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Planar Bistable Structures Detection via the Conley Index and Applications to Biological Systems

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Abstract: Bistability is a ubiquitous phenomenon in life sciences. In this paper, two kinds of bistable structures in two-dimensional dynamical systems are studied: one is two one-point attractors, another is a one-point attractor accompanied by a cycle attractor. By the Conley index theory, we prove that there exist other isolated invariant sets besides the two attractors, and also obtain the possible components and their configuration. Moreover, we find that there is always a separatrix or cycle separatrix, which separates the two attractors. Finally, the biological meanings and implications of these structures are given and discussed.

Keywords: bistable structure; dynamical system; biological system; Conley index

MSC: 37N25



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1. Introduction

Bistability is a common phenomenon in everyday life and life sciences. Here, bistability means that a dynamical system is in one of two stable states, and its state does not change under a slight disturbance. A simple example of this kind of phenomenon is the lamp switch, which has two mutually exclusive and stable states, ‘on’ and ‘off’. The memory unit in the electronic device, flip-flop circuit, which is always in one of two states, ‘0’ and ‘1’, is also an example of bistability. Moreover, interestingly, there are many examples of such bistability in life-related fields ranging from microscopic gene expression to macroscopic species competition. For example, at the molecular level, whether or not genes in cells are expressed [1], the switching of different genes [2], and the differentiation of cells in developmental biology [3], can be considered as bistable phenomena. There are also many examples at the population level, such as the outbreak of disease [4], the number of single species [5,6], the interaction between different species [7], including competition, symbiosis, and predation.

The study of bistability is of considerable significance in decoding the mysteries of life because this phenomenon can be served as a commonality shared by many life-related fields. On the one hand, bistability helps to understand how the biological object switches between different stable states so that we can assess conditions towards the desired state. On the other hand, bistability is a bridge between monostability and multistability. It can be regarded as a building block for the study of more complicated structures and dynamics.

Stable states may be described by attractors in dynamical systems. Typically, an attractor refers to the whole asymptotically stable orbit in the dynamical system. So, as its name suggests, the orbits neighboring the attractor will be attracted and will finally approach the attractor as time goes on. Some asymptotically stable orbits, such as asymptotically stable equilibria, asymptotically stable periodic orbits, and strange attractors, are attractors. However, sometimes attractors also refer to the attracting invariant sets that are composed of whole orbits. To avoid ambiguity, the attractor in this paper adopts the former definition, and the one-point attractor and the cycle attractor refer to the asymptotically stable equilibrium and the asymptotically stable periodic orbit, respectively.

In this paper, two classes of two-dimensional dynamical systems with precisely two attractors are studied. The first is the system with two one-point attractors, and the second is that with a one-point attractor and a cycle attractor. They are the two most common bistable structures in biological fields. With the help of the Conley index, we find that there exists another invariant set except for these two attractors, and also obtained its Conley index. We also obtain the possible compositions of this invariant set and their connecting structure with the attractors. Moreover, we find that there is always a separatrix or cycle separatrix between two attractors, which divide the region we considered into two sub-regions so that almost all the orbits in different subregion flow to different attractors.

Conley index, which is named after Charles Conley, is the significant generalization of Morse index [8–10]. In Morse index theory, the study object is the hyperbolic equilibrium, and its Morse index is defined as the dimension of the unstable manifold. However, in the Conley index theory, a hyperbolic equilibrium is generalized as an isolated invariant set. The primary strategy of the Conley index is to find a neighborhood that isolates the invariant set, then deduce the dynamical structure or the properties inside by examining the behavior of flow at the boundary.

Conley index can be used as a topological tool for the studying of a dynamical system [8,9]. For example, it can be employed to prove the existence of orbits, such as the connecting orbits in Theorems 1–3 in the next section, and to prove the existence of bifurcation points, such as in the boundary value problems of Vlasov–Maxwell systems [11]. In addition, the Conley index can also be used to exclude some structures within an isolating neighborhood, but if we want to obtain more refined structures, some additional information becomes indispensable, which is also the research idea of this paper.

The rest of the paper is organized as follows. In Section 2, a preliminary knowledge of the Conley index and attractor is provided. In Section 3, two kinds of bistable structures are studied, and the main results are presented as well. In Section 4, we present four examples and two applications that exactly have a bistable structure. Finally, the conclusion and further discussion are given in Section 5.

2. Preliminary

We first provide the definition of the Conley index and related notions. For more details about the Conley index, please refer to [8–10].

Let X denote a locally compact metric space, and $\varphi : \mathbb{R} \times X \rightarrow X$ represent a flow.

Definition 1. A compact set $N \subset X$ is an isolating neighborhood if

$$\text{Inv}(N, \varphi) := \{x \in N \mid \varphi(\mathbb{R}, x) \subset N\} \subset \text{int}N,$$

where $\text{int}N$ denotes the interior of N . S is an isolated invariant set if $S = \text{Inv}(N)$ for some isolating neighborhood N .

Definition 2. Let S be an isolated invariant set. A pair of compact sets (N, L) where $L \subset N$ is called an index pair for S if:

1. $S = \text{Inv}(\text{cl}(N \setminus L))$ and $N \setminus L$ is a neighborhood of S .
2. L is positively invariant in N ; that is given $x \in L$ and $\varphi([0, t], x) \subset N$, then $\varphi([0, t], x) \subset L$.

3. L is an exit set for N ; that is given $x \in N$ and $t_1 > 0$ such that $\varphi(t_1, x) \notin N$, then there exists $t_0 \in [0, t_1]$ for which $\varphi([0, t_0], x) \subset N$ and $\varphi(t_0, x) \in L$.

Definition 3. The homotopy Conley index of S is

$$h(S) = h(S, \varphi) \sim (N/L, [L]).$$

where “ \sim ” denotes homotopy equivalence relation, and $(N/L, [L])$ is pointed space, namely, the points in L are identical.

We also need to point out that the Conley index in this paper refers to the homotopy Conley index.

Then, we provide three useful properties of the Conley index and three theorems on its applications.

Property 1 (Ważewski Property). If N is an isolating neighborhood for the isolated invariant set S , and if $H(S) \neq \bar{0}$, then $S \neq \emptyset$; i.e., N contains a complete orbit.

Property 2 (Wedge Sum). If S_1 and S_2 are disjoint isolated invariant sets, then the disjoint union $S = S_1 \sqcup S_2$ is an isolated invariant set, and

$$H(S) = H(S_1 \sqcup S_2) = H(S_1) \vee H(S_2). \tag{1}$$

Property 3 (Continuation). If S_λ and S_μ are related by continuation, then they have the same Conley index.

Theorem 1 ([10,12,13]). Let $x' = f(x)$ be gradient-like in an isolated neighborhood N , and let N contain precisely two rest points x_1, x_2 , of f , not both of which are degenerate. Let $S(N)$ be the maximal invariant set in N . If $H(S(N)) = \bar{0}$, then there is an orbit of f connecting the two rest points.

Theorem 2 ([12,14]). Let N be an isolating neighborhood of the flow ϕ containing precisely two equilibria p_1 and p_2 . If $H(S(N)) \neq H(p_1) \vee H(p_2)$, then there exists an orbit γ of ϕ in N , different from p_1 and p_2 . If, moreover, ϕ is also gradient-like in N , then γ connects p_1 and p_2 .

Theorem 3 ([12,15]). If (A_μ, A_μ^*) is an attractor–repeller pair for the i.i.s. S_μ , which continues for $\mu \in [\mu_1, \mu_2] \subset \mathbb{R}$ and

$$S_\mu u_1 = A_{\mu_1} \cup A_{\mu_2}^*, S_\mu u_2 = A_{\mu_2} \cup A_{\mu_1}^*,$$

but $CSS(S_{\mu_1})$ is not the same as $CSS(S_{\mu_2})$, then, for some $\mu \in [\mu_1, \mu_2]$, there exists a connecting orbit from A_μ^* to A_μ .

The three properties indicate the importance of the Conley index as a topological tool. Ważewski Property lies in that the existence of a solution can be proven based on a non-zero index without providing an analytical expression. Wedge Sum provides the operations between indices. Continuation property implies that the Conley index captures a stable property of the dynamic system, that is, bifurcation may appear with a change in parameter, but the Conley index remains unchanged from a neighborhood perspective. The other three theorems also indicate that the Conley index can be used to prove the existence of connecting orbits without providing specific expressions of orbits.

In addition, we also provide the definition of attractor [16].

Definition 4. A set Λ is called an attractor if:

1. Λ is compact and invariant.

2. There is an open set U containing Λ such that for each $x \in U$, $\varphi(t, x) \in U$ and $\bigcap_{t \geq 0} \overline{\varphi(t, U)} = \Lambda$.
3. (Transitivity) Given any points $x_1, x_2 \in \Lambda$ and any open neighborhoods U_i about x_i in U , there is a solution curve that begins in U_1 and later passes through U_2 .

Transitivity guarantees a single attractor rather than an invariant set composed of dynamically different attractors. Moreover, this paper only considers two types of attractors: one-point attractors and cycle attractors, namely, asymptotically stable equilibria and asymptotically stable periodic orbits. The chaotic attractor is not considered here since the Poincaré–Bendixson Theorem completely eliminates the possibility of chaotic behavior in a planar system, and chaotic behavior only appears in a nonlinear, three or higher-dimensional system.

3. Main Results

The research object of this paper is the bistable structure in a two-dimensional dynamical system, which can be written as follows:

$$\frac{d\mathbf{x}(t)}{dt} = \mathbf{f}(\mathbf{x}(t)). \quad (2)$$

Here $\mathbf{x}(t)$ is the state vector in \mathbb{R}^2 , and the vector-valued function $\mathbf{f}(\mathbf{x}(t))$ is differentiable in its domain. In this section, we consider this system two cases: two one-point attractors and coexistence of a cycle attractor and a one-point attractor, since they are the two most common bistable structures in biological models.

3.1. Case 1: Two One-Point Attractors

In this case, we first make the following assumption:

H1. There exists a bounded and closed region U in the domain of system (2), such that there are precisely two asymptotically stable equilibria in the interior of U , say A_1 and A_2 , and on the boundary ∂U , all orbits run from outside into interior immediately.

Usually, researchers only care about the behaviors within some regions or the structure they are interested in. For example, for biological models, only the quadrants where all variables are non-negative are focused, since variables usually represent the number of population or concentration, and only the positive quantities make sense. Sometimes whether the model has a periodic orbit is concerned as well because this orbit can cause the variable to oscillate. However, in this paper, we are only interested in the structure in assumption H1, and there are three main reasons. First, U is an attracting region from the outside view of it, though there are two stable equilibria within U . That makes it possible to bifurcate between monostable and this kind of bistable structure. Second, the region with the bistable structure as a whole can be considered as one of the attractors in another bistable structure. That is, a bistable structure can be embedded into another bistable structure. As a result, we may be able to use the bistable structure as the cornerstone to study the multi-stable structure. Third, the whole region U is attracting, which is based on the fact that, basically, the number of biological objects can neither become negative nor increase indefinitely due to limited environmental carrying capacity, such as species population, and densities of cells or microorganism.

