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Multiple attractors in host-parasitoid interactions: coexistence and extinction

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Abstract

This paper considers the dynamics of a two-dimensional discrete-time model for host-parasitoid interactions, and show that the model has two attractors: the fixed point where two species coexist and the boundary cycle where the parasitoid is absent. The analysis with the Liapunov exponent confirms that this kind of bistability is common in this model. The generality of this phenomenon in host-parasitoid interactions is also discussed.

Running head:

Multiple attractors

Key words:

permanence, invasibility, Liapunov exponent, host density dependence, difference equations, Ricker map, Nicholson-Bailey model, overcompensatory dynamics

1 Introduction

It is known that host-parasitoid interactions are very popular in the insect world. According to Hassell [9], parasitoids comprise about 10% or more of all metazoan species, and few insect species escape the attack of parasitoids (see also Godfray [5], §1.4). Therefore, to focus on the interaction between hosts and parasitoids is important to uncover the mechanism which promotes species diversity.

The classical framework for discrete-time host-parasitoid models is given by

$$\begin{cases} H_{t+1} &= \lambda H_t f[P_t] \\ P_{t+1} &= bH_t(1 - f[P_t]), \end{cases} \tag{1}$$

where H_t and P_t are the population densities of hosts and parasitoids, respectively. The parameters $\lambda > 1$ and $b > 0$ denote the number of offspring of hosts in the absence of parasitoids and the number of parasitoids emerging from each host parasitized, respectively. The function f defines the fraction of hosts escaping parasitism. Therefore, $1 - f$ defines the fraction of hosts parasitized.

System (1) with $f[P] = \exp[-aP]$ is called the Nicholson-Bailey model. The parameter $a > 0$ represents the per capita searching efficiency of parasitoids. The Nicholson-Bailey model has a positive fixed point (H^*, P^*), $H^* > 0$ and $P^* > 0$, on which point two species can coexist as long as the initial condition satisfies $(H_0, P_0) = (H^*, P^*)$. However, it is well known that this fixed point is never stable, and the slightest perturbation leads to divergent oscillations. Since this instability disagrees with the fact that many hosts and parasitoids coexist in nature, a great effort has been made to find mechanisms which stabilize this positive fixed point.

One of such mechanisms is the density dependence in host populations (see Hassell [9] for other mechanisms which stabilize host-parasitoid interactions). The following model was proposed by Beddington *et al.* [1] as a host-parasitoid model with density dependence in a host population:

$$\begin{cases} H_{t+1} &= \lambda H_t \exp[-\mu H_t] \exp[-aP_t] \\ P_{t+1} &= bH_t(1 - \exp[-aP_t]), \end{cases} \tag{2}$$

where the newly introduced parameter $\mu > 0$ denotes the intensity of intra-specific competition in a host population. Beddington *et al.* [1] showed that the inclusion of the host density dependence stabilizes the Nicholson-Bailey model, i.e., System (2) can have a stable positive fixed point. They also illustrated that the destabilization of the positive fixed leads to quasi periodic and chaotic orbits (see also Gumowski and Mira [7] for the structure of positive attractors of (2)).

These results were obtained by addressing the dynamics in the interior of the non-negative corn (denoted by $\mathbb{R}^2_+$), especially the bifurcation of a positive fixed point. In contrast with these studies, there are some studies focusing on the dynamics on the boundary of $\mathbb{R}^2_+$. For example, Hadeler and Gerstmann [8] examined the dynamics of the discrete-time predator-prey model called the discrete-time Rosenzweig model. They showed that there are two attractors: the first is a positive fixed point where both species coexist, and the second is a cycle (or periodic orbit) where the predator is absent. Moreover, Neubert and Kot [26] found the similar phenomenon in other models (see also the recent works by Kon [15, 17] and Greenman and Benton [6]). These results imply that whether or not two species coexist could depend on their initial population densities. In this paper, we focus on the boundary orbits (in particular 2-, 4- and 8-cycles) of System (2) and consider how often such kinds of multiple attractors are observed in System (2).

