RIGOROUS METHOD FOR THE GLOBAL DYNAMICS OF THE SEMELPAROUS SPECIES

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ABSTRACT. We present a computer assisted method for automatic verification that in a given model of the competition of different age classes of semelparous species under the dynamics of the system in general only one age class will survive, the rest need to extinct. This extinction happens for almost all initial sizes of the age classes except the measure zero set related to the unstable fixed point.

1. INTRODUCTION

Individuals of the semelparous species reproduce only once in their life time and often die shortly afterwards. We will consider species with fixed life span length. Dynamics of the semelparous species was investigated by many authors . Recently Rudnicki and Wieczorek in [3] studied broad class of models. They proved for them several general properties and they end up with conjecture that *if a specie lives for even number of years then the competition of different age classes leads to the extinction of all but one year classes for almost all initial class sizes.* As they observe numerically in many cases it is also true for species that live for odd number of years. The remarkable example of such fenomena are periodical cicadas of eastern North America. They spend most of their life time underground and every 13 or 17 years (depending on specie) they appear synchronously in tremendous numbers. The primary motivation for this paper is to study the global dynamics of semelparous species and provide automatic way of checking if for given model the above conjecture is true.

We present a computer assisted method which for given model gives precise description of the global dynamics which in contrast to numerical simulations has all the mathematical rigour. All computations are performed using rigorous numerics in which floating points operations are replaced by interval arithmetic in such a way that returned bounds are guaranteed to contain the true result. All other numerical errors are also taken into account so that obtained estimates can be used to verify assumptions of suitable theorems.

Presented method consists of three steps. First we use analytic estimates of the trapping region to restrict interesting dynamics to a compact set. Next, inside such a set we obtain rough description of the dynamics given by Morse graph. Roughly speaking it stores in vertices upper estimates of the recurrent sets and directed edges represent all possible connection between recurrent sets. In the last step for each vertex we perform additional computations to get exact (or at least much sharper) description of the recurrent sets.

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The method joins together two approaches: the first one that is focused on global picture up to some finite resolution and the second one that study local phenomena such as fixed points, periodic orbits, connectiong orbits, etc. Although in this paper we apply the method only to the dynamics of the semelparous species, it can be easily used in the context of other dynamical systems.

A number of individuals at age a at time t we denote by $x_a(t)$. We assume that the maximal age a_{max} is finite, therefore the state of the population at time t can be represented as a vector $x(t) = (x_1(t), x_2(t), \ldots, x_{a_{max}}(t))$. For the most of the paper we will consider a general population model with discrete time

$$x(t+1) = F(x(t)) \tag{1}$$

where $F : \mathbb{R}^n_0 \to \mathbb{R}^n_0$ is a C^1 function.

2. Rough global dynamics

Definition 1. *A subset $S \subset X$ is called an* ***invariant set*** *if $f(S) = S$. A compact subset $N \subset X$ is called an* ***isolating neighborhood*** *if*

$$Inv(N, f) \subset int(N)$$

where $Inv(N, f)$ denotes the maximal invariant set under f contained in N. An invariant set S is called ***isolated*** *if $S = Inv(N, f)$ for some isolating neighborhood N.*

Definition 2. *A* ***Morse decomposition*** *of an isolated invariant set S is a finite collection*

$$M(S) = \{M(p) \subset S \mid p \in \mathcal{P}\}$$

of disjoint isolated invariant sets, called ***Morse sets****, which are indexed by the set $\mathcal{P}$ on which there exists a strict partial ordering $\succ$, called an* ***admissible order****, such that for every $x \in S$*
$\bigcup_{p\in\mathcal{P}} M(p)$ and any complete orbit γ of f through x in S there exist indices $p \succ q$ such that under f

$$\omega(\gamma) \subset M(q) \text{ and } \alpha(\gamma) \subset M(p).$$

The main purpose to compute Morse decomposition is to get global description of the dynamics on S. Every subset of S that is associated with recurrent dynamics e.g. a fixed point, a periodic orbit, chaotic dynamics must lie in some Morse set. The dynamics outside the Morse sets is gradient-like and all possible directions of trajectories between Morse sets are encoded in an admissible partial order. The Morse decomposition can be represented as an acyclic directed graph, called **Morse graph**, in which vertices correspond to Morse sets and edges are generated by ordering $\succ$.