The main results are presented below.

Theorem 4. For system (2), if H1 is satisfied, then we have the following conclusions:

- (i) There exists other isolated invariant set, denoted by S , besides of A_1 and A_2 , and its Conley index is Σ^1 .
- (ii) There also exists connecting orbits from the invariant set S to attractors, A_1 and A_2 .

Proof. (i) Firstly, let us construct an isolating neighborhood for invariant set S . Since $A_i, i = 1, 2$, is asymptotically stable equilibrium, there must exist two small open neighborhood U_1 and U_2 which are disjoint in $\text{Int}(U)$, i.e., the interior of U , such that $A_i \in U_i$ and all orbits that pass through the boundary of U_i will gradually approach the equilibrium A_i as time goes to infinity, $t \rightarrow \infty$. Then the region $N = U \setminus \{U_1 \sqcup U_2\}$ is an isolating neighborhood, which is shown in Figure 1.

It is not difficult to find that the exit set N_0 of isolating neighborhood N is the boundary of U_1 and U_2 , namely, $N_0 = \partial U_1 \sqcup \partial U_2$. Then by Definition 2 of the index pair in Section 2, we can easily verify that (N, N_0) is an index pair. By forming the cone over the exit set N_0 , we can obtain that the Conley index of index pair (N, N_0) is Σ^1 (see also Example 3 in [17]). According to the Ważewski Property 1, the interior of isolating neighborhood N must contain isolated invariant set S .

(ii) If we dig U_2 out from region U , then the remaining region and the corresponding exit set can be constructed as an index pair $(U \setminus U_2, \partial U_2)$, and its Conley index is $\bar{0}$. According to the conclusion (i) above, we know that the attractor A_1 and invariant set S are contained in $U \setminus U_2$. Thus, by Wedge Sum Property 2 in Section 2, there must exist connecting orbit from S to attractor A_1 . Otherwise, their Conley index will not $\bar{0}$ but $\Sigma^1 \vee \Sigma^0$, which is a contradiction. Similarly, there must be connecting orbit from S to the attractor A_2 . So the proof is completed. \square

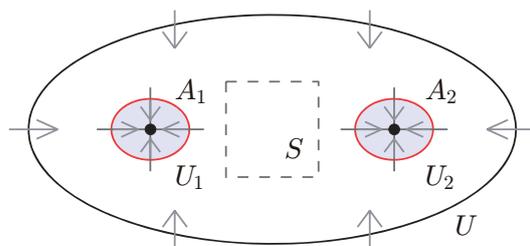


Figure 1. Diagram of the bistable structure. Arrows indicate the direction of the orbits. Only A_1 and A_2 are the two asymptotically stable equilibria in the interior of U . U_1 and U_2 , which are disjoint in $\text{Int}(U)$, are the open neighborhoods of A_1 and A_2 , respectively.

As mentioned in the introduction, more additional information would be necessary if one wants to obtain more details about an invariant set. So some of the prerequisites or limitations of the following study are based on this idea. Here, we make the following assumption:

H2. *The dynamical system is structurally stable.*

This assumption is mainly based on the fact that most biological objects, such as human metabolism or species population, are insensitive to small disturbances in the environment unless some massive changes are encountered. Corresponding to the mathematical model, it means that the dynamical behavior of the system is unaffected by small perturbations. Namely, the system is structurally stable, as we assumed above.

Before giving detailed results, we present the following lemma.

Lemma 1. *For the two-dimensional system (2), there are at most a finite number of hyperbolic equilibria within a bounded and closed region $D \subset \mathbb{R}^2$ in the domain of the system.*

Proof. We prove this lemma by contradiction. We first assume that there are an infinite number of hyperbolic equilibria within the bounded and closed region D . By Bolzano–Weierstrass Theorem (sometimes also called Sequential compactness theorem) we know that the subset consisting of all possible hyperbolic equilibria, denoted by E , is sequentially compact due to the compactness of D . That is, for each sequence of points in E it has a convergent subsequence converging to a point in E . For example, for sequence

$\{e_n\}_{n=1}^\infty \subset E$, its subsequence $\{e_{n_k}\}_{k=1}^\infty$ converge to point $e^* \in E$. In other words, for all $\varepsilon > 0$ there exists an $N \in \mathbb{N}^+$ such that when $k > N$ we have $|e_{n_k} - e^*| < \varepsilon$.

On the other hand, by Hartman–Grobman Theorem, we know that there exists a small neighborhood U^* of e^* , such that the solutions to system (2) are homeomorphic to that of linearization of (2) at e^* as long as it is inside U^* . System (2) have the unique equilibrium e^* inside U^* , due to the uniqueness of the equilibrium to linearization. That is, there exists $\varepsilon_1 > 0$, such that for any other equilibrium e if it exists we have $|e - e^*| > \varepsilon_1$. As a result, this contradicts the statement above, so there are at most a finite number of hyperbolic equilibria within $D \subset \mathbb{R}^n$. The proof is completed. \square

Then we introduce the concept of ‘loop’ to simplify the description of the following content. By ‘loop’ we mean the invariant set that consists of equilibrium and complete orbits and is homeomorphic to one-sphere, S^1 . Some examples are a periodic orbit, and an invariant set that is consist of a homoclinic orbit and the corresponding saddle, and invariant set that is composed of heteroclinic orbits and related equilibria.

Theorem 5. *For system (2), if H1 and H2 are satisfied, then*

- (i) *There must be a finite and odd number of equilibria in S , namely $2k + 1, k \in \mathbb{N}$ equilibria, in which $k + 1$ equilibria are the saddles, and k equilibria are unstable nodes or focuses;*
- (ii) *There is at most one loop in S , which is an unstable limit cycle or a loop consisting of saddles, unstable nodes or focuses, and the heteroclinic orbits that flow from the latter to the former. Moreover, if the loop does exist, it contains an attractor inside it, and another attractor is outside of it.*

Proof. (i) We prove that the invariant set S contains a finite number of equilibria first. By H1, we know that region U is bounded and closed. According to H2 and the Andronov–Pontryagin criterion [18,19], we obtain all the equilibria in U are hyperbolic. Then by Lemma 1, we can conclude that there are at most a finite number of hyperbolic equilibria in U . So the number of equilibria in S is also finite.

Then, we prove that S contains an odd number of equilibria. The winding numbers both of the boundary ∂U and each attractor are +1. Then by the fact that the winding number of a closed curve is equal to the sum of the winding numbers of all isolated equilibria contained in it, we know that S must contain equilibria other than the two attractors, and the sum of the winding number of these equilibria is -1 . Also, all equilibria are hyperbolic due to H2. So we can divide these equilibria into two types according to their winding number: saddle, whose index is -1 , and non-saddle, whose index is +1. Node and focus belong to the non-saddle class. Then S must contain an odd number of equilibria, where the amount of the saddle is one more than the number of non-saddle. Otherwise, the sum of the winding number of total equilibria in S can not be -1 . So in mathematical terms, S contains $2k + 1$ equilibria, where $k + 1$ ones are saddles, and k are non-saddle. Moreover, because of H1, the stable equilibrium cannot be included in S . Thus, the non-saddle can only be unstable nodes or focuses.

(ii) We prove it by the following four steps:

The first step is to show that the possible loop is an unstable limit cycle or a loop consisting of saddles, unstable nodes or focuses, and the heteroclinic orbits that flow from the latter to the former. If there is no equilibrium on the loop, it will be an unstable limit cycle. That is because S does not contain other attractors, including cycle attractor, by H1 and the system is also structurally stable by H2. If the loop contains equilibrium, it will be the loop consisting of saddles, unstable nodes or focuses, and the heteroclinic orbits that flow from the latter to the former. Because the asymptotically stable equilibria cannot appear again on the loop by H1, and both the homoclinic orbits and the heteroclinic orbits that flow from one saddle to another saddle are not present due to their structural instability by H2. So the loop can only be one of these two candidates if any.

The second step is to give the position of the loop if it exists, and we will show that the loop must be around an attractor. In other words, two attractors are located inside and

outside the loop, respectively. If it is not the case, then the loop either does not contain any attractor or contains two attractors.

For the first case, we assume that the loop does not contain any attractor. So there must be an infinite number of orbits in any small neighborhood inside the loop, and they flow further into the interior of the loop. Then their ω -limit sets are either cycles or points. The cycles are impossible because they must be hyperbolic according to structural stability. Stable cycles cannot appear, and unstable cycles cannot be served as ω -limit sets. Moreover, it is also impossible for their ω -limit sets to be points. Because an unstable node or focus cannot be served as the limit set as well, and the stable equilibrium is not contained inside this loop. The saddle is also impossible because the amount of saddles is finite by conclusion (i), and they cannot be the ω -limit sets of an infinite number of orbits. Therefore, the assumption is not correct, and the loop must contain at least one attractor.

For the second case, we assume that there are two attractors inside the loop. Then there must be an infinite number of orbits in the small neighborhood outside the loop, which are further away from this loop but still stay inside the region U . Their ω -limit sets are either cycles or points, but both are impossible based on the same analysis as the first case. So the loop cannot contain two attractors either.

In short, neither case is possible. So if the loop does exist, it must precisely contain one attractor.

The third step is to prove that there is at most one loop around each attractor. Assume there are two or more loops around each attractor. Then one can find two adjacent loops, say C_1 , C_2 , and C_1 is inside C_2 . There must be an infinite number of orbits in the small neighborhoods outside of C_1 and inside of C_2 . These orbits flow away from the two loops, respectively, and remain between these two loops. Then contradictions can be obtained based on the same analysis as the second step once again. Therefore, there is at most one loop around each attractor.

The final step is to show that it is impossible to have a loop for each attractor. We assume that is not true, then the outer neighborhood of each loop has an infinity number of orbits, which, respectively, away from these two loops and are still stay in the region U . Here the contradiction occurs again. So the assumption is not valid.

From the four steps above, we conclude that S contains at most one loop, which is an unstable limit cycle or a loop composed of saddles, unstable nodes or focuses, and heteroclinic orbits. Moreover, if the loop does exist, it must contain an attractor. The proof is completed. \square

In the context above, the Conley index of the invariant set S and its possible components were studied. Now, we are going to consider the configuration of the orbits globally outside of the invariant set S .

Here according to whether the invariant set S contains the loop structure, we make the following two mutually exclusive assumptions:

H3. *Invariant set S does not contain loop structure;*

H3'. *Invariant set S contains loop structure;*

Furthermore, we also consider two additional cases according to the connectivity of S :

H4. *The invariant set S is connected;*

H4'. *The invariant set S is disconnected, in which it has a finite number of connected components.*

Note that it is beyond the capability of the Conley index to judge whether the invariant set S is connected or not, unless with the help of other information. Here, we are trying to study all possible configurations to understand clearly the internal structure of region U .