The remainder of this paper is organized as follows. In Section 2, we review some known results addressing the stability of fixed points of (2) (see also [1, 4, 13, 24]). In Section 3, we address the boundary cycles (2-, 4- and 8-cycles) of (2) and examine their stability. The result of this stability analysis is used, in Section 4, to consider the existence of multiple attractors. By introducing the Liapunov exponent, Section 4 also considers the attractivity of boundary aperiodic orbits. The final section includes discussion.

2 Fixed points and their stability

We introduce the new variables $x_t = \mu H_t$ and $y_t = aP_t$ and the new parameters $r = \log\lambda > 0$ and $\theta = ab/\mu > 0$, which lead to the following rescaled equation:

$$\left\{\begin{array}{lcl} x_{t+1} & = & x_t \exp[r - x_t - y_t] \\ y_{t+1} & = & \theta x_t (1 - \exp[-y_t]). \end{array}\right. \tag{3}$$

In the rest of this section, we present the known results concerning the existence and stability of fixed points of this rescaled system.

System (3) has at most three fixed points: $E_{00} = (0, 0)$, $E_{+0} = (r, 0)$ and $E_{++} = (x^*, y^*)$, which is derived as a unique positive root of the following equations:

$$\begin{cases} r &= x^* + y^* \\ x^* &= y^*/\{\theta(1-\exp[-y^*])\}. \end{cases}$$

Fig. 1 illustrates the disposition of these fixed points. The fixed points E_{00} and E_{+0} always exist, and E_{++} exists if and only if $\theta r > 1$ (e.g., see Kon and Takeuchi [13]). Therefore, the r-$(1/\theta)$ parameter plane is divided into two regions depending on the existence of the fixed point E_{+0} (see Fig. 2). Kon and Takeuchi [16] showed that if $\theta r < 1$ holds, then $\lim_{t\to\infty} P_t = 0$ for every $(H_0, P_0) \in \mathbb{R}^2_+$. Therefore, except the critical case $\theta r = 1$, we see that if E_{++} does not exist, then the parasitoid goes extinct.

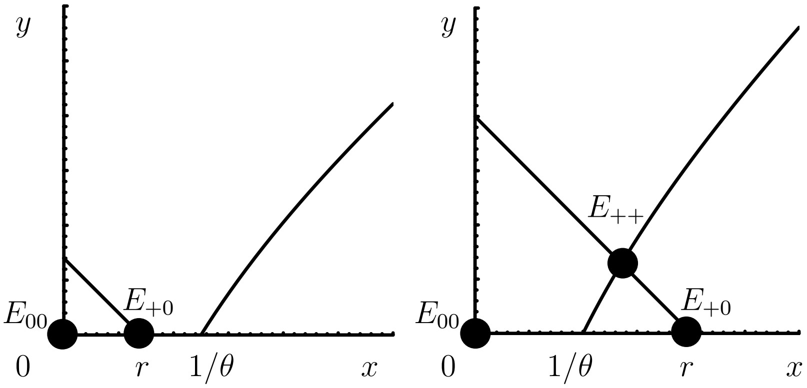

Figure 1: The x-y phase plane. The dots and lines represent fixed points and null clines of (3), respectively.