To construct Morse graphs we use conley-morse-database software [1]. The software adaptively grids the phase space, constructs combinatorial representation of the dynamics from which a Morse decomposition is computed (see [2] for detailed description). As a result one obtain Morse graph and upper estimates of Morse sets corresponding to vertices. In general Morse graphs are not unique. They often can be refined. Because we need to stop subdivision of the phase space at some level graphs can contain some 'artificial' vertices, which correspond to empty Morse sets. Due to overestimations graphs can also contain edges between Morse sets, that are not connected by any trajectory. Those two facts do not conflict with the above definition of the Morse decomposition.

3. Dynamics inside Morse sets

In this section we assume that we already have description of the global dynamics given by Morse graph $(\mathcal{P}, E)$. We would like to stress that this description can be very rough. Usually we do not know Morse sets explicitely, but we have only sets of boxes covering them.

On the one hand even if a Morse set is empty or contains single fixed point the estimates could be quite big. On the other hand narrow estimates of the Morse set usually do not guarantee that the set measure is zero.

To obtain rough description of the dynamics usually only values of the function are used.

3.1. **Repeller.**

Theorem 1. *Let $f : \mathbb{R}_0^n \to \mathbb{R}_0^n$ be differentiable and $f(0) = 0$. Let $0 \in V \subset \mathbb{R}_0^n$ be compact and convex. If $\sum_{j=1}^n \frac{\partial f_j}{\partial x_i} > \delta > 1$ for some δ and $i = 1, 2, \ldots, n$ then $Inv(V, f) = \{0\}$.*

Proof: Let $x = (x_1, x_2, \ldots, x_n) \in V$ and let $L(x) = \sum_{i=1}^n x_i$. If $x \neq 0$ we have

$$\begin{aligned} L(f(x)) &= L(\int_0^1 f'(sx)xds) = \sum_{j=1}^n \int_0^1 \sum_{i=1}^n \frac{\partial f_j(sx)}{\partial x_i} x_i ds \\ &= \sum_{i=1}^n x_i \int_0^1 \sum_{j=1}^n \frac{\partial f_j(sx)}{\partial x_i} ds > \delta \sum_{i=1}^n x_i = \delta L(x). \end{aligned}$$

Hence all points in V except 0 must leave V after a finite number of iterations. ∎

3.2. **Attractors.**

Definition 3. *A set of all natural numbers from 1 to n without i we denote by I_n^i i.e. $I_n^i := \{1, 2, \ldots, i-1, i+i, \ldots, n\}$.*

An i-th positive half-axis will be denoted by $\mathrm{OX_i}$ i.e. $\mathrm{OX_i} = \{(x_1, \ldots, x_n) \in \mathbb{R}^n \mid x_i \geq 0, x_j = 0$ for $j \in I_n^i\}$

$$\pi_i(x) = ...$$

$$hull_0^i(V) := \{(x_1, \ldots, x_n) \in \mathbb{R}_0^n \mid \exists (y_1, \ldots, y_n) \in V : x_i = y_i \text{ and } x_k \leq y_k \text{ for } k \neq i\}$$

Theorem 2. *Let $i \in \{1, 2, \ldots, n\}$ be one of the coordinates and $V \subset \mathbb{R}_0^n$ is compact. Let $f : \mathbb{R}_0^n \to \mathbb{R}_0^n$ be differentiable and $f(\mathrm{OX_i}) \subset \mathrm{OX_i}$. If there exists $k \in \mathbb{N}$ such that for all $x \in hull_0^i(V)$ and all $j \in I_n^i$ we have*

$$0 < \sum_{m \in I_n^i} \frac{\partial f_m^k(x)}{\partial x_j} < \gamma \quad \text{for some } \gamma < 1,$$

then $\mathrm{Inv}(V, f) \subset \mathrm{OX_i}$.
If $\mathrm{Inv}(V, f) \cap \mathrm{OX_i} = \emptyset$ *then* $\mathrm{Inv}(V, f) = \emptyset$.