In the case of connected, we can obtain the following lemma.

Lemma 2. For system (2), if H1–H4 are satisfied, then for invariant set S , there must be precisely two disjoint orbits, such that the points on it will gradually approach S as time goes to infinity. However, on the other orbits nearing S points will be gradually away from S finally.

Proof. We prove this lemma by contradiction. We assume that there exist n orbits, on which points gradually approach the invariant set S , but n is not equal to 2. Then these n orbits must be located on the stable manifolds of the saddles, and the orbits nearing these n orbits will away from the invariant set S finally. From H4, we know that S is connected, and from H2 and H3, we know that S does not have the loop structure, which can be thought of as a simple closed curve in a plane. Thus, S is simply connected, and it is homotopic to a point, denoted by P_s . Then, P_s have n stable manifolds, which are separated by n unstable manifold. So the Conley index of this point is the wedge sum of $n - 1$ multiple of Σ^1 . Since the Conley index is algebraic topological invariant, the Conley index of original invariant set S is the wedge sum of $n - 1$ multiple of Σ^1 as well. This result contradicts the conclusion (i) in Theorem 4, so there must be precisely two orbits considered above. The proof is completed. \square

Theorem 6. For system (2), if H1–H4 are satisfied, then there must exist two different points, p_1 and p_2 , on ∂U , such that the orbits through p_1 or p_2 will approach invariant set S , that is, their ω -limit sets are subset to S . In addition, the orbits passing through other points on ∂U will approach the corresponding attractor A_1 or A_2 .

Proof. By Lemma 2, we obtain that near S there precisely exist two different orbits, on which point are gradually approach S , that is to say, their ω -limit sets are subset to S . We denote these orbits by φ_1 and φ_2 , respectively. On the boundary of U , ∂U , there must exist two distinct points p_1 and p_2 , such that φ_1 and φ_2 flow into U through p_1 and p_2 , respectively. Otherwise, we assume that $\varphi_i, i = 1, 2$, comes from the interior of U . Thus, φ_i either flow from A_i or flow from S , which are both impossible.

We denote the ω -limit sets of φ_i by $E_i, i = 1, 2$. Thus, $E_i \in S$. Since S is connected, there must exist a path from E_1 to E_2 . Thus, the two orbits, φ_1 and φ_2 , together with invariant set S , can divide the region U into two sub-regions, as shown in Figure 2. For each sub-region, from H1 and Lemma 2, we obtain that it is a positively invariant set. So its limit set is nonempty. And then from H3, we know that there are no periodic orbits. So by Poincaré–Bendixson Theorem, the limit set must be equilibrium, namely A_1 or A_2 . In this case, the two stable equilibrium must be evenly distributed into two sub-regions. The proof is completed. \square

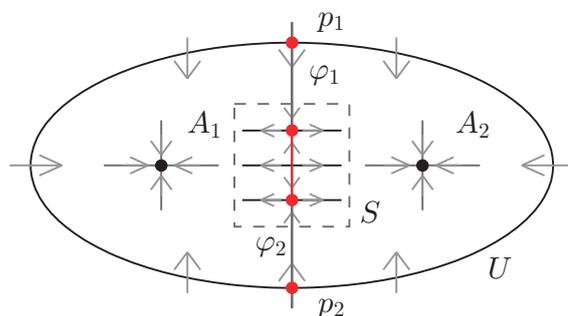


Figure 2. Diagram of the invariant set S in the bistable structure. This is a kind of possible configuration of invariant set S , in which there are two saddles and an unstable node, and S is connected.

The Theorem above describes the destination of the orbits through the boundary ∂U , i.e., their ω -limit sets. Here, we call the connected set that is composed of orbits φ_1, φ_2 , and invariant set S as separatrix. This is due to the fact that inside of region U , the orbits at each side of the connected set will approach different attractors, respectively.

Next, we consider the disconnected case. For this, we assume that S has K connected components and label these components by S_1, S_2, \dots, S_K . Similar to Lemma 2 and Theorem 6, we have the following results.

Lemma 3. *For system (2), if H2 and H3 are satisfied, and the connected invariant set S^* is composed of saddle, unstable nodes or focus and connecting orbits, in addition, its Conley index is $\bar{0}$, then there must be precisely one orbit, such that the points on it will gradually approach S^* as time goes to infinity. However, on the other orbits neighboring S^* , points will run away from S^* finally.*

Proof. The proof is similar to the one for Lemma 2, and we prove it by contradiction as well. Since S^* is connected and from H2 and H3, we know that it does not have a loop structure and S^* is simply connected. So S^* can be homotopically shrunk to a point, denoted by P_{S^*} . We assume that there exist precisely n orbits, on which point will gradually approach S^* as time goes to infinity, and n is not equal to 1. Then the Conley index of P_{S^*} is the wedge sum of the $n - 1$ multiple of Σ^1 . Since the Conley index is an algebraic topological invariant, the Conley index of the original invariant set S^* is also the wedge sum of the $n - 1$ multiple of Σ^1 . This contradicts $H(S^*) = \bar{0}$, so there must be one orbit as required. Thus the points on other orbits will be away from S^* finally. The proof is completed. \square

Theorem 7. *For system (2), if H1, H2, H3, H4' are satisfied, then there must be $K + 1$ disjoint points, p_1, \dots, p_K, p_{K+1} , on ∂U , such that the orbits through p_i will approach invariant set S . That is to say, their ω -limit set is a subset of S . In addition, orbits passing through other points on ∂U will approach corresponding attractor, A_1 or A_2 .*

Proof. From H4' and Property 2 in Section 2, one has

$$H(S) = H(S_1) \vee H(S_2) \vee \dots \vee H(S_K). \tag{3}$$

Due to the conclusion that $H(S) = \Sigma^1$ in Theorem 4, for invariant set S , there must be one connected component whose Conley index is Σ^1 and all the Conley index of other $K - 1$ connected component is the additive identity [8], namely $\bar{0}$. Otherwise, the Conley index of S will be the Wedge sum of some items, which contradicts $H(S) = \Sigma^1$.

To make it easier to describe, we re-label K connected components by exchanging the label of the first component and the component whose Conley index is Σ^1 . In the process, if the Conley index of component S_1 is exactly Σ^1 , then the label method remains the same. After this process, the Conley index of the first component S_1 will be Σ^1 , and the Conley index of others will be $\bar{0}$.

For connected component S_1 , by Lemma 2 above, we know that there must be two orbits whose ω -limit sets are subset to S_1 , and we label them by φ_1^1, φ_1^2 . Similar to the Theorem 6, φ_1^1, φ_1^2 must come from outside of region U . We denote the intersection points of these two orbits and boundary ∂U by p_1^1, p_1^2 .

For each of other components, say $S_i, i = 2, \dots, K$. By Lemma 3 above we also know that there must be one and only one orbit φ_i whose limit set is subset to S_i . This orbit must come from outside of U as well, and we denote the corresponding intersection point by p_i .

Finally, we obtain $K + 1$ different points on the boundary ∂U , and the orbits through them all approach the corresponding connected component of invariant set S . For other points on the boundary, the orbits that through them finally approach one of the two attractors. \square

Similar to the connected case, there is also a separatrix in the disconnected case. The difference is that this separatrix is composed of the connected component S_1 , which Conley index is Σ^1 , and the two orbits, φ_1^1 and φ_1^2 . On the boundary ∂U , the points on the same side of this separatrix will approach the same attractor except a finite number of points, namely $p_i, i = 2, \dots, K$ in the proof above.

To summarize, the separatrix acts as a role of the threshold, and the point on the boundary can be considered as an initial condition. Except for a finite set of initial boundary points that tend to the invariant set S , almost all the initial points tend to one of the two attractors. More importantly, those initial points located on the different sides of separatrix will have different destinies.

Theorem 8. For system (2), if $H1, H2, H3', H4$ are satisfied, then there must be one and only one point on the boundary of U , denoted by p_1 , such that its ω -limit set is a subset of S , and within the region bounded by S some attractor, say A_1 , is contained. Moreover, all the other points on the boundary flow to another attractor, A_2 .

Proof. First, by Theorem 5(ii) and $H3'$, there is one and only one loop in S , which is an unstable limit cycle or a loop consisting of saddles, unstable nodes or focuses, and heteroclinic orbits flowing from the latter to the former. Moreover, this loop must contain an attractor, say A_1 , and another attractor A_2 is outside this loop, as shown in Figure 3.

Next, we can obtain that S and the region bounded by S , where there are attractor A_1 and heteroclinic orbits flowing to A_1 , form a simply connected domain. Its Conley index is $\bar{0}$ because its isolating neighborhood can be obtained by digging out a small open neighborhood of A_2 , like U_2 in Theorem 4, and the exit set is precisely the boundary ∂U_2 .

Next, we prove that there is only one orbit that flows to S from the outside of S . There is only one loop in S , as shown in Theorem 5 above, so that we can deform homotopically the region bounded by this loop into a point. Then this point is asymptotically unstable since the original loop is unstable. As a result, the region bounded by S becomes a new invariant set, denoted by S' , which consists of unstable nodes or focuses, saddles, and heteroclinic orbits, and its Conley index is still $\bar{0}$. Therefore, it can be obtained from Lemma 3 that there is only one orbit that tends to S' . So there only exists an orbit that flows to invariant S as well, and the ω -limit set of this orbit must be a saddle, which is a subset of S but does not on the loop in S .

The orbit approaching S must flow from the outside of U , and it must intersect the boundary ∂U at a point, which is p_1 . The other orbits passing through ∂U will only eventually flow towards A_2 . The proof is completed. \square

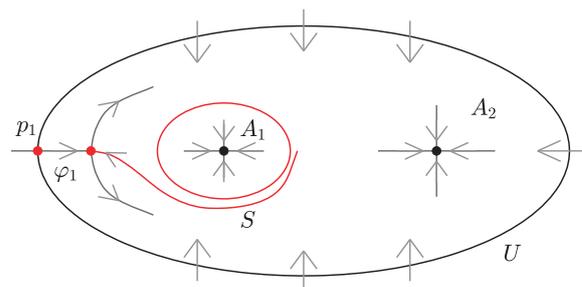


Figure 3. Diagram of the invariant set S in the bistable structure. This is a kind of possible configuration of invariant set S , in which there are a saddle and an unstable limit cycle, and S is connected.

Theorem 9. For system (2), if $H1, H2, H3', H4'$ are satisfied, then on the boundary of U , there must be K different points, whose ω -limit set is a subset of S , and other points eventually flow to attractor A_2 .