The local stability conditions of the fixed points are given by using the Schur-Cohn or Jury criteria (e.g., see May [20] and Kocic and Ladas [12] for the Schur-Cohn criterion and Murray [24] and Caswell [2] for the Jury criterion.) These criteria show that E_{00} is always unstable, and the stability of E_{+0} and E_{++} depends on the parameter values. In Fig. 2, the r-$(1/\theta)$ parameter plane demarcated with the stability of these fixed points is shown. Furthermore, the schematic phase portraits of (3) are given for each parameter region. E_{+0} is stable if $r < 2$ and $\theta r < 1$. E_{++} is stable in the gray region of Fig. 2. On the boundaries **T**, **H** and **F** in Fig. 2, transcritical, Naimark-Sacker (discrete-Hopf) and flip bifurcations of E_{++} occur, respectively (see Neubert and Kot [26] and Kot [18]). On the boundary **T**, E_{++} emerges from E_{+0}. There is an exchange of stability between E_{+0} and E_{++}. Below **H**, we observe an unstable focus E_{++}

and an attracting invariant circle surrounding E_{++}. On the boundary **F**, the destabilization of E_{++} gives rise to a 2-cycle. It is known that this 2-cycle is unstable, i.e., the flip bifurcation is subcritical (see Neubert and Kot [26] and Kot [18]).

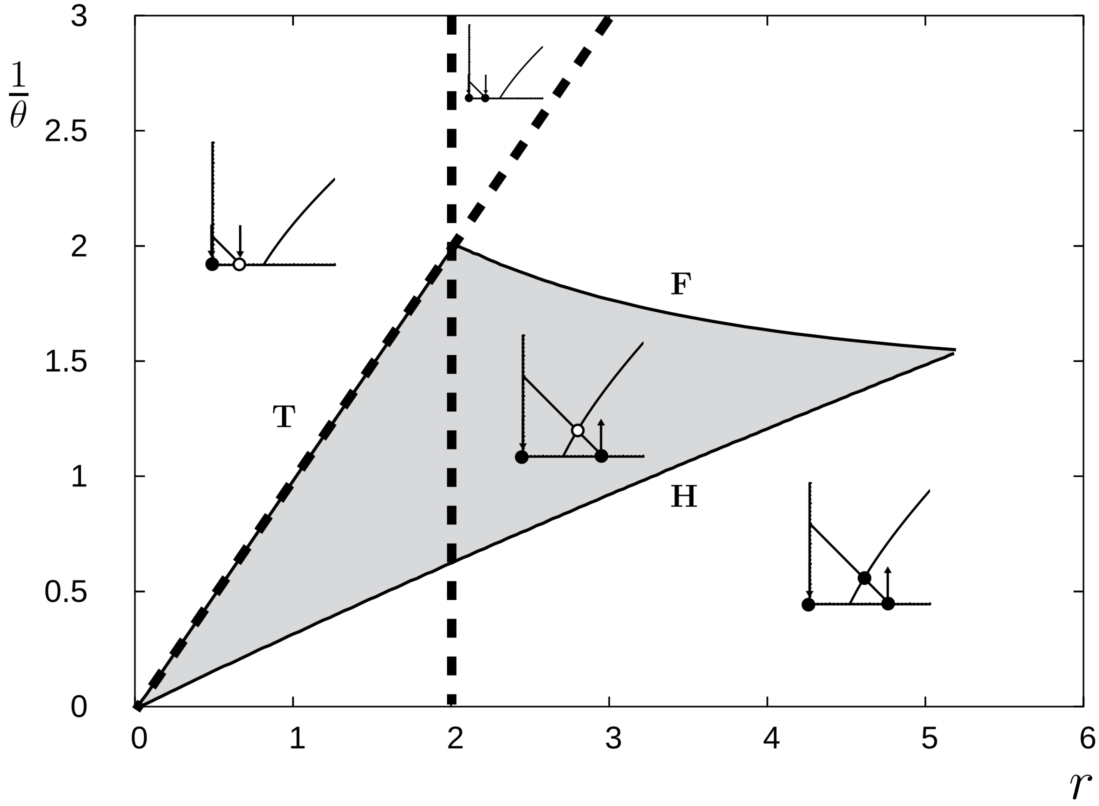

Figure 2: The r-$(1/\theta)$ parameter plane demarcated with stability of E_{+0} and E_{++}. E_{+0} is stable if $r < 2$ and $\theta r < 1$. The internal and transversal stabilities of E_{+0} change on the lines $r = 2$ and $\theta r = 1$, respectively. E_{++} is stable in the gray region. In the schematic phase portraits, the white and black dots represent stable and unstable fixed points, respectively.

