**Dynamical Properties of Discrete Negative Feedback Models**

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**Abstract.** Dynamical properties of tropically discretized and max-plus negative feedback models are investigated. Reviewing the previous study [S. Gibo and H. Ito, J. Theor. Biol. **378**, 89 (2015)], the conditions under which the Neimark-Sacker bifurcation occurs are rederived with a different approach from theirs. For limit cycles of the tropically discretized model, we ﬁnd that the ultradiscrete state emerges when the time interval in the model becomes large. For the max-plus model, stable and unstable limit cycles are found by the Poincaré map method. The relationship between these limit cycle states for the tropically discretized and the max-plus models is discussed.

# INTRODUCTION

When a continuous dynamical system is discretized, the discretized dynamical system can exhibit dynamical behaviors that the original continuous system never shows as in the well-known case of the logistic system for population of biological individuals [1]. Which model to apply, continuous or discrete, is determined by real phenomena focused on. The negative feedback model in biological systems is also a similar case, and its continuous equation is given as

 *dx* = *y−x,*

1

*y*

*dt dy*

(1)

 *dt* = 1 + *xm − b,*

where *x* = *x*(*t*), *y* = *y*(*t*), *b* and *m* are positive [2]. *m* is called the Hill coefﬁcient. For this continuous negative feedback model, it has been conﬁrmed that there is no limit cycle solution [2, 3]. On the other hand, based on eq.(1), the following discretized negative feedback model has been derived [4]:

*xn*



+

*xn* + τ*yn*

1 = *,*

1 + τ

*yn* + τ

*m*

(2)

*yn*+1 = 1+*xn ,*

*b*

1 + τ

where *xn* = *x*(*n*τ), *yn* = *y*(*n*τ), *n* = 0*,* 1*,* 2*,...*, and τ *>* 0 corresponds to the time interval. Gibo and Ito showed that the discretized model, eq.(2), exhibits Neimark-Sacker bifurcation and has limit cycle solutions [4]. For obtaining eq.(2), they applied the tropical discretization [5, 6] to eq.(1). They obtained conditions under which the Neimark-Sacker bifurcation occurs and the limit cycle solutions emerge in eq.(2). Furthermore, they derived the max-plus negative feedback model by ultradiscretization [7] and numerically showed the existence of oscillatory solutions. They argued that the negative feedback model with discrete time steps is appropriate for biochemical situations where the rate of degradation is lower than that of synthesis and the threshold for feedback regulation is small. Moreover, even if τ is inﬁnity, the tropically discretized model is considered to be still valid for systems where the successive reactions take place at prolonged intervals in biochemical processes. Then it is meaningful to understand the dynamical properties of eq.(2) for application to real phenomena.

In this paper, by adopting our approach for identifying the types and stability of ﬁxed points in tropically discretized dynamical systems [8], we review the previous study by Gibo and Ito [4]. After that, we report the results of further investigation for dynamical properties of the tropically discretized and the max-plus negative feedback models.

# DYNAMICAL PROPERTIES OF EQ.(2)

First, we apply our systematic approach [8] to eq.(2), which is formally in the form of the following set of equations:

*xn*+1 = *xn xn* + τ *f*1(*xn, yn*) *,*

*y y*

*xn* + τ*g*1(*xn, yn*)

*y*

+ τ *f* (*x , y* )

(3)

where

*n* 2 *n n*

*n*+1 = *n yn* + τ*g*2(*xn, yn*) *,*

 *f*1(*x, y*) = *y, g*1(*x, y*) = *x,*

 *f* (*x, y*) = *, g* (*x, y*) = *.*2 2

1

*y*

(4)

1 + *xm b*

It is easily found that eq.(3) becomes *dx* = *f*1(*x, y*)*−g*1(*x, y*), *dy* = *f*2(*x, y*)*−g*2(*x, y*) in the limit of τ *→* 0. Equation (1)

*dt*

has a positive ﬁxed point (*x*¯*, y*¯), where *x*¯ = *y*¯ = *b*

(1 + *x*¯*m*)

*dt*

* 0 holds. Note that (*x*¯*, y*¯) also becomes the ﬁxed point of eq.
  1. for arbitrary τ. The Jacobi matrix for eq. (1) at

( *,*

*x*¯ *y*¯

is given by *J*

( *−*1 1

*z*¯

) where *z*¯

∂ *f*2

*x*¯ *y*¯

*my*¯*m*+1 .