Proof. It can be obtained from $H3'$ and Theorem 5 that there is only one loop structure in S , and this loop bounds the attractor A_1 . Then, the invariant set S and the region it surrounds, containing A_1 and related heteroclinic orbits flowing to it, constitute a new invariant set, denoted by S' . It also has K connected components, and each component is simply connected. The Conley index of this new invariant set is the addition identity, $\bar{0}$, and the computation method is the same as that of Theorem 8. Then, by Property 2, the Conley index of each component is $\bar{0}$, as well.

For the new variant set S' , the structure of the connected component containing the loop is the same as that of the combined structure of S with the region bounded by it in Theorem 8. Therefore, for this component, there must be only one orbit tending to it, denoted by φ_1 . For the other $K - 1$ components, according to Lemma 3, there is only one orbit tending to each component, denoted, respectively, by $\varphi_i, i = 2, 3, \dots, K$. Here, K orbits must come from the outside of U , and they intersect with the boundary ∂U at K different points. Therefore, for the K orbits passing through these K points, their ω -limit sets are K components, respectively, subset to S , and all of the orbits passing through the remaining boundary points will eventually flow to the attractor A_2 . The proof is completed. \square

When a loop exists, it does have another kind of separatrix, namely, the cycle separatrix. Different from the separatrix above, cycle separatrix divides the region U into two sub-regions that are not homotopy equivalent. The first one is an annular region, which is outside of the separatrix, and another is simply connected, which is inside of the separatrix. The loop structure in Theorems 8 and 9 just happen to be the cycle separatrix. Inside of it, almost all orbits flow towards attractor A_1 , while outside of the loop, almost all orbits, including the orbits coming from outside of U , approach attractor A_2 .

In the preceding Theorems or Lemmas, H1 requires orbits must enter the interior of U immediately. This restriction is a little bit harsh, and it can be relaxed slightly as below. Now the outside orbits are allowed to run along the boundary ∂U for a while once they touch the boundary, but eventually, they must enter the interior of the U the same as before. In other words, the boundary ∂U can contain orbit segments that comes from the outside of U and eventually enters the inside of U . So the new assumption is

H1'. *There exists a closed region U in the domain of system (2), such that there are precisely two asymptotically stable equilibria in the interior of U , say A_1 and A_2 , and on the boundary ∂U , orbits run from outside into interior immediately, or firstly run along the boundary for a while then into its interior.*

With the assumption H1 replaced by H1', the invariant set S within U and its connection with two attractors are the same as those in previous studies. Thus, Lemmas 1–3, Theorems 4 and 5 are still valid, but Theorems 6–9 need to be modified appropriately. That is because the last four Theorems involve the points in boundary ∂U . And the expression “disjoint points” in each theorem or lemma should be replaced with “disjoint points or boundary segments”. Here, we do not take these related results as corollaries or new theorems. Accordingly, their proofs are omitted as well since they are almost the same as the proofs in related theorems. No matter whether the boundary is composed of points or orbit segments, as long as they all run into the interior of U , the internal structure of U will not be affected.

3.2. Case 2: A Cycle Attractor and a One-Point Attractor

In this case, we consider the second bistable structure, which contains a cycle attractor and a one-point attractor. Here, we first give the following two assumptions, which have the same boundary conditions as H1, and the relative positions of two attractors are also considered.

H5. *There exists a closed region U in the domain of system (2), such that there are precisely two attractors, an asymptotically stable periodic orbit C_1 and an asymptotically stable equilibrium A_1 , where A_1 is inside C_1 , and on the boundary ∂U , all orbits run from outside into interior immediately;*

H6. *There exists a closed region U in the domain of system (2), such that there are precisely two attractors, an asymptotically stable periodic orbit C_1 and an asymptotically stable equilibrium A_1 , where A_1 is outside C_1 , and on the boundary ∂U , all orbits run from outside into interior immediately;*

Similar to Theorem 4, we have the following results.

Theorem 10. For system (2), if H5 is satisfied, then

- (i) There is other isolated invariant set, denoted by S , in the annular region bounded by the circle C_1 and the point A_1 , and its Conley index is $\Sigma^2 \vee \Sigma^1$.
- (ii) There are the connecting orbits from S to both attractors, C_1 and A_1 , as well.

Proof. The proof is similar to that of Theorem 4.

(i) Firstly, we construct an isolating neighborhood of invariant set S . We can find an open neighborhood U_1 of A_1 since A_1 is asymptotically stable, such that the orbits passing through the boundary ∂U_1 will flow into the interior of U_1 and be attracted by A_1 in the end. Moreover, we can also find an annular neighborhood R_1 of C_1 , which is bounded by two simple closed curves L_1 and L_2 , as shown in Figure 4, such that the orbits passing through the boundary points will run into the interior of R_1 and be attracted by attractor C_1 . Then the annular region bounded by curves ∂U_1 and L_1 is an isolating neighborhood, and the exit set is precisely composed of two boundary curves ∂U_1 and L_1 . So its Conley index is $\Sigma^2 \vee \Sigma^1$ computed by collapsing the exit set into a point. By the Ważewski Property 1 of Conley index, we obtain that its isolated invariant set is not empty, and there must exist other isolated invariant set S except two attractors.

(ii) The region bounded by curve L_1 is an isolating neighborhood, and its Conley index is Σ^2 , which does not equal the wedge sum of the two Conley indices of invariant A_1 and S , $\Sigma^0 \vee (\Sigma^2 \vee \Sigma^1)$. So, by Wedge Sum Property 2 of Conley index, in addition to S and A_1 , there must be at least one connecting orbit from S to A_1 . Similarly, we also obtain the existence of connecting orbit from S to C_1 . The proof is completed. \square

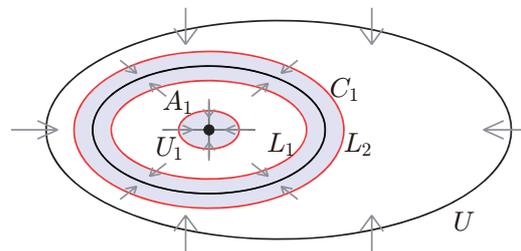


Figure 4. Diagram of bistable structure with a cycle attractor C_1 and a one-point attractor A_1 , where A_1 is inside of C_1 . Annular neighborhood R_1 of cycle attractor C_1 is bounded by L_1 and L_2 .

We should note that the system considered in H5 and H6 contains the periodic orbits, which are a kind of loop structure, so we do not consider the assumption H3 (or H3') in the current situation. Nevertheless, considering H2 is still rational. Given this, we have the following result.

Theorem 11. For system (2), if H5 and H2 are satisfied, then

- (i) There must be a finite and even number of equilibria in S , namely $2k$, $k = 0, 1, \dots$, in which k equilibria are saddles, and other k equilibria are unstable nodes or focuses.
- (ii) There is one and only one loop structure in S , and it contains A_1 in its interior.
- (iii) Invariant set S is connected.
- (iv) Denote the isolated invariant set within the region bounded by cycle attractor C_1 and boundary ∂U by S_2 . Then it must contain a finite and even number of equilibria, which is the same as (i).

Proof. (i) The proof of (i) is omitted here since its strategy and process are analogous to that of Theorem 5.

(ii) The proof of (ii) is divided into the following four steps:

The first step is to give the possible loop structure in S . There are two candidate types, an unstable limit cycle and the loop structure consisting of saddles, unstable nodes or

focuses, and heteroclinic orbits. The loop must be an unstable limit cycle if there are no equilibria on it. Moreover, it must be the second type of loop if there are some equilibria on it. That is because there is no possibility of an additional stable equilibrium in S by H5, and also, no homoclinic orbit of the saddle flow to itself and the heteroclinic orbit of saddle flow to another saddle according to the structure stability assumption in H2.

The second step is to illustrate the position of the loop, that is, the loop, if any, must contain A_1 inside it. We prove it by contradiction. We first assume that the region bounded by the loop does not contain A_1 . Then in any small neighborhood inside either loop mentioned in the previous step, there must be an infinite number of orbits, which further flow into the interior of the loop. Then the ω -limit sets of these infinite orbits are either equilibria or periodic orbits. The periodic orbit is impossible because the stable periodic orbit cannot appear again due to H5, and the unstable periodic orbit cannot be served as a ω -limit set. Moreover, the equilibria are also impossible. Because unstable focus or nodes cannot be used as a limit set as well, and stable equilibria cannot reappear. Saddles are also impossible because their total number is finite, and it is impossible for an infinite number of orbits with a finite number of saddles as their ω -limit set. So the assumption we made is not correct, and the loop must contain A_1 inside of itself.

The third step is to prove the existence of the loop by contradiction as well. First, we assume that a loop structure of any kind does not exist. Then the invariant set S must consist of saddles, unstable nodes or focuses, and heteroclinic orbits according to Theorem 11 (i). Next, freely choose a saddle in S , such as s_1 , whose two stable manifolds must come from distinct unstable nodes or focuses, say n_1 and n_2 . We continue to check if both equilibria are connected to other saddles. It may assume that n_1 is not, but n_2 is connected to another saddle, denoted by s_2 . Next, we continue to consider the stable manifold of s_2 . Analogously, we can always end this process because the number of equilibria in S is finite. In the end, we can obtain a simply connected invariant set similar to Figure 5a, and its Conley index is Σ^2 due to its asymptotical instability. We continue to count all other saddles, then obtain a finite number of the invariant set like Figure 5a. If this process does not pick up all the unstable nodes or focuses, they can be considered as unstable invariant set disconnected from each other, and their Conley indices are still Σ^2 . Finally, we obtain that the invariant sets S is a collection of invariant set just like Figure 5a and unstable equilibria. In this view, the Conley index of S is the wedge sum of a finite number of Σ^2 , which contradicts the Theorem 10 (i). So, there must be a loop structure.

The final step is to prove the uniqueness of the loop. We assume this is not true. That means there are two or more loops. From the second step, we know that A_1 must be contained in the smallest loop, which is then contained in the second smallest loop again. And so forth, just like the Russian doll. These loops are finite due to the compactness of region U and the structural stability of the system. Next, let us consider the two outermost loops, as shown in Figure 5b (other cases are similar). Any small inner neighborhood of the outer loop must have an infinite number of orbits that further flow into the interior of this loop. Their ω -limit sets are either equilibria or loops. However, neither is possible through the same analysis as the second step. So the assumption is not valid, and the loop structure is unique.

(iii) We assume that the invariant set S is not connected. We know that S contains a loop, and the Conley index both of this loop and S is $\Sigma^2 \vee \Sigma^1$. Therefore, if there are other invariant sets, which are not connecting to the loop and also disconnected from each other, then their Conley index must be $\bar{0}$ by Property 2. From (i), we know that S only can contain unstable nodes or focuses, saddles, and heteroclinic orbits. Also, Lemma 3 shows that there must be an orbit that is approaching this invariant set. Because the invariant sets are disconnected from each other, this orbit cannot come from S , and it cannot come from other invariant sets and A_1 as well. So, the contradiction occurs, and S must be connected.