Proof: Let $L(x) = \sum_{k \in I_n^i} x_k$ and $\mathrm{Inv}(V, f) \neq \emptyset$. From compactness of V it follows that $\mathrm{Inv}(V, f)$ is also compact and therefore there exists $\hat{x} \in \mathrm{Inv}(V, f)$ such that $L(\hat{x}) = max\{L(x) \mid x \in Inv(V,f)\}$. Moreover we have $\hat{x} = f(y)$ for some $y \in \mathrm{Inv}(V,f)$. Let $\bar{y} = \pi_i(y)$.

$$\begin{aligned} L(\hat{x}) &= L(f(y)) = L(f(\bar{y})) + L\left(\int_0^1 f'(\bar{y}+s(y-\bar{y}))ds(y-\bar{y})\right) \\ &= \sum_{j\in I_n^i}\int_0^1 \sum_{k=1}^n \frac{\partial f_j(\bar{y}+s(y-\bar{y}))}{\partial x_k}ds(y_k-\bar{y}_k) \\ &= \sum_{k\in I_n^i} y_k \int_0^1 \sum_{j\in I_n^i}\frac{\partial f_j(\bar{y}+s(y-\bar{y}))}{\partial x_k}ds \\ &< \delta \sum_{k\in I_n^i}(y_k) = \delta L(y). \end{aligned}$$

It is only possible if $L(\hat{x}) = 0$ and hence $Inv(V,f) \subset \mathrm{OX_i}$. ∎

3.3. **Saddle fixed point.** To give more precise description of a Morse set we can use also more general tools. First we will recall from [4] the notions of h-sets, covering relations, cones conditions.

Definition 4. [4, Definition 1] *An h-**set**, N, is a quadruple $(|N|, u(N), s(N), c_N)$ such that*

- *$|N|$ is a compact subset of $\mathbb{R}^n$*
- *$u(N), s(N) \in \{0,1,2,\dots\}$ are such that $u(N)+s(N)=n$*
- *$c_N : \mathbb{R}^n \to \mathbb{R}^n = \mathbb{R}^{u(N)} \times \mathbb{R}^{s(N)}$ is a homeomorphism such that*

$$c_N(|N|) = \overline{B_{u(N)}} \times \overline{B_{s(N)}}.$$

We set

$$\begin{aligned} \dim(N) &:= n, \\ N_c &:= \overline{B_{u(N)}} \times \overline{B_{s(N)}}, \\ N_c^- &:= \partial B_{u(N)} \times \overline{B_{s(N)}}, \\ N_c^+ &:= \overline{B_{u(N)}} \times \partial B_{s(N)}, \\ N^- &:= c_N^{-1}(N_c^-), \quad N^+ = c_N^{-1}(N_c^+). \end{aligned}$$

Hence an h-set, N, is a product of two closed balls in some coordinate system. The numbers $u(N)$ and $s(N)$ are called the **nominally unstable and nominally stable dimensions**, respectively. The subscript c refers to the new coordinates given by homeomorphism c_N. In the sequel to make notation less cumbersome we will sometimes drop the bars in the symbol $|N|$ and we will use N to denote both the h-sets and its support.

Definition 5. [4, Definition 6] *Assume that N, M are h-sets, such that $u(N) = u(M) = u$, $s(N) = s(M) = s$ and let $f : N \to \mathbb{R}^{\dim(M)}$ be continuous. Let $f_c = c_M \circ f \circ c_N^{-1} : N_c \to \mathbb{R}^u \times \mathbb{R}^s$.*

We say that

$$N \stackrel{f}{\Longrightarrow} M$$

*(N f-**covers** M) iff the following conditions are satisfied*

1.: *there exists a continuous homotopy* $h : [0,1] \times N_c \to \mathbb{R}^u \times \mathbb{R}^s$, *such that the following conditions hold true*

$$\begin{aligned} h_0 &= f_c, \\ h([0,1], N_c^-) \cap M_c &= \emptyset, \\ h([0,1], N_c) \cap M_c^+ &= \emptyset. \end{aligned}$$

2.: *If* $u > 0$, *then there exists a map* $A : \mathbb{R}^u \to \mathbb{R}^u$, *such that*

$$\begin{aligned} h_1(p,q) &= (A(p), 0), \ \text{for } p \in \overline{B_u}(0,1) \text{ and } q \in \overline{B_s}(0,1), \\ A(\partial B_u(0,1)) &\subset \mathbb{R}^u \setminus \overline{B_u}(0,1). \end{aligned}$$

Moreover, we require that

$$\deg(A, \overline{B_u}(0,1), 0) \neq 0,$$

Sometimes if map is know from the context we may drop the symbol f and write $N \Longrightarrow M$.