Note that *z*¯ *<* 0. The trace *T* and determinant ∆ of *J* are *T* Tr *J* = (*b−*1 + 1) *<* 0 and ∆ det *J* = *b−*1 *z*¯ *>* 0, respectively.

*≡ − ≡ −*

)

=

*−b−*1

*,*

*≡*

∂ *x* ( *,*

) = *−*

*b*2

Here we consider the function *Pnd* (τ) given as

*Pnd* (τ) *≡ And* τ2 + *Bnd* τ + *Cnd,* (5)

where

*And* = *F*2 4*x*¯*y*¯ *f*¯1 *f*¯2∆*,*

 *−*

 ( )

*Bnd* = 2*x*¯*y*¯*T F −* 4*x*¯*y*¯ *x*¯ *f*¯2 + *y*¯ *f*¯1 ∆*,*

*Cnd* = (*x*¯*y*¯)2 (*T* 2 *−* 4∆) *,*

(6)

*F ≡ x*¯ *f*¯2*J*11 + *y*¯ *f*¯1*J*22 , and *Ji j* denotes the (*i, j*) component of the matrix *J* (*i, j* = 1*,* 2) [8]. The sign of *Pnd* (τ) determines whether the ﬁxed point (*x*¯*, y*¯) is spiral or not. Now *And* = 4*x*¯4*b−*1*z*¯ *<* 0 and *Bnd* = 4*x*¯4*z*¯(1 + *b−*1) *<* 0. If *Cnd <* 0, where the ﬁxed point (*x*¯*, y*¯) is spiral in eq.(1), *T* 2 *<* 4∆, then *Pnd* (τ) *<* 0 holds for all τ and the ﬁxed point (*x*¯*, y*¯) is also spiral in eq. (2) for all τ *>* 0. On the other hand, when *Cnd >* 0, (*x*¯*, y*¯) becomes a spiral for τ satisfying *Pnd* (τ) *<* 0.

( )

Regarding the stability of (*x*¯*, y*¯), the following values of α and β are focused on [8]:

β = *T x*¯*y*¯ = *−x*¯2 (*b−*1 + 1) *<* 0*.*

{α = ∆*x*¯*y*¯ + *F* = *−x*¯2 (*b−*1 + *z*¯) *,*

(7)

Note that the sign of α determines the stability of the spiral ﬁxed point. When α *<* 0, or *b−*1 + *z*¯ *>* 0, (*x*¯*, y*¯) is stable for any τ *>* 0. If 0 *< m* 1, then *b−*1 + *z*¯ *>* 0 is always satisﬁed for any τ *>* 0, and (*x*¯*, y*¯) becomes stable. On the other hand for *m >* 1, when *b−*1 + *z*¯ *<* 0, (*x*¯*, y*¯) is stable (unstable) for 0 *<* τ *<* γ (τ *>* γ), respectively, where

*≤*

γ β *b−*1 + 1

*≡ −* α = *− b−*1 + *z*¯ . Therefore, at τ = γ, the Neimark-Sacker bifurcation occurs. Note that these results for the

spiral ﬁxed points are consistent with the previous studies done by Gibo and Ito [4].