3 Boundary cycles

In this section, we focus on cycles on the boundary of the non-negative corn $\mathbb{R}_+^2$, which is composed of the x- and y-axes. From Eq. (3), we can easily see that these axes are invariant, i.e., every orbit on the x- and y- axes does not leave the respective axes.

It is clear that on the y-axis there are no cycles except the origin E_{00}. In fact, we see that every orbit on the y-axis is mapped to the origin by one iteration. In contrast to such simple dynamics, the dynamics on the x-axis is much more complicated. From Eq. (3), we see that the dynamics on the x-axis is governed by the following map:

$$x_{t+1} = x_t \exp[r - x_t]. \tag{4}$$

This map is called the Ricker map and its dynamics is extensively studied by many authors (e.g., see May [21] and May and Oster [22]). Fig. 3 is a bifurcation diagram of this map. Fig. 3 (a) captures stable cycles and (b) captures some cycles (2-, 4- and 8-cycles) irrespective of their stability, which are originated from the positive fixed point $x = r$ (see Appendix A of Mylius and Diekmann [25] for analytical expression of the 2-cycle). These cycles are embedded in the x-axis of System (3).

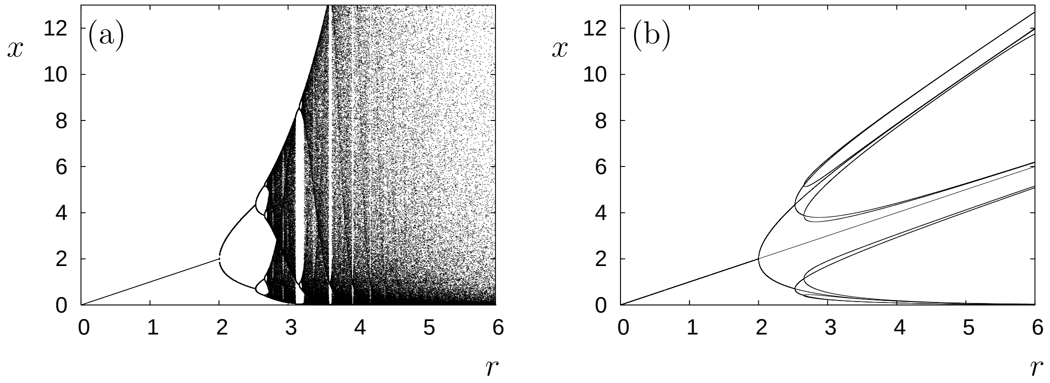

Figure 3: The bifurcation diagrams of (4). (a) The orbits for $t = 1000$-1200 are plotted. This diagram shows attractive orbits. (b) The fixed point $x = r$ and 2-, 4- and 8-cycles are plotted.

Let $\{(p_t, 0)\}_{t=1}^{m}$ be an m-cycle on the x-axis. The stability conditions of $\{(p_t, 0)\}_{t=1}^{m}$ are given by using the Schur-Cohn or Jury criteria. These criteria show that $\{(p_t, 0)\}_{t=1}^{m}$ is stable if

$$\left|\prod_{t=1}^{m}(1 - p_t)\exp[r - p_t]\right| < 1 \quad \text{and} \quad \prod_{t=1}^{m}\theta p_t < 1$$

hold (e.g., see Kon and Takeuchi [14]). Note that the first inequality is identical to the stability condition of a cycle $\{p_t\}_{t=1}^{m}$ of the Ricker map (4), i.e., the so-called internal stability. Whether or not this inequality holds can be numerically evaluated by using the bifurcation diagram in Fig. 3 (a). For example, the first inequality holds for a 2-cycle (resp. 4-cycle) when $2 < r < 2.526\cdots$ (resp. $2.526\cdots < r < 2.692\cdots$) (see also May [21]). The second inequality determines the so-called transversal stability. If the inequality $\prod_{t=1}^{m} \theta p_t \leq 1$ holds, then the cycle $\{(p_t, 0)\}_{t=1}^{m}$ is said to be *saturated*, otherwise *unsaturated*.