Definition 6. *Let* N *be an h-set and* $Q : \mathbb{R}^{dim(N)} \to \mathbb{R}$ *be a quadratic form*

$$Q(x,y) = \alpha(x) - \beta(y), \qquad (x,y) \in \mathbb{R}^{u(N)} \times \mathbb{R}^{s(N)},$$

where $\alpha : \mathbb{R}^{u(N)} \to \mathbb{R}$ *and* $\beta : \mathbb{R}^{s(N)} \to \mathbb{R}$ *are positively definite quadratic forms.*

The pair (N, Q) *will be called an* ***h-set with cones***.

Definition 7. *Let* (N, Q_N) *and* (M, Q_M) *be h-sets with cones such that* $u(N) = u(M)$ *and let* $f : |N| \to \mathbb{R}^{dim(M)}$. *Assume that* $N \overset{f}{\Longrightarrow} M$. *We say that* f *satisfies the* ***cone condition*** *(with respect to the pair* $((N, Q_N), (M, Q_M))$*) if any* $x_1, x_2 \in N_c$ *with* $x_1 \neq x_2$ *satisfy*

$$Q_M(f_c(x_1) - f_c(x_2)) > Q_n(x_1 - x_2).$$

By $(N, Q_N) \overset{f}{\Longrightarrow} (M, Q_M)$ *we denote the fact that* $N \overset{f}{\Longrightarrow} M$ *and additionally* f *satisfies the cone condition.*

Theorem 3. *Let* (N, Q_N) *be an h-set with cones. If* $(N, Q_N) \overset{f}{\Longrightarrow} (N, Q_N)$, *i.e.* N *covers itself and* f *satisfies the cone condition, then*

$$Inv(N, f) = \{x^*\}$$

where x^* *is a hyperbolic fixed point and the dimension of its stable manifold is equal to the nominally stable dimension* $s(N)$. *If the nominally unstable dimension* $u(N) > 0$ *then everything leaves* $|N|$ *in forward time except the stable manifold which is of measure 0.*

4. Model

The model described in this section is exactly the same as in [3].

We consider discrete time model hence the age a and the time t are positive integers. We assume also that $a < a_{max}$ where $a_{max} < \infty$ is maximal age.

We use the following notation

- $x_a(t)$ is a number of individuals at age a and time t,
- $N(t) = \sum_{a=1}^{a_{max}} x_a(t)$ is a total number of individuals at time t. We assume that $N(t) \leq N_{max}$ for some $N_{max} < \infty$.
- $q_a(N(t))$ and $b_a(N(t))$ denote the *survivorship* and the *birth* rates for an individual at age a at time t. We assume that all rates are continuous.

As a starting point we consider general non-linear Leslie model

$$
\begin{aligned}
N(t) &= \sum_{a=1}^{a_{max}} x_a(t), \\
x_{a+1}(t+1) &= q_a(N(t))x_a(t), \\
x_1(t+1) &= \sum_{a=1}^{a_{max}} b_a(N(t))x_a(t).
\end{aligned} \tag{2}
$$

Since we restrict our attention to *semelparous species* we will assume that only individuals at age n can reproduce and then they die i.e. $b_a(N(t))$ is non zero only for $a = n$. We also assume that the survivorship rate depends only on the age a i.e. $q_a(N(t)) = q_a$. Finally we obtain model

$$
\begin{aligned}
x_{a+1}(t+1) &= q_a x_a(t) \text{ for } a = 1, \dots, n-1, \\
x_1(t+1) &= b(N(t))x_n(t).
\end{aligned} \tag{3}
$$

where n is the maximal age and b is a continuously differentiable function defined on some interval $[0, M)$ where $0 < M \leq \infty$.(

Three typical models and the corresponding birth functions b are

- the logistic model: $b(x) = \sigma\left(1 - \frac{x}{M}\right)$,
- the Ricker model: $b(x) = \sigma e^{-cx}$,
- the Beverton-Holt model: $b(x) = \frac{\sigma}{1+cx}$.

5. Results

In this section we will apply methods from Sections 2 and 3 to semelparous species models described in Section 4. For given model and given parameters our method will try to prove that almost all points converge to the axes except repelling fixed point in the origin, a hyperbolic fixed point and points from its stable manifold. We would like to stress that if the algorithm succeeds the results has all the mathematical rigor

As a first step using conley-morse-database software [1] we obtain Morse graph. We assume that our grid is fine enough that Morse graph consists of one repeller set M_O (that contains origin), a set M_H that is at some distance from all axes and n paths $(M_H, M_i^1, \dots, M_i^{k_i}, M_i)$ connecting M_H with the set M_i "laying" on the i-th axis for $i = 1, \dots, n$. For various parameters different number of subdivisions of the phase space was needed to obtain Morse graphs of the above structure.