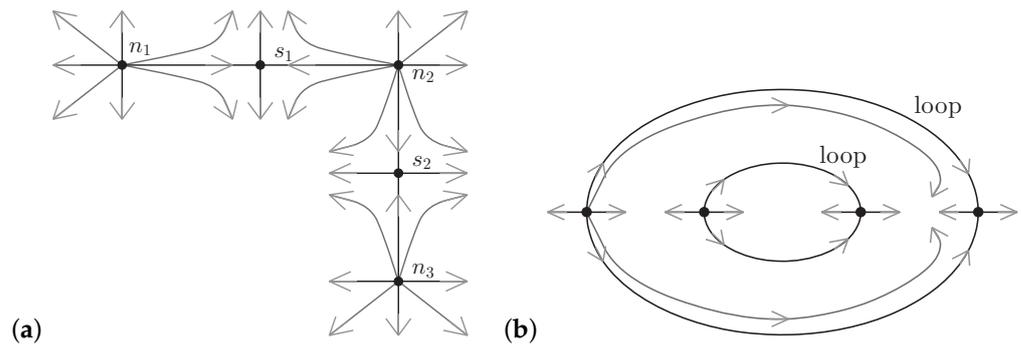


Figure 5. (a) A schematic diagram of one possible unstable invariant set consists of saddles and unstable nodes or foci. (b) Schematic diagram of the loop structure.

(iv) We omit the proof of (iv) again because it can be proved via the winding number and the same idea as Theorem 5. The proof is completed. \square

Similar to the case of two one-point attractors with the loop structure appears, the loop in Theorem 11 is the cycle separatrix. Almost all the orbits outside and inside of the separatrix flow towards the cycle attractor C_1 and the one-point attractor A_1 , respectively.

Theorem 12. For system (2), if H6 is satisfied, then

(i) There is an isolated invariant set, denoted by S_1 , in the region bounded by cycle attractor C_1 , and its Conley index is Σ^2 .

(ii) There is also an isolated invariant set, denoted by S_2 , outside the cycle attractor C_1 but except the one-point attractor A_1 , and its Conley index is Σ^1 . Moreover, there are connecting orbits from S_2 to C_1 and A_1 , respectively.

Proof. (i) Known from H6, C_1 is an asymptotically stable periodic orbit. Therefore, there must be a simple closed curve, denoted by L_1 , in the small inner neighborhood of C_1 , so that the orbits passing through L_1 will flow to its outside and eventually approach C_1 , as shown in Figure 6. Thus, the closed region bounded by L_1 together with the curve L_1 form an index pair, and its Conley index is Σ^2 , which is not equal to $\bar{0}$. So, according to Property 1, there must be an isolated invariant set, S_1 , in the region bounded by L_1 , and it is also within the region bounded by C_1 .

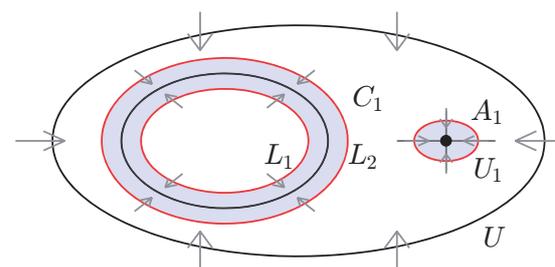


Figure 6. Diagram of bistable structure with a cycle attractor C_1 and a one-point attractor A_1 , where A_1 is outside of C_1 .

(ii) Similar to the L_1 above, we can also find a simple closed curve L_2 in the small outer neighborhood of C_1 so that the orbits passing through L_2 will flow to C_1 . Moreover, for A_1 , we can find an open neighborhood U_1 as well, similar to Theorem 4, so that the orbits passing through the boundary will flow to A_1 . Next, we dig out the interior of L_2 along with U_1 , resulting in a region with two holes. As a result, this region, together with the boundary of these two holes, constitutes an index pair, whose Conley index is not $\bar{0}$ but Σ^1 . So, there is also an isolated invariant set S_2 between C_1 and A_1 .

Finally, we can prove the existence of connecting orbits by the same idea as Theorem 4. Firstly, digging out the region bounded by L_2 forms the index pair $(U \setminus \text{Int}(L_2), L_2)$, which

proves the existence of connecting orbit from S_2 to A_1 . Similarly, digging out the region U_1 shows the presence of connecting orbit from S_2 to C_1 . The proof is completed. \square

When H6 and H2 are satisfied, we can refer to the situation of two one-point attractors. That is because if we see the cycle attractor from its outside, the cycle attractor and the one-point attractor have the same dynamics. Moreover, if we contract homotopically the region bounded by the cycle attractor, it would be a one-point attractor. In this case, there can be different separatrices. When the unstable loop structure appears, which must around C_1 or A_1 , this loop structure would be the cycle separatrix. However, when the unstable loop structure does not appear, the separatrix would be similar to the situations discussed below of Theorems 6 and 7.

Corresponding to the previous subsection, the assumption H5 and H6 can also be relaxed to the followings, respectively.

H5'. *There exists a closed region U in the domain of system (2), such that there are precisely two attractors, an asymptotically stable periodic orbit C_1 and an asymptotically stable equilibrium A_1 , where A_1 is inside C_1 , and on the boundary ∂U , all orbits run from outside into interior either immediately or firstly run along the boundary for a while then into its interior.*

H6'. *There exists a closed region U in the domain of system (2), such that there are precisely two attractors, an asymptotically stable periodic orbit C_1 and an asymptotically stable equilibrium A_1 , where A_1 is outside C_1 , and on the boundary ∂U , all orbits run from outside into interior either immediately or firstly run along the boundary for a while then into its interior.*

4. Examples and Applications

In this section, some examples are provided to indicate that the bistable structures we considered are common phenomena in certain biological systems. At the same time, some applications are given to illustrate how to use the conclusions of the previous section.

4.1. Some Examples in Biological Systems

As mentioned in the introduction, the bistable structure can occur in many biological models, such as the insect population model [5], genetic control model [1], interactive model between two populations, including mating between the sexes [20], obligate mutualism between two species [21], predator–prey relationship [22,23], etc., epidemic model [4,24,25], and so on. Here, we briefly introduce four biological models, all of them exhibit a bistable structure.

The first one is the spruce budworm population model that was proposed and analyzed by Ludwig et al. [5,6,26]. This model is aimed at studying the outbreak of spruce budworm in eastern Canada. This kind of insect is a serious pest, for it can defoliate and kill most of the fir trees in the forest in about four years.

This model can be written as follows:

$$\frac{dN}{dt} = RN \left(1 - \frac{N}{K} \right) - \frac{BN^2}{A^2 + N^2}, \tag{4}$$

where $N(t)$ denotes the budworm population at time t . In this model, $N(t)$ is assumed to have a logistic growth rate, as well as a saturated mortality rate due to predation, chiefly by birds. Although (4) is one-dimensional, we can think of it as a sub-system of a two-dimensional system combined (4) with $\frac{dX}{dt} = -X$. By analysis, we find that model (4) can have four equilibria, the origin o , and the other three positive equilibria, as shown in Figure 7. There are precisely two stable equilibria, a and c , which correspond to the refuge level and outbreak level of budworm, respectively, and can be seen as two point-attractors. It is effortless to find a closed interval covering a and c to the right of origin as the region U in H1. In this case, equilibrium b acts as a separatrix, since orbits to the left side of b flow to attractor a , while orbits to another side flow to c .

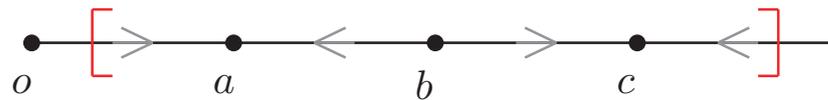


Figure 7. The bistable structure diagram for the model (4).

The second one is the genetic control model discussed by Griffith [1,26]. We all know that in a cell, genes are transcribed into message RNA (mRNA), and then mRNA acts as a template to produce proteins. Here, this model assumes that the activity of the genes is directly induced by a certain amount of protein for which it codes. In other words, genes control the production of proteins, and in turn, proteins stimulate the genes. In this way, an autocatalytic feedback process is formed. The model can be written in the following dimensionless form:

$$\begin{cases} \frac{dx}{dt} = -ax + y, \\ \frac{dy}{dt} = \frac{x^2}{1+x^2} - by, \end{cases} \quad (5)$$

where variables $x(t)$ and $y(t)$ denote the concentration of mRNA and protein at time t , respectively. Either rate of growth is proportional to the other, and both will be degraded, which are controlled by parameters a and b , respectively. We should note that there is no equation for DNA since it is externally supplied in this process.

For model (5), we can easily obtain its x -nullcline, $y = ax$, and y -nullcline, $y = \frac{x^2}{b(1+x^2)}$. They are denoted by μ and ν , respectively, as before. Under certain conditions, line μ and Sigmoidal curve ν can intersect transversely, thus obtaining three equilibria o , a , and b , which are schematically shown in Figure 8a. By linearization, we obtain o and b are two stable equilibria, and a is unstable. Then we can apply the conclusions in the previous section by constructing a region U that contains these two stable equilibria precisely. As a result, equilibrium a must be a saddle. This result also can be obtained by linearization. However, the purpose of doing this here is to illustrate that this model shows the bistable structure we are interested in.

For this model, the separatrix is composed of two orbits, $\varphi_1(t)$ and $\varphi_2(t)$, and one saddle, a . To the bottom left of the separatrix, the orbits flow to origin o , which corresponds to the silent state of the gene. However, on the other side of the separatrix, the orbits flow to equilibrium b , which corresponds to the activated state. Its biological interpretation is that genes can be switched between two opposite states, silent and activated, depending on the external environment. In other words, the concentrations of mRNA and the corresponding protein determine if the gene is expressed.

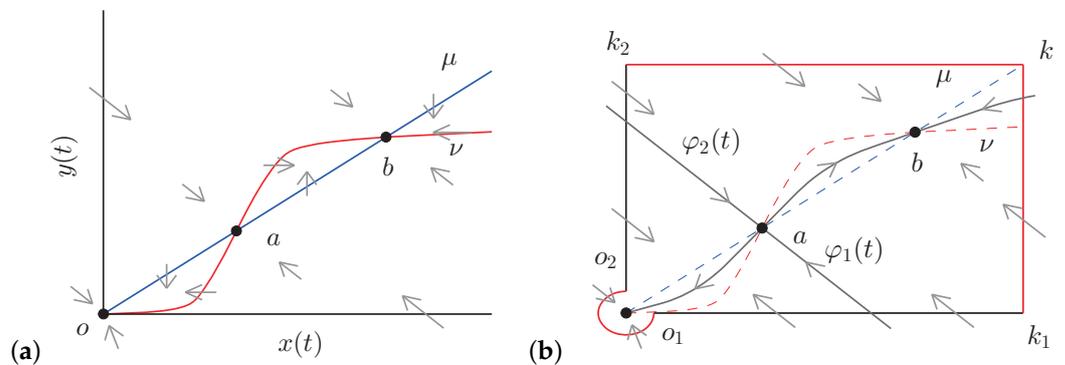


Figure 8. The bistable structure diagram for the model (5). (a) Line μ and Sigmoidal curve ν are x -nullcline and y -nullcline, respectively. Moreover, there are three equilibria here, o , a , and b , where o and b are stable. (b) The region U is bounded by four line segments and one arc. Furthermore, the separatrix is composed of two orbits, $\varphi_1(t)$ and $\varphi_2(t)$, and equilibrium a .

