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On the Concept of Attractor in Community-Dynamical Processes

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Abstract

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

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1 Introduction

The aim of this paper is to introduce a modification of Conley-Ruelle attractors, as introduced in [6] and [7], that is adapted to the asymptotic behaviour of the dynamical systems studied in community ecology. The construction of Conley-Ruelle attractors is based on the idea that any mathematical system is but an idealization of reality and that neither physical nor numerical experiments produce the precise orbits of the theoretical system under consideration, but rather so-called pseudoorbits that occur as a consequence of small disturbances or roundoff errors. Below we shall give a short review of this construction and some of its properties (Section 2). In addition we some useful new terms such as pseudoreachability and basin of introduce pseudoattraction that do not figure in [6] and [7]. Next we propose the modification (Section 3), followed by two 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 pseudoorbit 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 the Conley-Ruelle attractors, which in essence have their motivation in physics rather than biology.

2 Conley-Ruelle Attractors, Pseudoreachability and Basins of Pseudoattraction

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 formalizing the ubiquitous presence of small perturbations is in terms of pseudoorbits, to be defined below, leading to a characterization of their asymptotic behaviour by means of Conley-Ruelle attractors, which are constructed in terms of those pseudoorbits. In this section we summarize this construction as presented in [6] and Section 8 of [7]. 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* be a compact and metrizable manifold, with a metric *d* and the topology derived from it. Let $\phi : \mathrm{R}_{\geq 0} \times M \to M$ be continuous, and let $(\phi^t)_{t \geq 0}$ denote the induced semiflow on *M*.

An ε-pseudoorbit in *M* is by definition a (not necessarily continuous) curve, i.e., a family $(n_t)_{t\in[t_0,t_1]}$ with $t_1 \geq t_0$, of points in *M* such that $d\left(\phi^{\beta}(n_{t+\alpha}), \phi^{\alpha+\beta}(n_t)\right) < \varepsilon$ whenever $\alpha, \beta \geq 0$, $\alpha + \beta \leq 1$, and $t, t+\alpha \in [t_0, t_1]$. The ε-pseudoorbit then goes from n_{t_0} to n_{t_1} and has length $t_1 - t_0$. By concatenation of two ε-pseudoorbits, one going from *a* to *b* and of length *T*, the second one going from *b* to *c* and of length T', we obtain a 2ε-pseudoorbit of length $T + T'$ going from *a* to *c*.

A point *n* is chain-recurrent if, for every ε, $T > 0$, there is an ε-pseudoorbit of length $\geq T$ going from *n* to *n*. Chain-recurrency captures the notion of recurrency under arbitrarily small perturbations by means of (a sequence of) pseudoorbits. The set of chain-recurrent points is the chain-recurrent set.

On *M* the following relation $\succ$, to be called *pseudoreachability*, is defined: $a \succ b$ ('*b* is *pseudoreachable* from *a*') if for every $\varepsilon > 0$ there exists an ε-pseudoorbit going from *a* to *b*. (Roughly stated $a \succ b$ means that there is an orbit or an arbitrarily little perturbed orbit on *M* going from *a* to *b*.) The relation $\succ$ is reflexive ($a \succ a$, trivially by means of an ε-pseudoorbit of length 0) and transitive ($a \succ b$ and $b \succ c$ imply $a \succ c$), and thus is a preorder on *M*. The relation $\succ$ is also closed: if $x \succ y$ and $x \to a$, $y \to b$, then $a \succ b$. (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. Let $a,b \in M$. $a \succ b$ if and only if there is a $t \geq 0$ such that $\phi^t(a) = b$ or for all $t \geq 0$: $\phi^t(a) \succ b$.

The relation ~ on M is defined in the following way: $a \sim b$ if $a \succ b$ and $b \succ a$. Since $\succ$ is a preorder, ~ is an equivalence relation on M, to be called *mutual pseudoreachability*. $[a]$ denotes the equivalence class of a under ~. Clearly ~ is a closed relation, and therefore every equivalence class is closed.