Once we have Morse graph we will use theorems from Section 3 to give more detailed information about each of Morse sets. We will prove that:

S1. $\mathrm{Inv}(M_O, f) = \{0\}$.
S2. $\mathrm{Inv}(M_H, f)$ contains only a saddle fixed point.
S3. A set $\mathrm{Inv}(M_i, f)$ is a subset of i-th axis.
S4. Each set M_i^j is empty or lies on one of the axis.

All the models we consider fulfills the general assumptions of theorems in the paper [3] and therefore we know that

- origin is a repelling fixed point,
- there exists exactly one positive fixed point and its stability is easy to determine (e.g. for even number of age classes it is always unstable),
- if we are close enough to the axis we will be attracted to it.

But this information is not enough to prove statements (S1) - (S4). There is still possibility of an existence of an invariant sets other then fixed point in each of the Morse sets in the Morse graph since we know only their rough upper estimates.

To prove statements (S1)-(S4) we perform rigorous computations to obtain estimates of function values and derivatives which verifies assumptions of theorems from Section 3.

5.1. **Results for logistic model.** The logistic birth function is given by

$$b(x) = \begin{cases} \sigma\left(1 - \frac{x}{M}\right) & \text{for } x \in [0, M] \\ 0 & \text{for } x \in (M, \infty) \end{cases}$$

For this model of semelparous species the set $S = [0, M]^n$ is a trapping region for all choices of σ and q_a we will use it as an initial domain for conley-morse-database software. In the following we fix M equal to 1.

First we will apply our algorithm to bienials model (i.e. model with two age classes) for parameters values for which Rudnicki and Wieczorek performed simulation in [3] and we obtained the following rigorous results

Theorem 4. *For the bienials models with logistic birth rate and for parameters values*

- $q = 2/3, \sigma = 3$,
- $q = 0.99, \sigma = 3.3$,

almost all initial conditions converge to the one of the axis under second iteration of the map.

References

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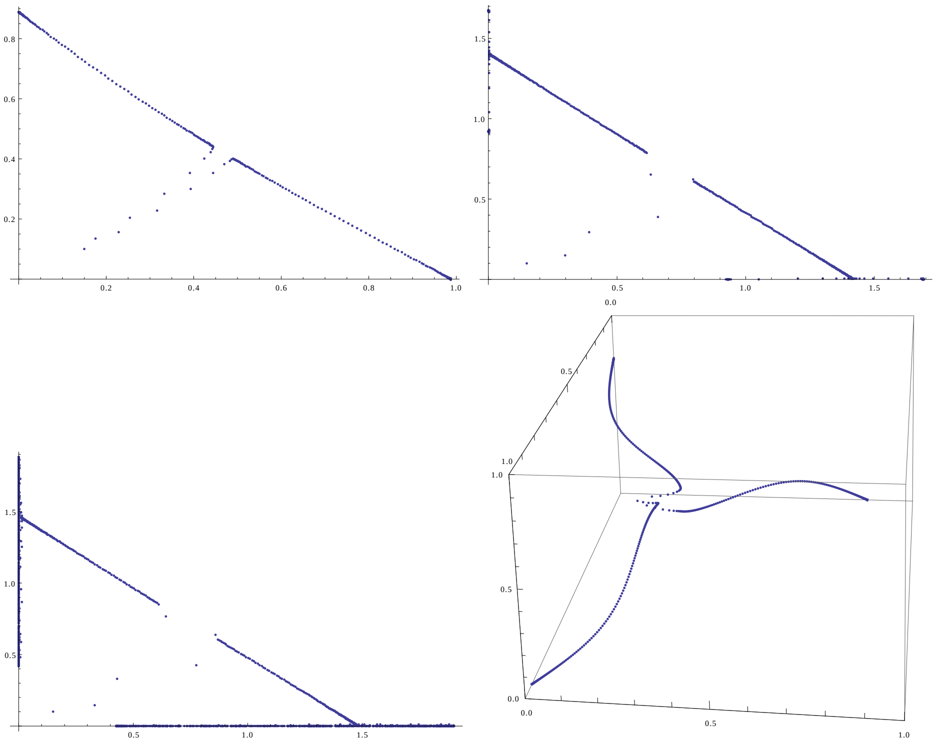