The third model is a predator–prey system with group defense, which is studied by Freedman, Wolkowicz [7], and other researchers [27,28]. Group defense describes the phenomenon that predation becomes harder, even prevented altogether, due to the growing ability of the prey to defend or disguise themselves when their population is large enough, so it is considered as a nonmonotonic functional response of predator to prey density. The study of this model was about to exhibit the so-called paradox of enrichment, and, interestingly, the second case of the bistable structure is observed here as well, namely, the bistable structure of the coexistence of a cycle attractor and a one-point attractor.

The model is written as

$$\begin{cases} \frac{dx}{dt} = xg(x, K) - yp(x), \\ \frac{dy}{dt} = y(-s + q(x)), \end{cases} \tag{6}$$

where $x(t)$ and $y(t)$ denote the densities of prey and predator at time t , respectively. Also, functions $g(x, K)$, $p(x)$, and $q(x)$ are assumed to be continuously differentiable and represent the specific growth rate of the prey in the absence of predation, predator response function, and the conversion rate of prey to predator, respectively. For their requirements, please refer to the literature [7]. Here, we only consider the model with the following forms, and it is also researched in [7].

$$\begin{cases} \frac{dx}{dt} = 2x(1 - \frac{x}{K}) - \frac{9xy}{x^2 + 3.35x + 13.5}, \\ \frac{dy}{dt} = y(-1 + \frac{11.3x}{x^2 + 3.35x + 13.5}). \end{cases} \tag{7}$$

With the increasement of parameter K , the carrying capacity of prey, the model exhibits different dynamics. When $K = 4$, equilibrium e_λ is asymptotically stable, and its position is illustrated in Figure 9a. If K increases to $K = 6$ due to enrichment, e_λ becomes unstable, and a unique asymptotically stable periodic orbit around it will appear. Then when K is growing to $K = 7$, the periodic orbit will coalesce with a homoclinic orbit that is stable from within and unstable from without. Here, we focus on the situation of $K = 6$, as shown in Figure 9. By linearization, e_K is an asymptotically stable node, e_μ is a saddle, and e_λ is asymptotically unstable, as shown in Figure 9b. Moreover, by using the function ode45 in MATLAB to simulate the solution orbits, it can be determined that there is a stable periodic orbit located around e_λ , and the nearby orbits will approach it finally, as shown in Figure 9c. In addition, the two orbits that tend to equilibrium e_μ must be located or almost located at the unstable manifold of e_μ , and other orbits either approach the periodic orbit or the equilibrium e_K . In this case, the system exactly embeds the second bistable structure, and the asymptotically stable periodic orbit is the cycle attractor C_1 and the asymptotically stable equilibrium e_K is the one-point attractor A_1 .

The region U required in $H6'$ can be constructed as illustrated in Figure 9d, which is bounded sequentially by line segment $\overline{k_1k_2}$, orbit segment $\widehat{k_2k_3}$, line segments $\overline{k_3k_4}$, $\overline{k_4e_K^1}$, arc $\widehat{e_K^1e_K^2}$, and line segment $\overline{e_K^2k_1}$. The asymptotically stable periodic orbit C_1 and stable equilibrium e_K are the only two attractors within region U . As described in Theorem 12, within the region bounded by C_1 , there is an unstable equilibrium e_λ , which is an isolated invariant set, and outside periodic orbit C_1 , there is a saddle e_μ . Moreover, there also exist connecting orbits from e_μ to both periodic orbit C_1 and equilibrium e_K . Moreover, the combination of orbits $\varphi_1(t)$, $\varphi_2(t)$, and saddle e_μ are served as the separatrix of region U , on each side of which orbits approach different attractors. Its biological meaning is that different initial states will lead to different destinies, coexistence, or extinction of predators.

The final one is an SIR compartment model in epidemiology, which was analyzed by Zhou and Fan [4]. Here the limited medical resources and their supply efficiency were considered, which was inspired by the treatment functions in [24] by Wang and in [25] by Zhang. Backward bifurcation, a kind of transcritical bifurcation, may occur, and one

can also find bistability here. By convention, the total population is divided into three compartments: susceptible (S), infected (I), and removed (R). The susceptible can become infected by touching with the infected individuals, and can then recover naturally or receive treatment, thus becoming a remover. This model is written as

$$\begin{cases} \frac{dS}{dt} = \Lambda - f(S, I) - dS, \\ \frac{dI}{dt} = f(S, I) - (d + \gamma + \varepsilon)I - h(I), \\ \frac{dR}{dt} = \gamma I + h(I) - dR, \end{cases} \tag{8}$$

where $S(t)$, $I(t)$ and $R(t)$ denote the number of people in the three compartments at time t , respectively. Λ denotes the recruitment of the population. d and ε denote the natural death rate and disease-related mortality, respectively. γ denotes the natural recovery rate. Saturated type incidence function, $f(S, I) = \frac{\beta SI}{1 + \kappa I}$, is considered here since it can reflect the “psychological” or inhibition effect [29]. Moreover, the treatment function $h(I)$ is taking the form of $\frac{\alpha I}{\omega + I}$, which is based on the fact of limited medical resources and supply efficiency.

The change rates of variables S and I are independent of R , so we can just focus on the first two equations in (8), leading to

$$\begin{cases} \frac{dS}{dt} = \Lambda - \frac{\beta SI}{1 + \kappa I} - dS, \\ \frac{dI}{dt} = \frac{\beta SI}{1 + \kappa I} - (d + \gamma + \varepsilon)I - \frac{\alpha I}{\omega + I}. \end{cases} \tag{9}$$

For this model, backward bifurcation can occur when parameters ω and α are located in a particular region. For details, one can refer to work [4]. Employing the function ode45 in MATLAB again to simulate the solution orbits, we can see that given specific parameters there are three equilibria: one disease-free equilibrium, e_0 , and two endemic equilibria, e_1 and e_2 , as shown in Figure 10a. By linearization, it can be obtained that e_0 and e_2 are asymptotically stable, and e_1 is a saddle, which is unstable. Alternatively, by the conclusions in the previous section, one can also obtain e_1 is a saddle. That is because we can construct a required region U which precisely contains e_0 and e_2 .

The region U is constructed as shown in Figure 10b, where the line segments $\overline{oe_0^1}$ and \overline{ok} are located on the x -axis and y -axis, respectively. The major arc $\widehat{e_0^1 e_0^2}$ is a segment of the boundary of a certain attracting neighbor of e_0 . Line segment $\overline{ke_0^2}$ is located on the line $S + I = \frac{\Lambda}{d}$, and this is because the derivatives $\frac{d(S+I)}{dt}$ at the points on this line segment are negative, which means the points on this line segment will go into the interior of U as the time goes on. e_0 and e_2 are the only two attractors in U . Furthermore, the existence of limit cycles can be excluded [4], and appropriate parameters can be found to make the model structurally stable. So, by Theorem 5 and the number of equilibria, it can be concluded that e_1 must be a saddle. In addition, by Theorem 6, orbits $\varphi_1(t)$ and $\varphi_2(t)$ are located on the two stable manifolds of e_1 . They, together with equilibrium e_1 , constitute the separatrix, as sketched in Figure 10b. The orbits above it will approach the endemic e_2 as time goes on, whereas the orbits below it will approach the disease-free equilibrium e_0 .

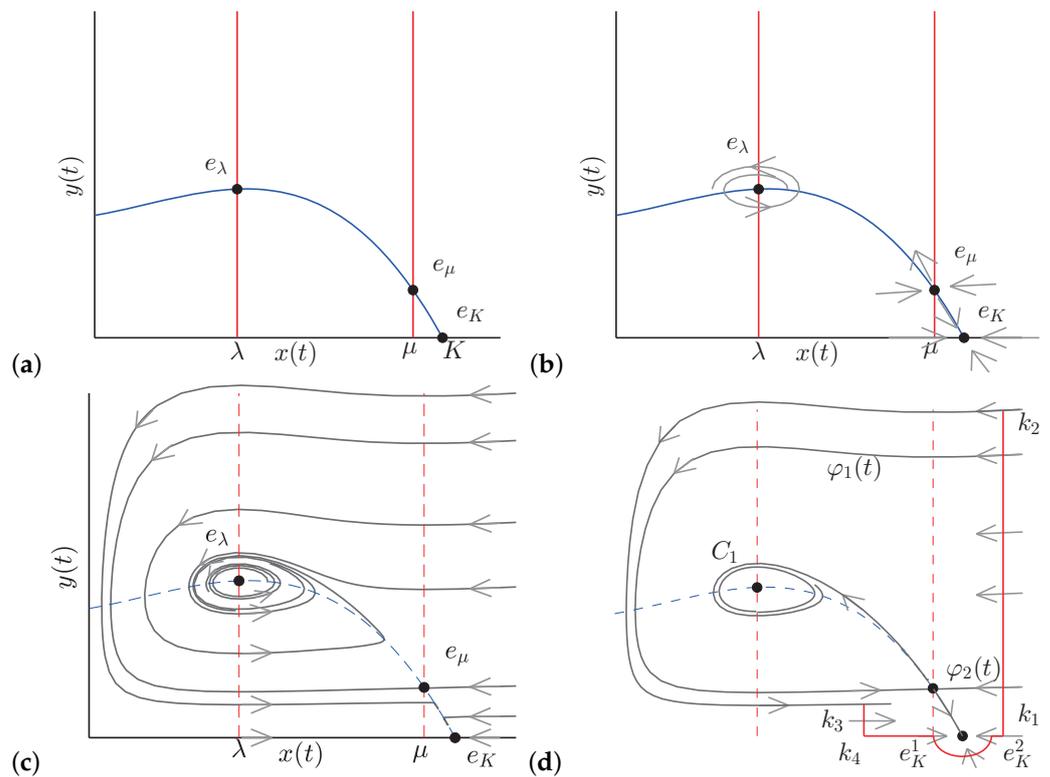


Figure 9. The bistable structure diagram for model (7), where $K = 6$. (a) The y -axis and the curve are x -nullclines, and x -axis, $x = \lambda$, and $x = \mu$ are y -nullclines. (b) Equilibrium e_λ is asymptotically unstable. Equilibrium e_μ is a saddle, and equilibrium e_K is asymptotically stable. (c) Numerical solutions with different initial values are simulated using the function ode45 in MATLAB. This function implements the Runge–Kutta method with a variable time step. The time span used is 0–30. The slight perturbations in the initial value will not cause significant changes in the solution orbits, except for the two orbits that originally tend towards e_μ become incline towards the periodic trajectory or equilibrium e_K . (d) The region U required is constructed. Orbits $\varphi_1(t)$, $\varphi_2(t)$, and equilibrium e_μ form the separatrix.