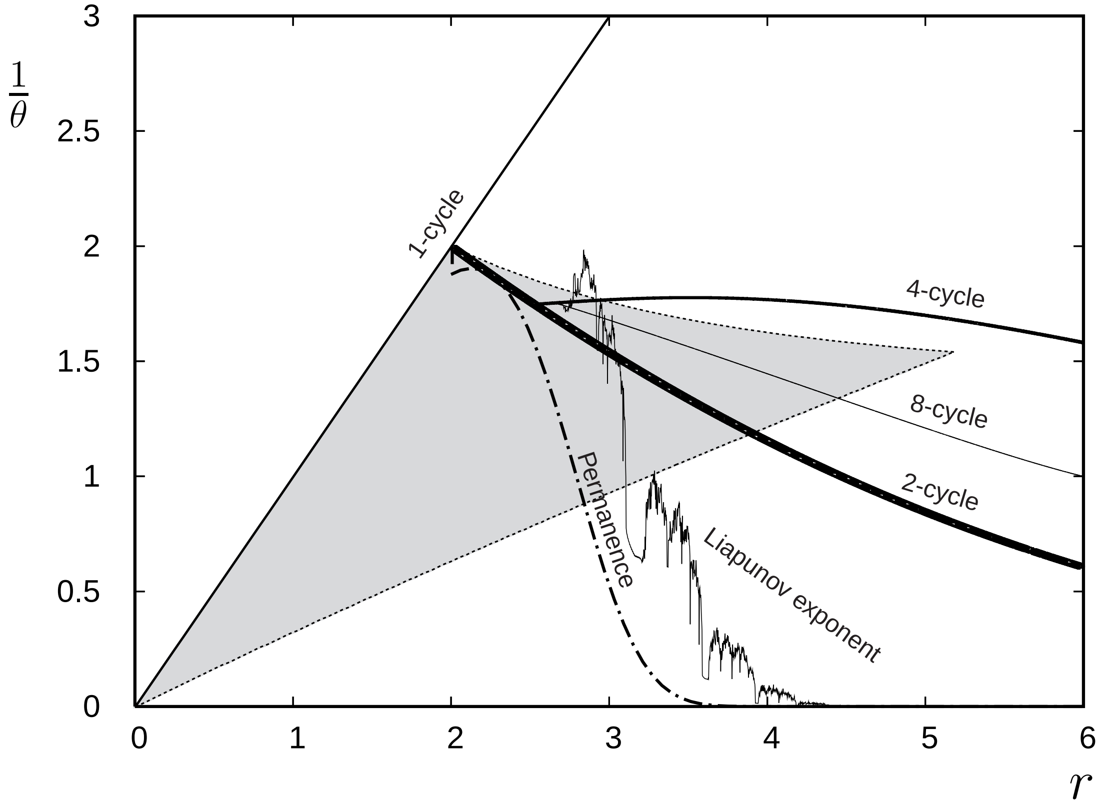

Figure 4: The r-$(1/\theta)$ parameter plane. The boundaries of transversal stability of cycles (1-,2-,4- and 8-cycles, which are shown in Fig. 3 (b)) on the x-axis are plotted. Above these boundaries, the associated cycles are saturated. Above the line labeled "Liapunov exponent", $s(x_0) < 0$ holds for an attractive orbit $\{x_t\}$ of (4), which are shown in Fig. 3 (a). Below the line labeled "Permanence", System (3) is permanent.