Now we set *m* = 2 and *b* = 10 as an example. In this example, we obtain (*x*¯*, y*¯) = (2*,* 2), *And* = *−*1*.*024, *Bnd* =

*−*11*.*264, and *Cnd* = +2*.*72. Then (*x*¯*, y*¯) becomes spiral for τ *>* 0*.*236397 *· · ·* . Figures 1 (a) and (b) show the graphs

of *b−*1

*z*¯ *b*

and γ *b*

*b−*1 + 1

, respectively. From Fig.1(a), it is found that *b−*1

*z*¯ *b*

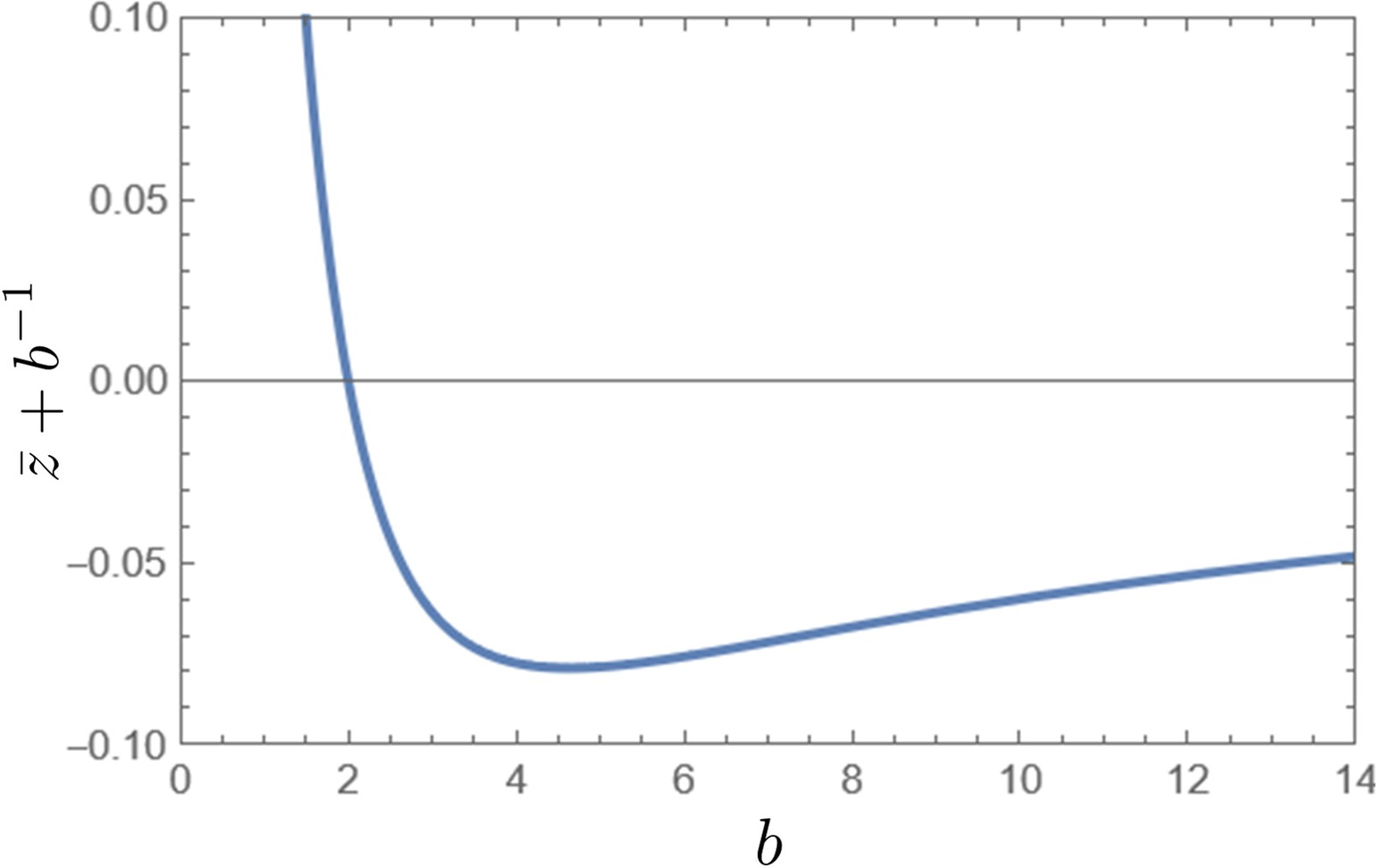
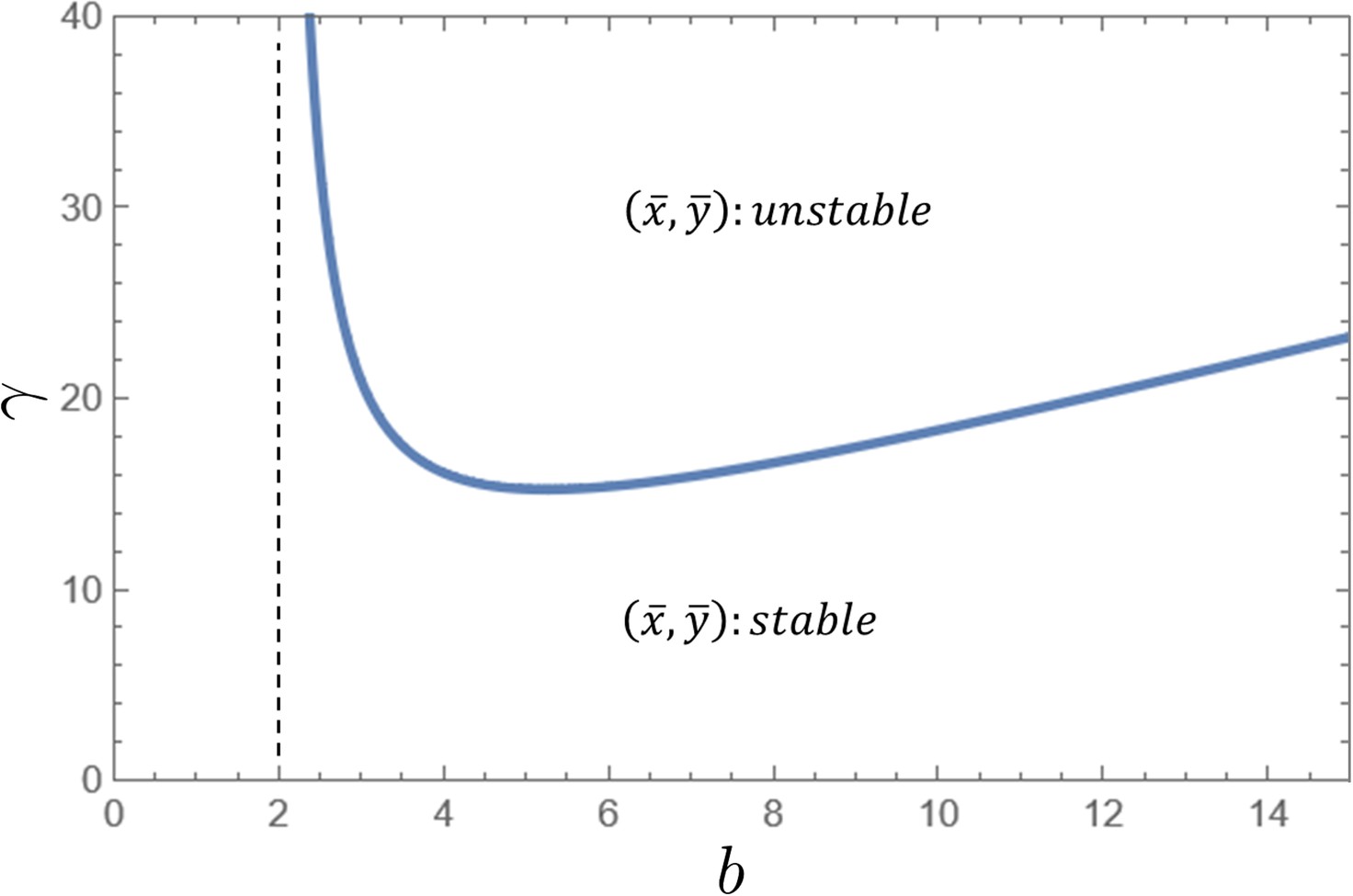
0 holds when *b* 2.