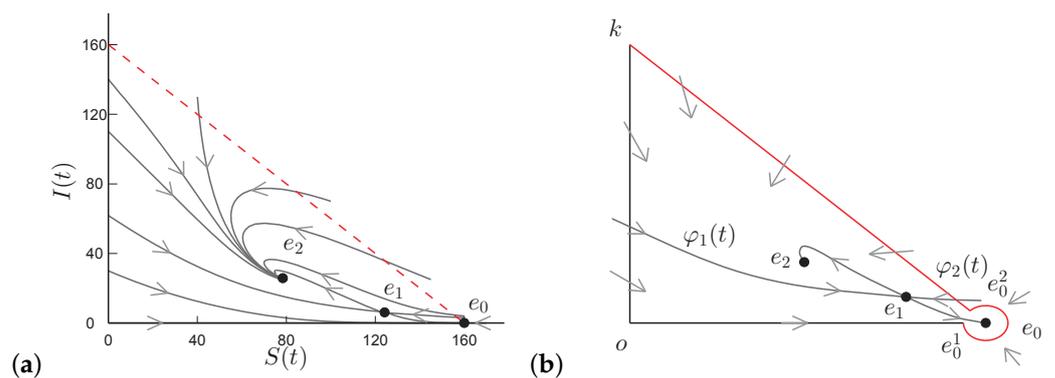


Figure 10. The bistable structure diagram for model (9). (a) This is the phase portrait of (9) simulated by function ode45 in MATLAB. Here $\Lambda = 16$, $\beta = 0.005$, $\kappa = 0.01$, $d = 0.1$, $\gamma = 0.01$, $\varepsilon = 0.02$, $\alpha = 6$, $\omega = 7$ and time span is 0–130. There are three equilibria, e_0 , e_1 , and e_2 , in which e_0 and e_2 are stable and e_1 is a saddle. The slight perturbations of the initial value will also not cause significant changes in the phase portraits. (b) The region U is bounded by two line segments, one orbit section and an arc. And the separatrix is composed of two orbits, φ_1 and φ_2 , and saddle e_1 .

4.2. Applications to a Competitive Eco-System

Here we consider a competitive model with two species competing for the same food supply [16,26,30], which can exhibit bistability. Instead of analyzing specific equations, we adopt a different approach; that is, we only consider the qualitative features to obtain the behavior of the model. This method can give more general conclusions than analyzing a specific model. At the same time, the difficulty of solving specific equations can be avoided, which can occur when other detailed factors, such as predators, seasonal effects, and other sources of food, are taken into account.

First, let $x(t)$ and $y(t)$ denote the populations of the two species at time t . For instance, rabbits and sheep, who are all fed on grass. Thus, the model can be written as

$$\begin{cases} \frac{dx}{dt} = M(x, y)x, \\ \frac{dy}{dt} = N(x, y)y, \end{cases} \tag{10}$$

where $M(x, y)$ and $N(x, y)$ are the growth rates of the two species, and both are functions of variable x and y . We consider the following assumptions:

1. In the absence of either species, the other would grow to its carrying capacity, a for species x and b for y . Therefore,

$$\begin{aligned} M(x, 0) > 0 \quad \text{for } x < a \quad \text{and} \quad M(x, 0) < 0 \quad \text{for } x > a, \\ N(0, y) > 0 \quad \text{for } y < b \quad \text{and} \quad N(0, y) < 0 \quad \text{for } y > b. \end{aligned} \tag{11}$$

2. Because of the interspecies competition, if the population of any species increases, then the population of another species will decrease. Thus

$$\frac{\partial M}{\partial y} < 0 \quad \text{and} \quad \frac{\partial N}{\partial x} < 0. \tag{12}$$

3. In addition, if either population is very large, then both the population will decrease. So there exists $K > 0$ such that

$$M(x, y) < 0 \quad \text{and} \quad N(x, y) < 0 \quad \text{if } x \geq K \text{ or } y \geq K. \tag{13}$$

We can see from the model (10) that no matter what $M(x, y), N(x, y)$ are there always exist three equilibria: $(0, 0)$, $(a, 0)$, and $(0, b)$, as shown in Figure 11. In order to obtain their stability, we compute the Jacobian:

$$J \triangleq \begin{pmatrix} \frac{\partial}{\partial x} \left(\frac{dx}{dt} \right) & \frac{\partial}{\partial y} \left(\frac{dx}{dt} \right) \\ \frac{\partial}{\partial x} \left(\frac{dy}{dt} \right) & \frac{\partial}{\partial y} \left(\frac{dy}{dt} \right) \end{pmatrix} = \begin{pmatrix} xM_x + M & xM_y \\ yN_x & yN_y + N \end{pmatrix}, \tag{14}$$

where $M_x = \frac{\partial M}{\partial x}, M_y = \frac{\partial M}{\partial y}$, and so on. Then we analyze these equilibria in turn.

$(0, 0)$: It is an unstable node. This is because the eigenvalues of matrix J valued at this point are M and N , and both are positive according to assumption 1 above.

$(a, 0)$: When it is to the left of v , it is a saddle. This is because the eigenvalues of matrix J valued at this point are a negative number, $aM_x(a, 0) < 0$, and a positive number $N(a, 0) > 0$. However, when $(a, 0)$ is to the right of v , eigenvalue $N(a, 0)$ will be negative. So, it is a stable node in the latter case. In either case, the positive half-axis of x is located on the stable manifold of $(a, 0)$.

$(0, b)$: Similar to $(a, 0)$, when $(0, b)$ is below μ , it is a saddle. Conversely, when $(0, b)$ is above μ , it is a stable node. And the positive half-axis of y is located on the stable manifold of $(0, b)$ correspondingly.

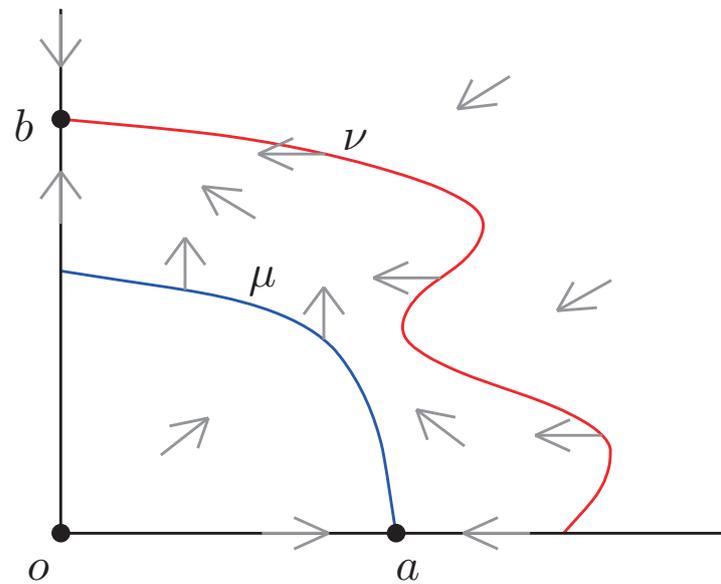


Figure 11. Equilibria and nullclines μ and ν for a competitive model. Curve μ corresponds to equation $M(x, y) = 0$, and Curve ν corresponds to equation $N(x, y) = 0$.

Moreover, there can be other equilibrium, say e , in the first quadrant, that is, the intersection point of μ and ν if they intersect. One can find that if both have the negative slope at equilibrium e but μ is steeper, then it is asymptotically stable. By implicit differentiation, this condition can also be formulated as

$$\text{slope of } \mu = -\frac{M_x}{M_y} < \text{slope of } \nu = -\frac{N_x}{N_y} < 0. \tag{15}$$

This can be proved by checking the trace is negative and the determinant is positive for matrix J evaluated at e , which means matrix J_e has two negative eigenvalues. This condition is necessary, as well. Namely, if the intersection point is asymptotically stable, Equation (15) must be held at that point.

Next, we begin to study the competitive model (10) using the results above and the conclusion in the previous section. Firstly, let the right-hand side of (10) equal to 0. Then we obtain the x -nullclines, $x = 0$ and curve $M(x, y) = 0$ labeled by μ , and the y -nullclines, $y = 0$ and curve $N(x, y) = 0$ labeled by ν . We assume that the nullclines can be sketched as (a) in Figure 12. Based on the above analysis, we obtain that the equilibrium $(0, 0)$ labeled o is an unstable node, and equilibrium $(a, 0)$ labeled a is a stable node since it is located to the right of ν . Similarly, the equilibrium $(0, b)$ labeled b is also a stable node. For equilibrium c , the slope of ν is positive, as can be seen in (b) in Figure 12, while the slope of μ is negative. Thus, equilibrium c is unstable.

To date, we have obtained precisely two stable equilibria, a and b . In order to apply the relevant conclusions in the previous section, we need a region U in which the stable equilibria is exactly a and b . So let us obtain started dealing with its construction first. Because a is a stable node, we can find a closed curve surrounding a in its basin of attraction, such that all the points on this curve will immediately run into its interior and approach equilibrium a eventually. Moreover, the two intersections with the x -axis are labeled with a_1 and a_2 , as shown in Figure 12c. The same method is applied to equilibrium b , and we can obtain another closed curve and intersections, b_1 and b_2 . However, a closed curve surrounding o can be found, such that the internal points, not o , will run outside through this curve. The intersections with the x -axis and y -axis are labeled with o_1 and o_2 . By Assumption 3, we know that the direction vector point to the bottom left when the component x or y is greater than K . Then we can find line segments, $\overline{k_1k}$ and $\overline{k_2k}$, to the right of $x = K$ and to the top of $y = K$, respectively, such that the points on those segments flow

to the lower left. The relevant labels can be seen in Figure 12c. Finally, a region bounded by line segments, $\overline{k_2k}$ and $\overline{k_1k}$, flow sections, $\overline{o_1a_1}$, $\overline{k_1a_2}$, $\overline{o_2b_1}$, and $\overline{k_2b_2}$, and arcs, $\overline{b_1b_2}$, $\overline{o_1o_2}$, and $\overline{a_1a_2}$, are constructed. As shown in Figure 12d, this region meets the requirements in H1'.