FIGURE 1. Simulations

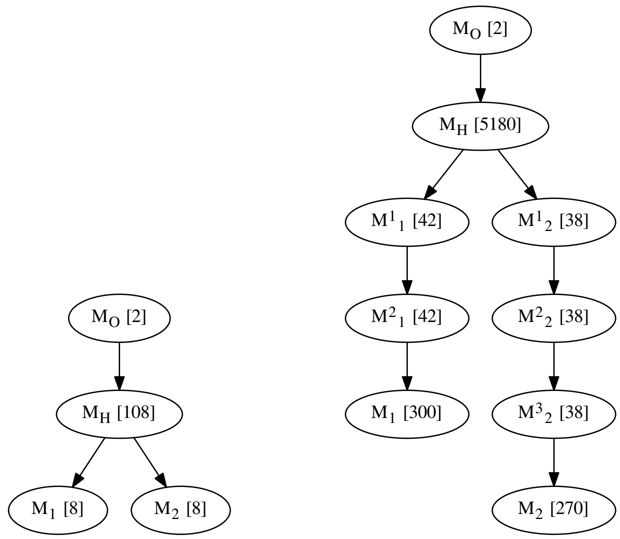

Figure 2. Morse graphs obtained for model with logistic birth rate and parameters values $q = 2/3, \sigma = 3$ (left), $q = 0.99, \sigma = 3.3$ (right). The number of boxes contained in an upper estimate of the recurrent set related to given vertex are displayed in the square brackets.

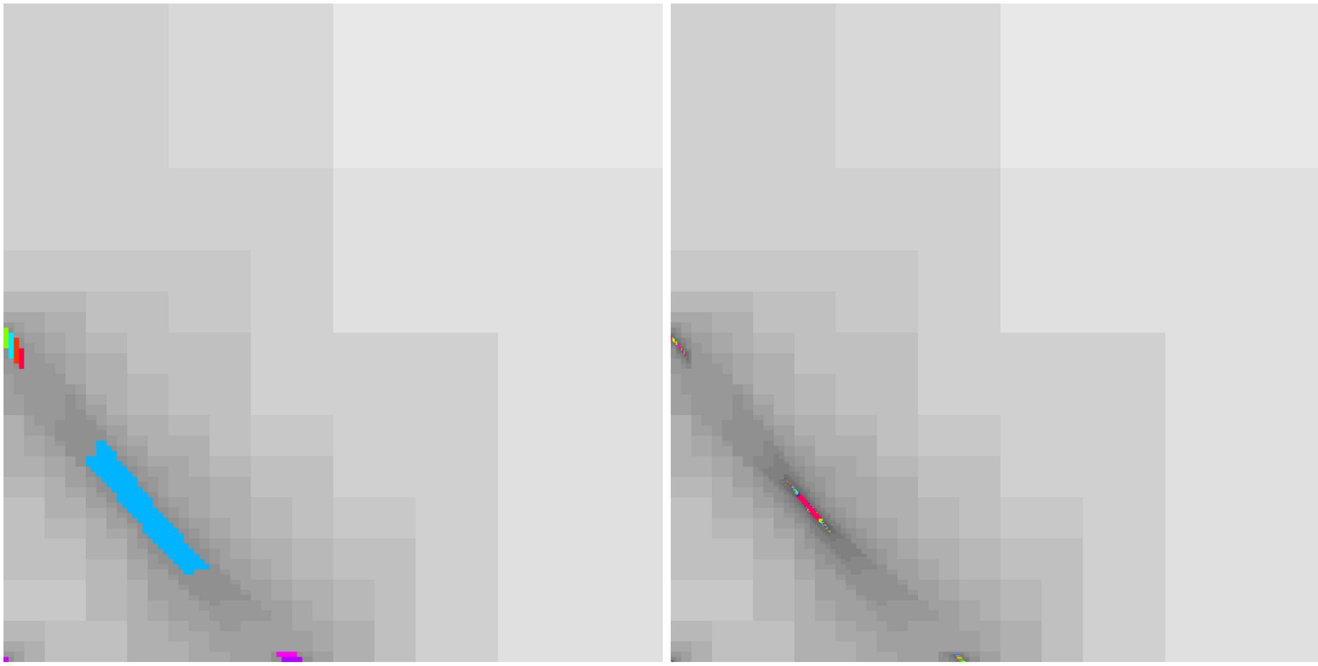

Figure 3. Morse sets