+ ( )

( ) = *−b−*1 + *z*¯(*b*)

+ ( ) *< >*

The Neimark-Sacker bifurcation occurs at *b* = 2, and the limit cycle solutions can emerge in the region τ *>* γ(*b*) as shown in Fig.1(b). Figure 2 shows the time evolution of eq. (2) from the initial state (*x*0*, y*0) = (1*.*5*,* 5) when (a)

1. (b)

**FIGURE 1.** The graphs of (a) *b−*1

*z*¯ *b*

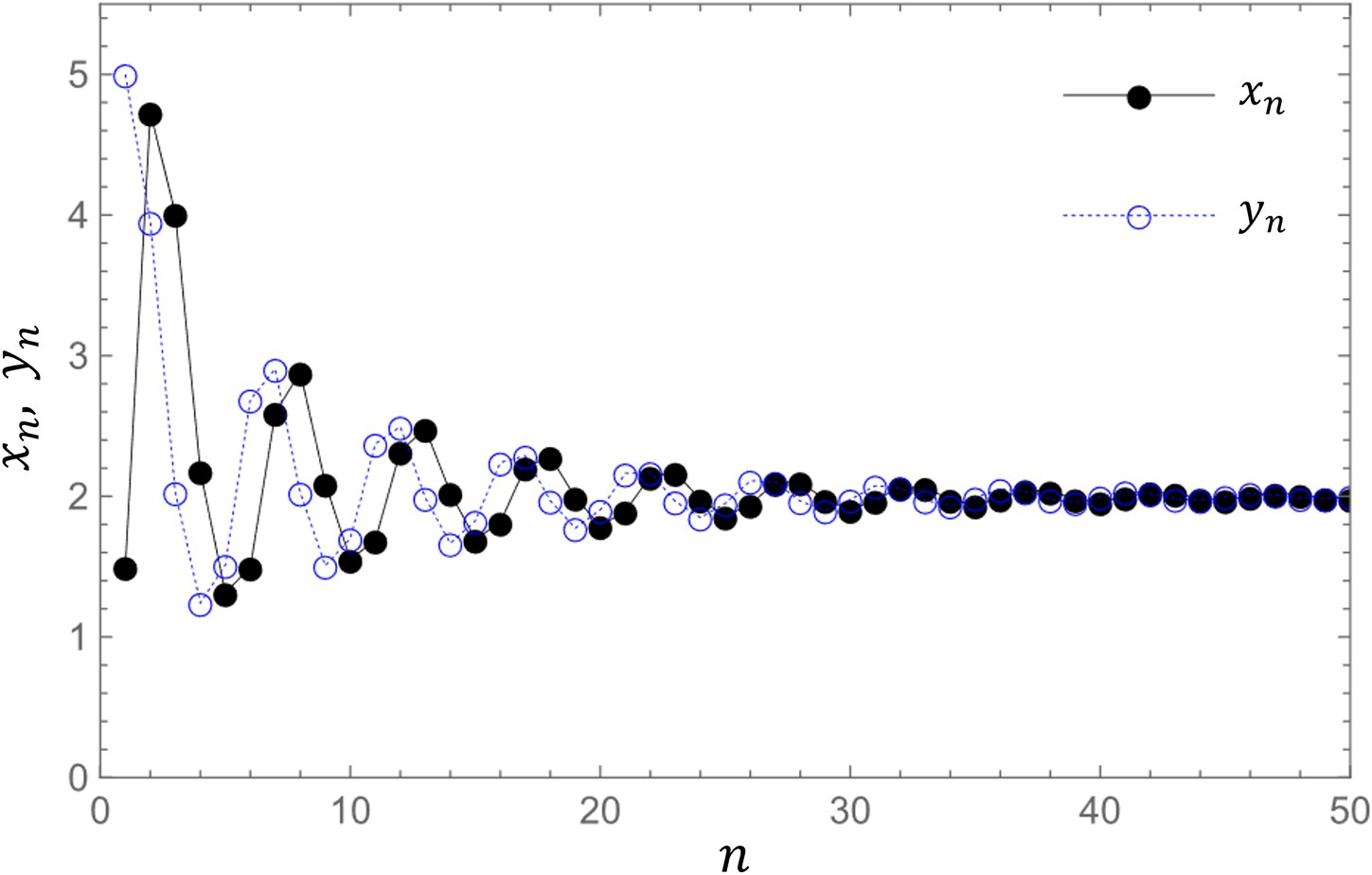
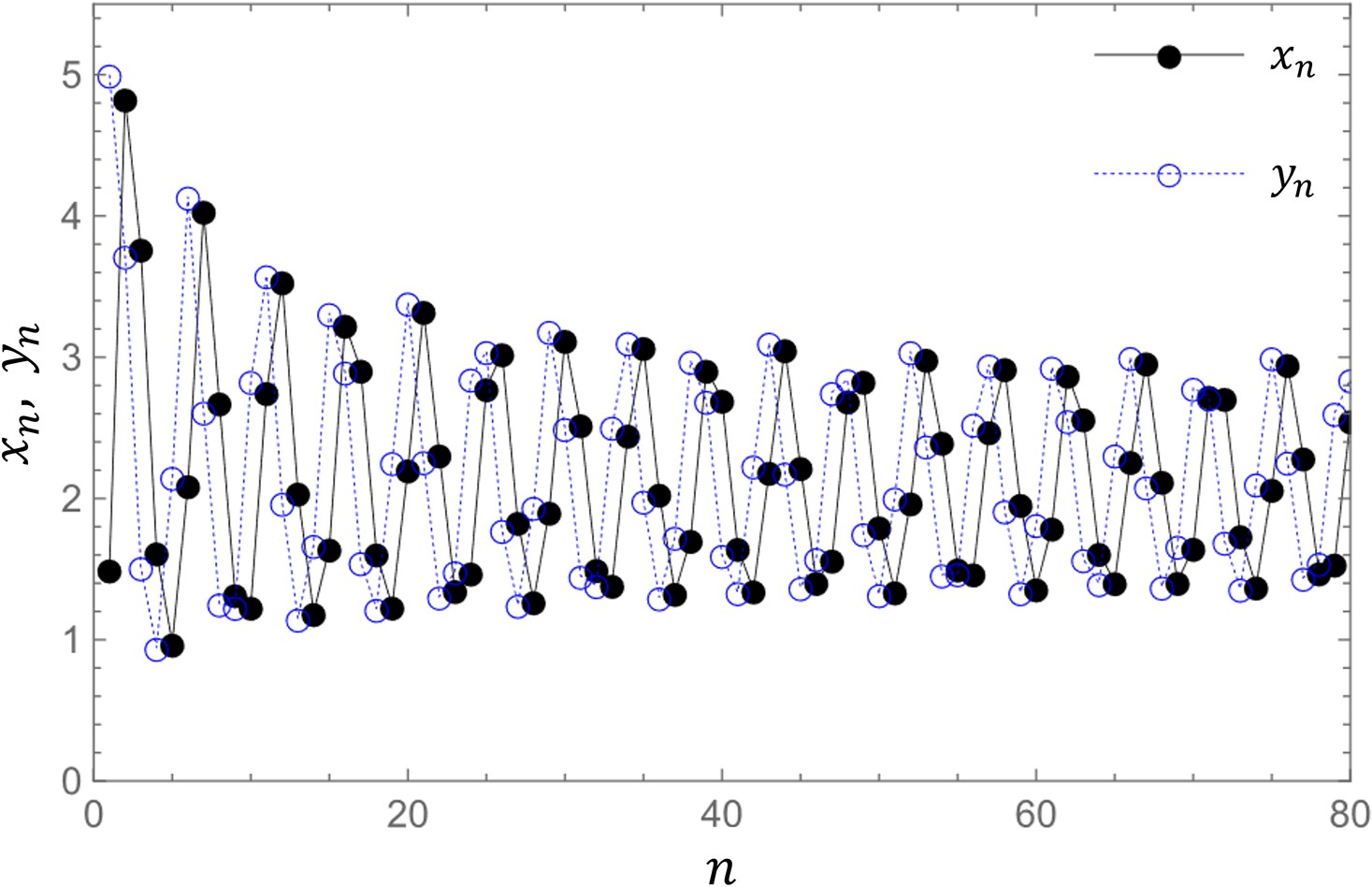
and (b) γ *b*

*b−*1 + 1

. We set *m* 2.

