain attractors

*Example 4*

This example illustrates that the ep-chain recurrent set does not necessarily have to be a closed set. In the dynamical system represented in Figure 4.5, a community in the interior of the community state space is attracted to a plane in whose interior the dynamics is determined by neutrally stable cycles. The ep-chain recurrent set consists of the interior of this plane together with three single species equilibria and the origin. Eventually any arbitrary community starting outside the origin will be confined to one of the three non-trivial ep-chain attractors of the system (the three non-trivial single species equilibria). The origin again is a degenerate ep-chain attractor.

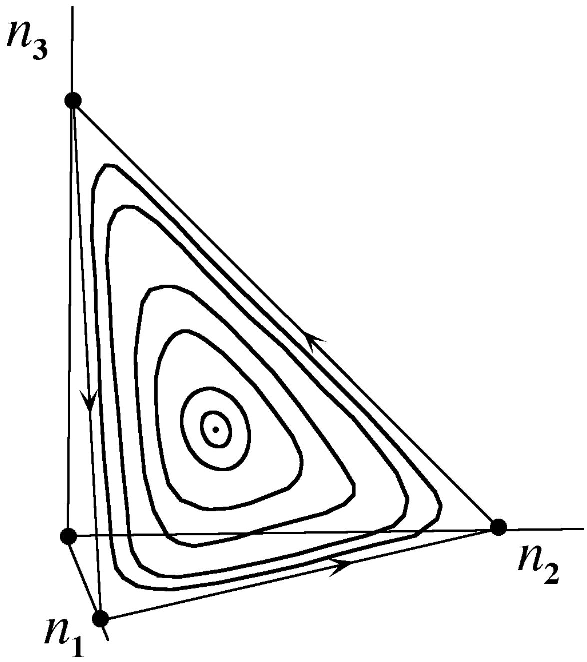


Figure 4.5: An example of a dynamical system with an open ep-chain recurrent set

## 4.5 DISCUSSION

We can expect that eventually the populations in a closed community-dynamical system will end up close to an ep-chain attractor in the interior of an $\mathbb{R}^l_+$ (for an appropriate $l \leq k$, with $k$ the number of populations initially present in the community). The actual attractor that will be reached may depend on the perturbations that the community is exposed to.

A word of warning may be in order though: Along its way towards an (ep-) chain attractor, a community may pass through a cascade of (ep-)chain saddles to which it initially is attracted but from which it subsequently moves away. These phases each have their own specific timescale, measured by a relaxation and excitation time. Since these times can be considerably larger than the eventual relaxation time to the (ep-)chain attractor, it may in empirical practice sometimes be hard to decide whether or not a community is already approaching one of its (ep-)chain attractors.

A bifurcation theory for a class of community-dynamical systems $(\phi^t_\mu)_{t\geq 0}$, depending on a parameter (or a vector of parameters) $\mu$, in essence must study the relation between $\mu$ and the induced ordering $\geqslant_{ep}$ on $\mathcal{M}_{ep}$. The bifurcation points are those values of $\mu$ for which in any neighbourhood there are parameter values for which $\langle \mathcal{M}_{ep}, \geqslant_{ep} \rangle$ (i.e., the set $\mathcal{M}_{ep}$ provided with the partial ordering relation $\geqslant_{ep}$) belongs to a different order isomorphism class.

In the context of phenotypic trait evolution as studied in adaptive dynamics (e.g. [17], [39], [38], [73]), it is assumed that a mutant population emerges from a resident community on an attractor. This assumption is based on the notion that the time needed for a community to reach its attractor is shorter than the timespan between the occurrences of successful mutant populations (successful in the sense that a mutant population invades the resident community and increases its density, causing a change from residental community dynamics into a dynamics of the resident populations with the mutant population; as regards the justification of the assumption of timescale separation the proof of the pudding is in the eating.). However, it never was made very clear what was meant with an attractor. Basically the theory was developed only for systems having classical attractors with pretty strong properties, such as equilibria or limit cycles. The concept of ep-chain attractors provides one possible step towards a further extension of the reach of adaptive dynamics theory. In the special case of Lotka-Volterra community dynamics, it is more or less clear how one can build a theory starting from this attractor concept only (see [53]). In order to arrive at a well-structured theory of adaptive dynamics for more general types of community dynamics, at least some restrictions will be necessary on the properties of the attractors that can occur. In any case, ep-chain attractors appear to be the minimal ingredients from which to start.