In Fig. 4, the boundaries of transversal stability of the fixed point E_{+0} (1-cycle) and the 2-, 4- and 8-cycles on the x-axis are superimposed over the r-$(1/\theta)$ parameter plane demarcated with stability of the positive fixed point E_{++}. The boundary of transversal stability of the fixed point E_{+0} is the line $1/\theta = r$, below which E_{+0} is transversally unstable (unsaturated). This instability leads to the positive fixed point E_{++} due to transcritical bifurcation (e.g., see Caswell [2] and Neubert and Kot [26]). Similarly, below the boundaries of transversal stability of 2-, 4- and 8-cycles, the respective cycles are transversally unstable (unsaturated). These instabilities also lead to positive cycles due to transcritical bifurcation (see Neubert and Kot [26] and Kot [18] for schematic phase portraits illustrating such bifurcations of boundary cycles).

As mentioned in Section 2, every positive orbit converges to the x-axis if the fixed point E_{+0} is strictly saturated in the sense that $\theta r < 1$ holds. This suggests that every cycle on the x-axis is saturated as long as the fixed point is strictly saturated. This assertion can easily be confirmed by using the property of the Richer map that the time average of cycles is identical to the positive fixed point, i.e., every cycle $\{p_t\}_{t=1}^{m}$ of (4) satisfies $\sum_{t=1}^{m} p_t/m = r$ (e.g., see Hofbauer *et al.* [10]). Therefore, the relationship between arithmetic and geometric means leads to

$$(\prod_{t=1}^{m} \theta p_t)^{1/m} \leq \frac{1}{m} \sum_{t=1}^{m} \theta p_t = \theta r.$$

This implies that if E_{+0} is strictly saturated, then all other cycles are also strictly saturated. In fact, Fig. 4 shows that the boundaries of transversal stability of 2-, 4- and 8-cycles are always below that of E_{+0}.

4 Multiple attractors

Fig. 5 contains the magnified picture of Fig. 4. In Fig. 5, the schematic phase portraits in the neighborhood of the x-axis are also shown. From Fig. 5, we see that both the boundary cycles (2-, 4- and 8-cycles) and the positive fixed point E_{++} can be stable simultaneously. At the point (a) (resp. (b)) in Fig. 5, both the boundary 2-cycle (resp. 4-cycle) and the positive fixed point E_{++} are stable. At the point (c), no boundary cycles are stable. But there exists an orbit converging to the boundary 2-cycle.

The following Liapunov exponent estimates the existence of attractors on the x-axis:

$$s(x_0) := \lim_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \ln \theta x_t,$$

where $\{x_t\}$ is a solution of (4). If $s(x_0) < 0$, then the Liapunov exponent roughly estimates that there is an attractor on the x-axis (see de Feo and Ferriere [3] for an example of riddled basin of attraction of boundary orbits). In Fig. 4, the boundary $s(x_0) = 0$ is superimposed over the r-$(1/\theta)$ parameter plane. In this figure, the Liapunov exponent is evaluated by the attractive orbits displayed in Fig. 3 (a). These analyses with the Liapunov exponent show that bistability is frequently observed, in particular for large r. If r is around 3.14, where the host dynamics has an attractive 3-cycle, then the positive fixed point E_{++} is never a unique attractor. From Fig. 4, we see that as r increases (i.e., the host dynamics becomes complex), System (3) tends to have multiple attractors. Fig. 6 illustrates the bistable dynamics of (3) with the parameter $(r, 1/\theta) = (3.14, 1.4)$. Fig. 6 shows that a solution around the positive fixed point converges to it and a solution around the x-axis converges to the boundary 3-cycle.