$[a]$ is called a basic class if a (and consequently every $x \in [a]$) is chain-recurrent, and the chain-recurrent set then is the union of all basic classes. By means of the Proposition above the following three statements are equivalent:

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

On the set of equivalence classes $M/\sim$ the relation $\geq$ is defined by: $[a] \geq [b]$ if $a \succ b$. This relation is reflexive and transitive. In addition, $[a] \geq [b]$ and $[b] \geq [a]$ together imply that $[a] = [b]$. $\geq$ thus imposes a partial ordering on $M/\sim$. A Conley-Ruelle attractor is a minimal element in $M/\sim$ under $\geq$, and consequently is a basic class. (The name Conley-Ruelle attractor is adopted from [2]).

In addition to the above review of the idea of Conley-Ruelle attractors we introduce the sometimes useful terms basin of pseudoreachability and basin of pseudoattraction.

Definition. Let $a \in M$.

(*i*) The *basin of pseudoreachability* of *a*, denoted $B_{\succ}(a)$, is the collection of points $b \in M$ such that for every $\varepsilon > 0$ there exists an ε-pseudoorbit going from *b* to *a*: $B_{\succ}(a) = \{b \in M \mid b \succ a\}$.

(*ii*) The *basin of pseudoreachability* of the equivalence class [*a*], denoted $B_{\succ}([a])$, is: $B_{\succ}([a]) = B_{\succ}(a)$.

(*iii*) If $[a]$ is a Conley-Ruelle attractor, we refer to its basin of pseudoreachability as its *basin of pseudoattraction*, and shall denote it as $Att([a])$.

Note that for each $a \in M$, $B_{\succ}(a) \neq \varnothing$ (since $a \in B_{\succ}(a)$). An element of M can belong to several basins of pseudoreachability, and each element of M belongs to the basin of pseudoattraction of at least one Conley-Ruelle attractor. 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 Conley-Ruelle attractors.

3 Strong Conley-Ruelle Attractors for Community-Dynamical Processes

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 and metrizable manifold *M* 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 $n_1,\ldots,n_k$, *M* is the intersection of $\mathrm{R}^k_{\geq 0} \subset \mathrm{R}^k$ with the closure of a simply connected neighbourhood of 0 in R^k. *M* is supposed to be provided with the standard (Euclidean) metric and topology.

For $l \in \mathrm{N}$, with $1 \leq l \leq k$, and for $i_1,\ldots,i_l \in \{1,\ldots,k\}$ such that $1 \leq i_1 < \ldots < i_l \leq k$, $bd_{i_1,\ldots,i_l}\left(\mathrm{R}^k_{\geq 0}\right)$ denotes the boundary set $\left\{(n_1,\ldots,n_k) \in \mathrm{R}^k_{\geq 0} : n_{i_1} = \ldots = n_{i_l} = 0\right\}$ of $\mathrm{R}^k_{\geq 0}$, and $bd\left(\mathrm{R}^k_{\geq 0}\right)$ denotes the union of the boundary sets of $\mathrm{R}^k_{\geq 0}$; furthermore, we write $bd_{i_1,\ldots,i_l}(M)$ for $bd_{i_1,\ldots,i_l}\left(\mathrm{R}^k_{\geq 0}\right) \cap M$.

The assumption of no immigration translates into the invariance of the $bd_{i_1,\ldots,i_l}(M)$ under the semiflow $(\phi^t)_{t\geq 0}$. For $a \in bd_{i_1,\ldots,i_l}(M)$ the equivalence class generated by the relation of mutual pseudoreachability connected to the semiflow $\left(\phi^t\big|_{bd_{i_1,\ldots,i_l}(M)}\right)_{t\geq 0}$ will be denoted as $[a]_{i_1,\ldots,i_l}$.

In the theory reviewed in Section 2, an ε-pseudoorbit which has a point in common with (or, more generally, comes arbitrarily close to) a boundary set $bd_{i_1,\ldots,i_l}(M)$ of *M*, may again get away from this boundary set and proceed in the interior $int(M)$ of the community state space. This is unrealistic in the case of community-dynamical processes, in which populations that attain almost zero densities are bound to go irreversibly extinct by demographic stochasticity. To incorporate this biological restriction into our considerations we introduce the following notion:

Definition. An ε-pseudoorbit $(n_t)_{t\in[t_0,t_1]}$ in M is called *strong* if it satisfies the following property: if $t_\alpha \in [t_0,t_1]$ is such that $n_{t_\alpha} \in bd_{i_1,\dots,i_l}(M)$ or $\lim\limits_{t\to t_\alpha} n_t \subset bd_{i_1,\dots,i_l}(M)$, then for all $t\in[t_\alpha,t_1]$: $n_t \in bd_{i_1,\dots,i_l}(M)$.