In this case, the model is assumed to be structurally stable, since typically the ecosystem is insensitive to the small disturbance of the external environment, and it is also impossible to have periodic orbits [26]. So, H2 and H3 are satisfied. Then by Theorem 5, we obtain that the invariant set S , namely the equilibrium point c , is a saddle point. Also, by the comment below Theorem 6, there must be a separatrix, as shown in Figure 12d, which consists of saddle c and two orbits, $\varphi_1(t)$ and $\varphi_2(t)$. The orbits to the lower right of the separatrix will flow to equilibrium a , while the orbits on the other side will flow to equilibrium b .

Now we consider the competitive model (10) again, where the nullclines μ and ν are slightly more complicated than the previous one, as shown in Figure 13a. The same as before, the origin o is an unstable node, and equilibrium b is a stable node. However, the differences are that equilibrium a becomes a saddle, and equilibrium c becomes a stable node, which can be obtained by checking condition (15). Moreover, there are three other equilibria, d , e , and f , as shown in Figure 13b.

The construction for region U is also a little different since equilibrium a is not stable anymore. Because a is a saddle and its stable manifold is on the positive x -axis, there must exist an orbit $\varphi^1(t)$ above the x -axis which comes from the origin and flows towards equilibrium a , and then flows upward along the unstable manifold of a , as shown in Figure 13c. Similarly, to the right side of equilibrium a , there must exist orbit $\varphi^2(t)$ which flows towards a to the right of a and then flow upward along the unstable manifold. Near equilibrium a , we can find a line segment $\overline{a_1a_2}$, such that it intersects transversely with $\varphi^1(t)$ at point a_1 and with $\varphi^2(t)$ at a_2 and with other orbits between them. The point on the $\overline{a_1a_2}$ will leave the line segment immediately and flow upward. For the other part of the boundary ∂U , the construction method is the same as above. We need to note that, in the present case, o_1 becomes the intersection point of orbit $\varphi^1(t)$ with a closed curve surrounding o , and k_1 is the intersection point of orbit $\varphi^2(t)$ with vertical line segment $\overline{k_1k}$. Now the relevant curves and orbit segments can form a closed region U required in H1', as shown in Figure 13c.

Since there are precisely three unstable equilibria, d , e , and f , it can be obtained from Theorem 5 that these three equilibria must be two saddles and one repeller. Moreover, by analyzing the direction of the vector field around these three equilibria, we can obtain that there must exist two heteroclinic orbits, such that both of them come from e and flow towards to d and f , respectively. That is to say, the invariant set S consisting of three equilibria and two heteroclinic orbits is connected. Thus, we can conclude that e is an unstable node, and d and f are saddles. What is more, by the comment below Theorem 6, there exists a separatrix, which is similar to the above conclusion and is composed of two orbits, $\varphi_1(t)$ and $\varphi_2(t)$, three equilibria, d , e , and f , and corresponding connecting orbits. As the name suggests, the separatrix divides the region into two parts, such that the orbits on the boundary will flow into its corresponding attractor, b or c , as shown in Figure 13d.

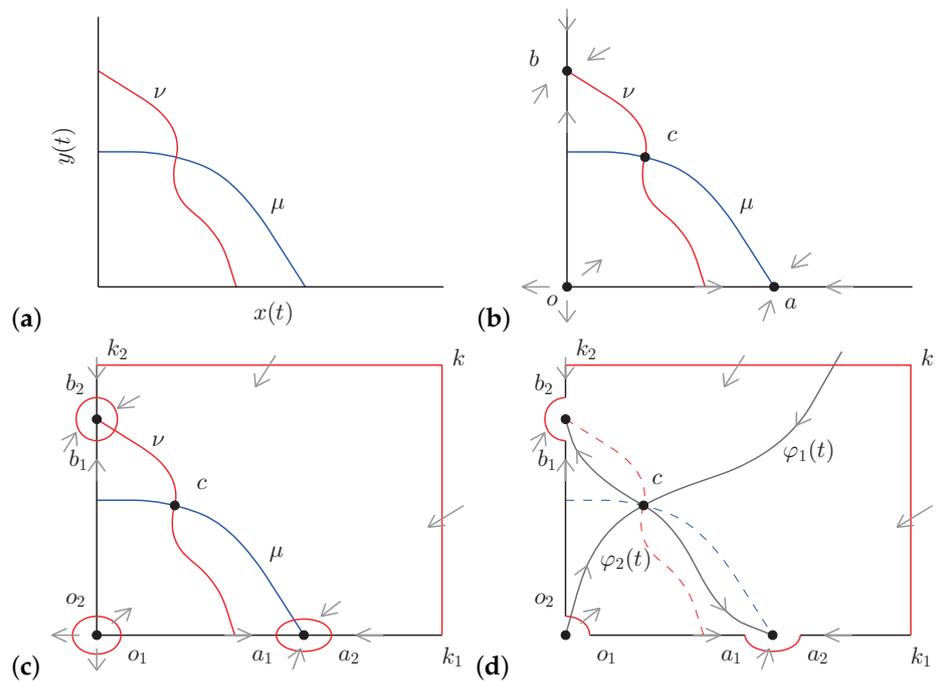


Figure 12. The bistable structure diagram for the competitive model (10). (a) The curves μ and ν are x -nullcline and y -nullcline, respectively, and they correspond to the equations $M = 0$ and $N = 0$, respectively. (b) There are four equilibria, a , b , c , and o , in which a and b are stable nodes, and o is an unstable node, and c is unstable. (c) The region U required in $H1'$ is being constructed. (d) The orbits, φ_1 and φ_2 , together with equilibrium c , form the separatrix. These two orbits are precisely located on the stable manifold of c .

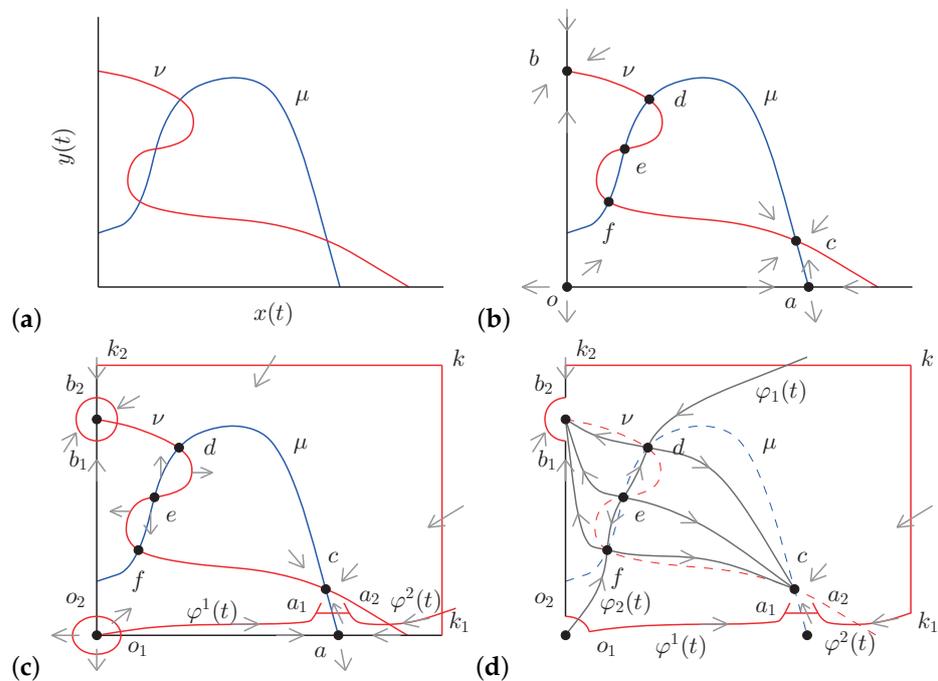


Figure 13. The bistable structure diagram for another competitive model (10). (a) The curves μ and ν are x -nullcline and y -nullcline, respectively, and they correspond to the equations $M = 0$ and $N = 0$, respectively. (b) There are seven equilibria, in which o is an unstable node, a is a saddle, and b and c are stable nodes. (c) The region U in $H1'$ is being constructed. (d) Two orbits, φ_1 and φ_2 , together with isolated invariant set S , form the separatrix.

5. Conclusions and Discussion

Bistability is a widespread phenomenon, whether in daily life or life-related fields. Based on this observation, we study two kinds of bistable structures in two-dimensional dynamical systems, which are very common in the study of biological models. The research method we use is mainly the Conley index theory, which is a topological tool in dynamical systems. Its idea is to find an isolated neighborhood first, and then deduce the dynamics of the isolated invariant set in it by checking the direction of the orbits on the neighborhood boundary. Moreover, if we want to obtain a more detailed structure of isolated invariant sets, some more information would be needed. This idea is precisely the strategy of this paper.

In this paper, two kinds of bistable structures with exactly two attractors in an attracting region are studied. The first is two one-point attractors, and another is the coexistence of a cycle attractor and a one-point attractor. We prove that in both cases, there are other isolated invariant sets except two attractors within this attracting region, and there are also connecting orbits from the invariant set to two attractors, respectively. Moreover, if the dynamical system we considered is structurally stable, we can obtain the requirement for the number of equilibria contained in the invariant set. More importantly, we find that no matter which case, there is always a separatrix or cycle separatrix between two attractors. It divides the whole attracting region into two sub-regions so that almost all the orbits within each sub-region flow to the corresponding attractor. Then, we briefly analyze four different biological models to indicate that many models have the bistable structure we considered in this paper, which are the spruce budworm population model, genetic control model, a predator–prey system with group defense, and a kind of SIR compartment model with limited medical resources and supply efficiency. Finally, we use the competitive ecosystem to show how to apply the related conclusions to analyze the global behavior of the model with two attractors.

We should note that although this paper mainly considers bistable structure in two-dimensional systems, some conclusions are still true in n -dimensional systems since Conley index is insensitive to dimension. Take Theorem 4 as an example, if system (2) is n -dimensional, $n \in \mathbb{N}^+$, we can still prove that in addition to attractor A_1 and A_2 within attracting area U , there is still isolated invariant set S , and its Conley index is Σ^1 as well. In addition, one can also prove the existence of connecting orbits from invariant set S to attractors A_1 and A_2 , respectively. The other is Theorem 5 (i), if it can be guaranteed that all the equilibria contained in S are hyperbolic, by the generalized winding number [31] it can be proved that S contains a finite and odd number of equilibria.

Finally, there are still challenges related to the bistable structure. The first is the study of bistable structure in high-dimensional systems because many biological models are built to be high-dimensional. Thus, the dynamic behavior of orbits here can be very complicated, which makes it hard to analyze. Moreover, researching the bistable structure with a strange attractor is also extremely difficult, and the strange attractor itself is a tricky object. Also, it is not easy to study a multistable structure, which is likely to appear in biological models due to the complexity and diversity of the corresponding biological system.

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