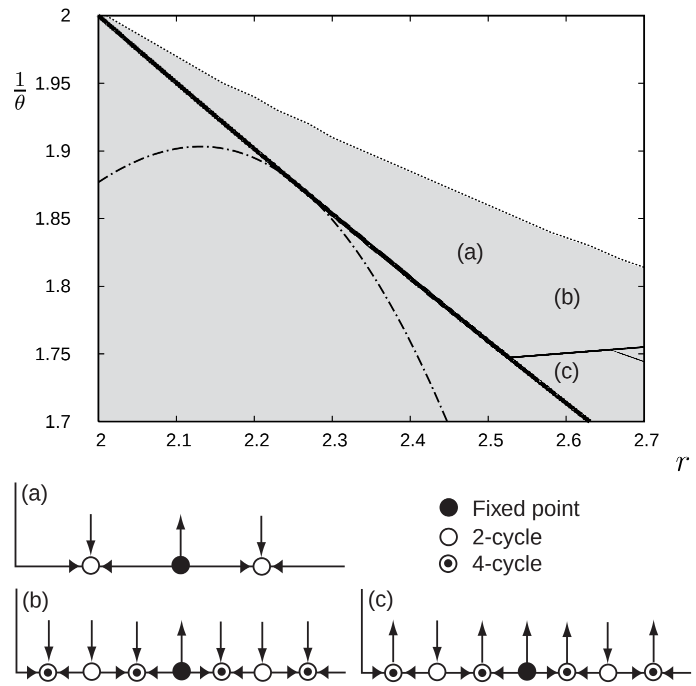

Figure 5: The magnified r-$(1/\theta)$ parameter plane. The schematic phase portraits in the neighborhood of the x-axis are shown for the points labeled (a), (b) and (c).

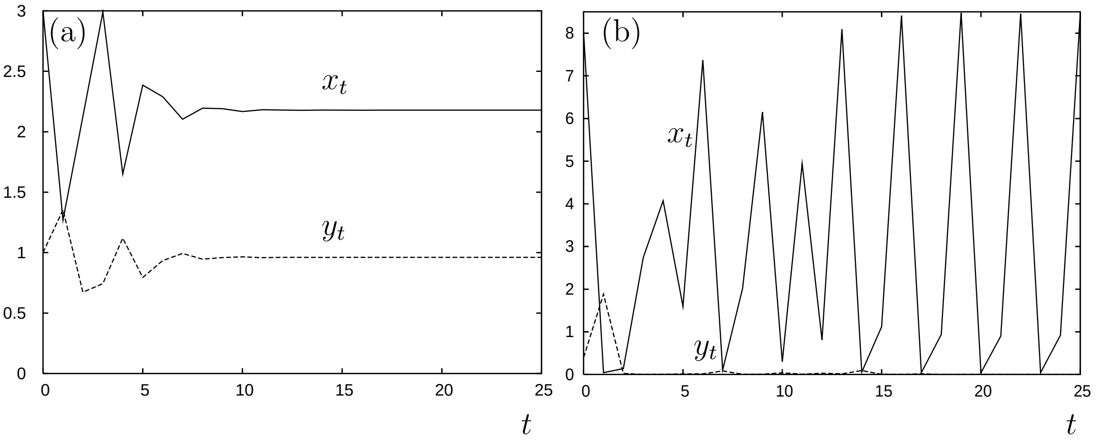

Figure 6: The temporal fluctuation of population densities of (3). The parameter set is $(r, 1/\theta) = (3.2, 1.4)$. The initial conditions are $(x_0, y_0) = (3.0, 1.0)$ for (a) and $(8.0, 0.4)$ for (b).

5 Discussion

In this paper, we investigated the dynamics of the specific host-parasitoid model (3) (or (2)) proposed by Beddington *et al.* [1]. Our investigations confirmed that this model has multiple attractors: the positive fixed point where both species coexist and the boundary cycle where the parasitoid is absent. Furthermore, the analysis with the Liapunov exponent showed that this type of coexistence of attractors is often found in System (3), in particular for large r. This result insists that it is very important to know the global behavior of systems when we consider coexistence of species.