In addition we define:

Definition. A point *n* is *strongly chain-recurrent* if for every ε, $T>0$ there is a strong ε-pseudoorbit of length $\geq T$ going from *n* to *n*. The set of strongly chain-recurrent points is the *strongly chain-recurrent set*.

Note that a strongly chain-recurrent point $n\in M$ satisfies either one of the following two mutually exclusive conditions:

1. *n* as well as every strong ε-pseudoorbit going from *n* to *n* belongs to $int\left(\mathrm{R}^k_{\geq 0}\right)$;
2. *n* as well as every strong ε-pseudoorbit going from *n* to *n* belongs to the interior of a unique boundary set $bd_{i_1\dots i_l}(M)$ (with the interior here with regard to the relative topology on $bd_{i_1\dots i_l}(M)$).

Furthermore, the strongly 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 strong ε-pseudoorbits.

Definition. Let $a,b\in M$. $a\succ_s b$ ('*b* is *strongly pseudoreachable* from *a*') if for every $\varepsilon>0$ there exists a strong ε-pseudoorbit going from *a* to *b*.

The relation $\succ_s$ (to be called *strong pseudoreachability*) is a preorder on *M*. It is not necessarily closed: if $x\succ_s y$ and $x\to a$, $y\to b$, then not always $a\succ_s b$ (take e.g. *a* and *b* in different boundary sets of *M* and not in their intersection).

Definition. Let $a,b\in M$. $a\sim_s b$ if $a\succ_s b$ and $b\succ_s a$.

Since $\succ_s$ is a preorder, $\sim_s$ is an equivalence relation on *M*, to be called *mutual strong pseudoreachability*. $[a]_s$ denotes the equivalence class of *a* under $\sim_s$, and $M/\sim_s$ the set of equivalence classes in *M* under $\sim_s$. Note that the relation $\sim_s$ is not closed. $a\sim_s b$ ('*a* and *b* are *mutually strongly pseudoreachable*') implies that either both *a* and *b* belong to $int\left(\mathrm{R}^k_{\geq 0}\right)$, or that *a* and *b* both belong to the interior of a unique boundary set $bd_{i_1,\dots,i_l}(M)$.

Notation. For $U\subseteq M$, let $\overline{U}$ denote the closure of *U* in *M*.

Proposition. If $\overline{[a]_s} \subset int(M)$, then $[a]_s = [a]$; if $\overline{[a]_s} \subset int\left(bd_{i_1,\ldots,i_l}(M)\right)$ (with regard to the relative topology on $bd_{i_1,\ldots,i_l}(M)$), then $[a]_s = [a]_{i_1,\ldots,i_l}$. Consequently, in both cases $[a]_s$ is closed.

Proof. M is a normal space, and so are the $bd_{i_1,\ldots,i_l}(M)$. Therefore, under the constraints of the proposition, if $b \in [a]_s$ there exists a $\delta > 0$ such that for every $\varepsilon < \delta$ all ε-pseudoorbits between b and a are confined to $int(M)$ or to $int\left(bd_{i_1,\ldots,i_l}(M)\right)$. Consequently, all of these ε-pseudoorbits are strong ε-pseudoorbits.

Definition. $[a]_s$ is called a *strong basic class* if a (and consequently every $x \in [a]_s$) is strongly chain-recurrent.

The strongly chain-recurrent set is the union of all strong basic classes. Three equivalent statements similar to the characterization of basic classes in Section 2 can be made for strong basic classes:

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

Definition. Let $[a]_s, [b]_s \in M/\sim_s$. $[a]_s \geq_s [b]_s$ if $a \succ_s b$.

$\geq_s$ is a partial ordering on the set of equivalence classes of $\sim_s$.

Definition. $[a]_s$ is a *strong Conley-Ruelle attractor* if it is a minimal element of the ordering $\geq_s$.

Proposition. A strong Conley-Ruelle attractor is closed.

Proof. If not ($\overline{[a]_s} \subset int(M)$ or $\overline{[a]_s} \subset int\left(bd_{i_1,\ldots,i_l}(M)\right)$ for some $i_1,\ldots,i_l$), then $[a]_s$ is not a minimal element of $\geq_s$. The result now follows from the previous Proposition.