System (3) is said to be *permanent* if there exist positive constants $\delta > 0$ and $D > 0$ such that $\delta < \liminf_{t\to\infty} x_t \leq \limsup_{t\to\infty} x_t < D$ and $\delta < \liminf_{t\to\infty} y_t \leq \limsup_{t\to\infty} y_t < D$ for all $x_0 > 0$ and $y_0 > 0$. We see that permanence implies coexistence of hosts and parasitoids. If System (3) is permanent, then as long as the initial population densities are positive there are no possibilities that the parasitoid goes extinct. In Fig. 4, the region where System (3) is permanent is shown (see Kon and Takeuchi [14] for the explicit expression of this region). Since this region only provides the sufficient condition for permanence of (3), we do not know whether or not this system is permanent outside the region. However, it is ensured that above the line labeled “2-cycle”, System (3) is not permanent since the stable manifold of the 2-cycle on the x-axis intersects with the interior of $\mathbb{R}^2_+$. To obtain a necessary and sufficient condition for permanence of (3) is an important future work.

Let us consider the generality of the bistable dynamics observed in the specific host-parasitoid system (2). System (2) can be generalized as follows:

$$\begin{cases} H_{t+1} &= \lambda H_t g[H_t] f[P_t] \\ P_{t+1} &= b H_t (1 - f[P_t]), \end{cases} \tag{5}$$

where $g[H]$ and $f[P]$ are strictly decreasing functions and satisfy the following equations:

$$g\left[\frac{\ln\lambda}{\mu}\right] = \frac{1}{\lambda} \quad \text{and} \quad \left.\frac{\partial f}{\partial P}\right|_{P\to +0} = -a.$$

System (5) is reduced to (2) if $g[H] = \exp[-\mu H]$ and $f[P] = \exp[-aP]$. Let $\{(p_t, 0)\}_{t=1}^{m}$ be an m-cycle on the H-axis. It is straightforward to show that the cycle is transversally stable if

$$\prod_{t=1}^{m} b p_t \left(\left.\frac{1 - f[P]}{P}\right|_{P\to +0} \right) = \prod_{t=1}^{m} a b p_t < 1.$$

We see that this condition is similar to that of System (2) (see the transversal stability condition of the rescaled system (3) in Section 3). If the host dynamics obeys the Ricker map, i.e., $g[H] = \exp[-\mu H]$, then the transversal stability condition is completely identical to that of System (2) irrespective of the form of the function f, and has the same picture in the r-$(1/\theta)$ parameter plane of Fig. 4 after the rescaling $x_t = \mu H_t$, $y_t = a P_t$, $r = \ln\lambda$ and $\theta = ab/\mu$. Therefore, in this case, if the generalized system has a positive stable fixed point in a wide area of the r-$(1/\theta)$ parameter plane, then the system is easy to have multiple attractors composed of a positive fixed point and a boundary cycle on the H-axis. For example, if $g[H] = \exp[-\mu H]$ and $f[P] = (1 + aP/k)^{-k}$, then System (5) has a stable fixed point in the wider range of parameter space than System (2) (see Lane *et al.* [19] and Hassell [9]). Although we need further investigations, the generalized system (5) seems to have the bistable dynamics if the host dynamics exhibits complex behavior due to overcompensatory dynamics like the Ricker map.

System (5) can be further generalized by replacing $f[P]$ with $f[H, P]$. An example model included in such a general framework is found in Kaitala *et al.* [11]. They showed that the model has several attractors simultaneously in the interior of $\mathbb{R}^2_+$. Therefore, the model seems to have a stable positive fixed point together with a local attractor on the host axis. It is a future work to investigate such bistable dynamics of System (5) with $f[H, P]$ instead of $f[P]$. It is also interesting to examine the dynamics of host-parasitoid models with the framework differing from (5). For example, it is known that the order of the events in host's life cycle leads to the different framework and is influential in the dynamics of host-parasitoid interactions (see May *et al.* [23] and Kon [15]).

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