In addition to the modification of the Conley-Ruelle attractor we adapt the definition of the basin of pseudoreachability.

Definition. Let $a \in M$.

(i) The *basin of strong pseudoreachability* of a, denoted $B_{\succ_s}(a)$, is the collection of points $b \in M$ such that for every $\varepsilon > 0$ there exists a strong ε-pseudoorbit going from b to a: $B_{\succ_s}(a) = \{b \in M \mid b \succ_s a\}$.

(ii) The *basin of strong pseudoreachability* of the equivalence class $[a]_s$, denoted $B_{\succ_s}([a]_s)$, is: $B_{\succ_s}([a]_s) = B_{\succ_s}(a)$.

(iii) If $[a]_s$ is a strong Conley-Ruelle attractor, we refer to its basin of strong pseudoreachability as its *basin of strong pseudoattraction*, and shall denote it as $Att_s([a]_s)$.

The basins of strong pseudoreachability have properties similar to the ones for the basins of pseudoreachability. That is: for each $a \in M$, $B_{\succ_s}(a) \neq \varnothing$; also, an element of M can belong to several basins of strong pseudoreachability, and each element of M belongs to the basin of strong pseudoattraction of at least one strong Conley-Ruelle attractor.

4 Two Examples

Example 1. In the May-Leonard system as described in [4], the community state moves towards a Conley-Ruelle attractor in the form of a heteroclinic cycle in $bd(\mathrm{R}^3_{\geq 0})$, connecting three single species equilibria; see Figure 1. These three equilibria are the strong Conley-Ruelle attractors of the system.

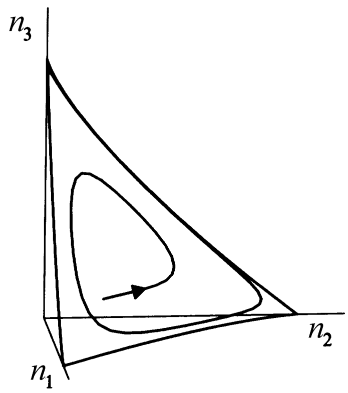

Figure 1

Example 2. Figure 2 depicts a dynamical system consisting of two populations, the members of which differ only in some neutral marker, and are population-dynamically equivalent.

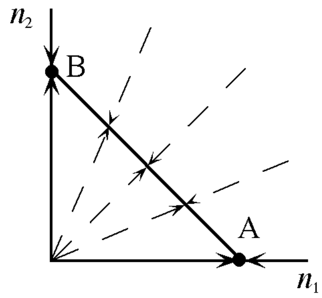

Figure 2

The dynamics is degenerate, in the sense that there exists a line AB of neutrally stable equilibria. Each equilibrium on this line is a global attractor for the dynamics confined to the straight line through this equilibrium and the origin (except for the origin itself, which is an unstable equilibrium on each line). Especially, 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 ε-pseudoorbits consisting of movement at a fixed speed $\varepsilon/2$ along the line AB. Consequently, the line AB is the (unique) Conley-Ruelle attractor for the dynamics depicted in figure 2. The strong Conley-Ruelle attractors are given by equilibria A and B.

5 Discussion

Eventually the populations in a closed community-dynamical system will end up close to a strong Conley-Ruelle attractor in the interior of an $\mathrm{R}^{l}_{\geq 0}$ (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: Along its way towards a (strong) Conley-Ruelle attractor, a community may pass through a cascade of (strong) basic classes to which it initially is attracted but from which it subsequently moves away. These phases each have their own specific time scale, expressed by a relaxation and excitation time. Since these times can be of the same order of magnitude as the eventual relaxation time to the (strong) Conley-Ruelle attractor, it may in empirical practice sometimes be hard to decide whether or not a community is already approaching one of its (strong) Conley-Ruelle attractors.

In the context of phenotypic trait evolution as studied in adaptive dynamics (e.g. [3], [5]), 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 they invade the resident community and increase their density, causing a change from residential community dynamics into a dynamics of the resident populations with the mutant population; as regards the justification of the assumption of time scale 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 strong Conley-Ruelle 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 [3]). 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, strong Conley-Ruelle attractors appear to be the minimal ingredients from which to start.

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