+ ( )

( ) = *−b−*1 + *z*¯(*b*) =

(a) (b)

**FIGURE 2.** Time evolutions of eq. (2) for *m* = 2*, b* = 10. (a) τ = 12, (b) τ = 20.

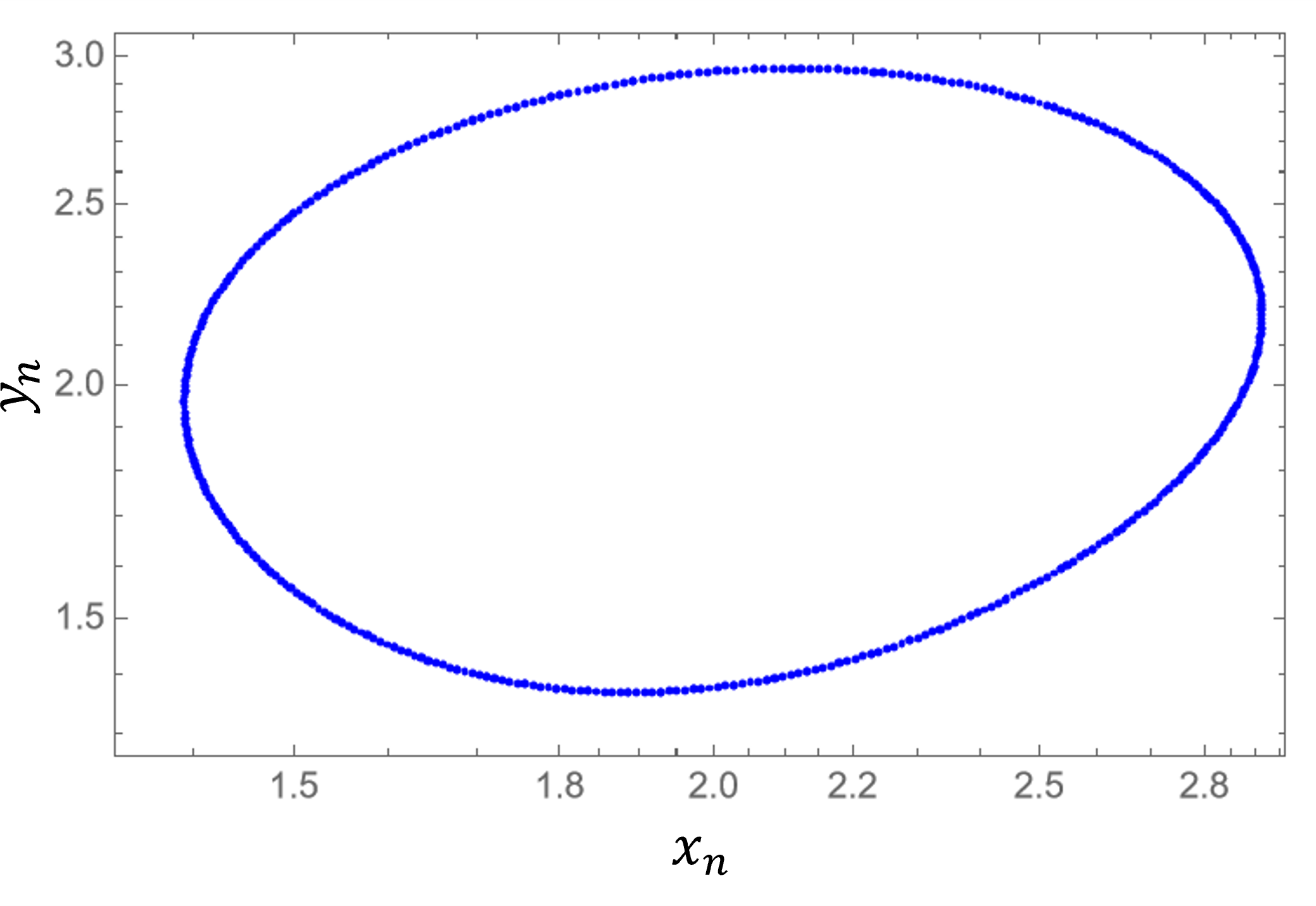
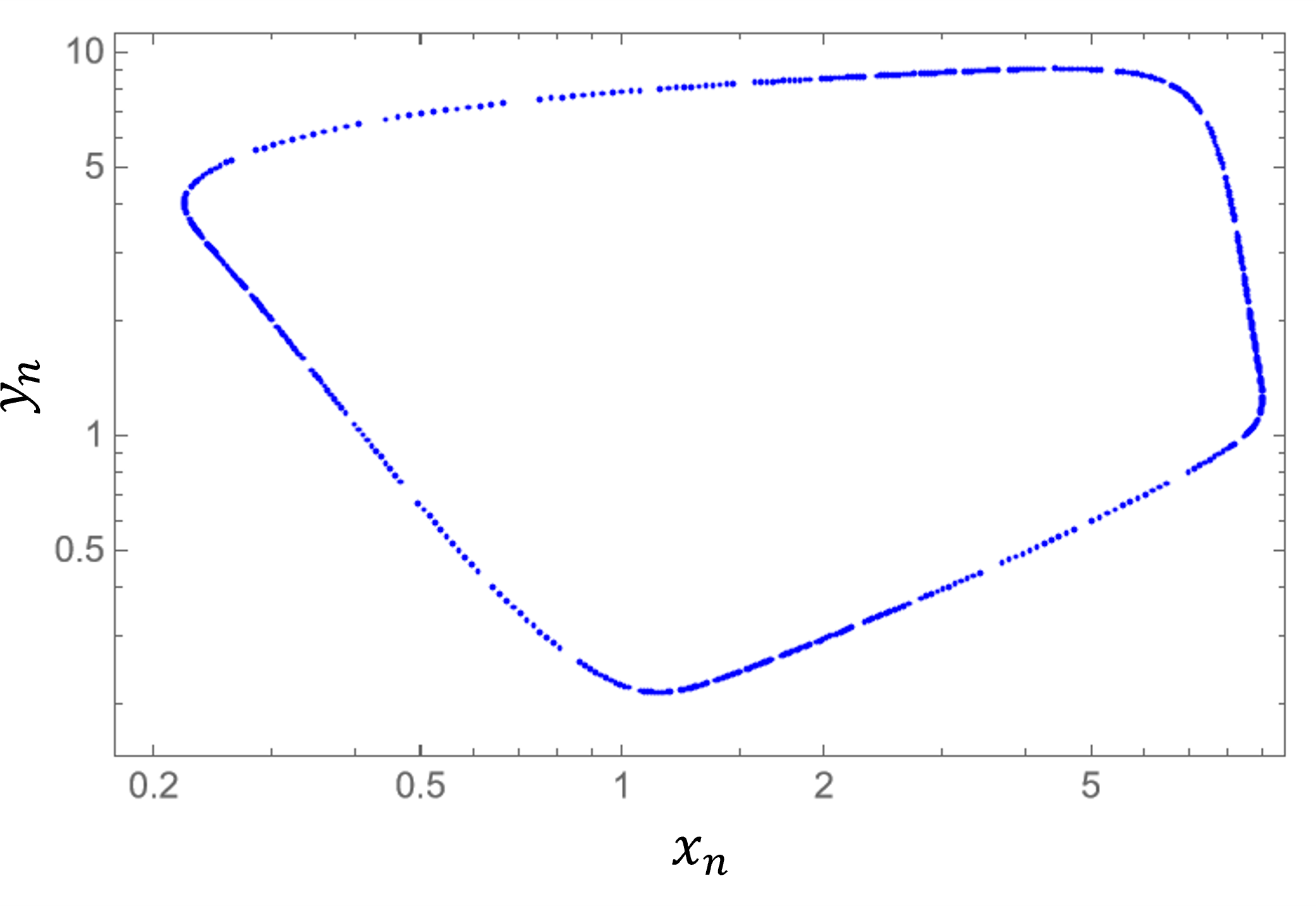
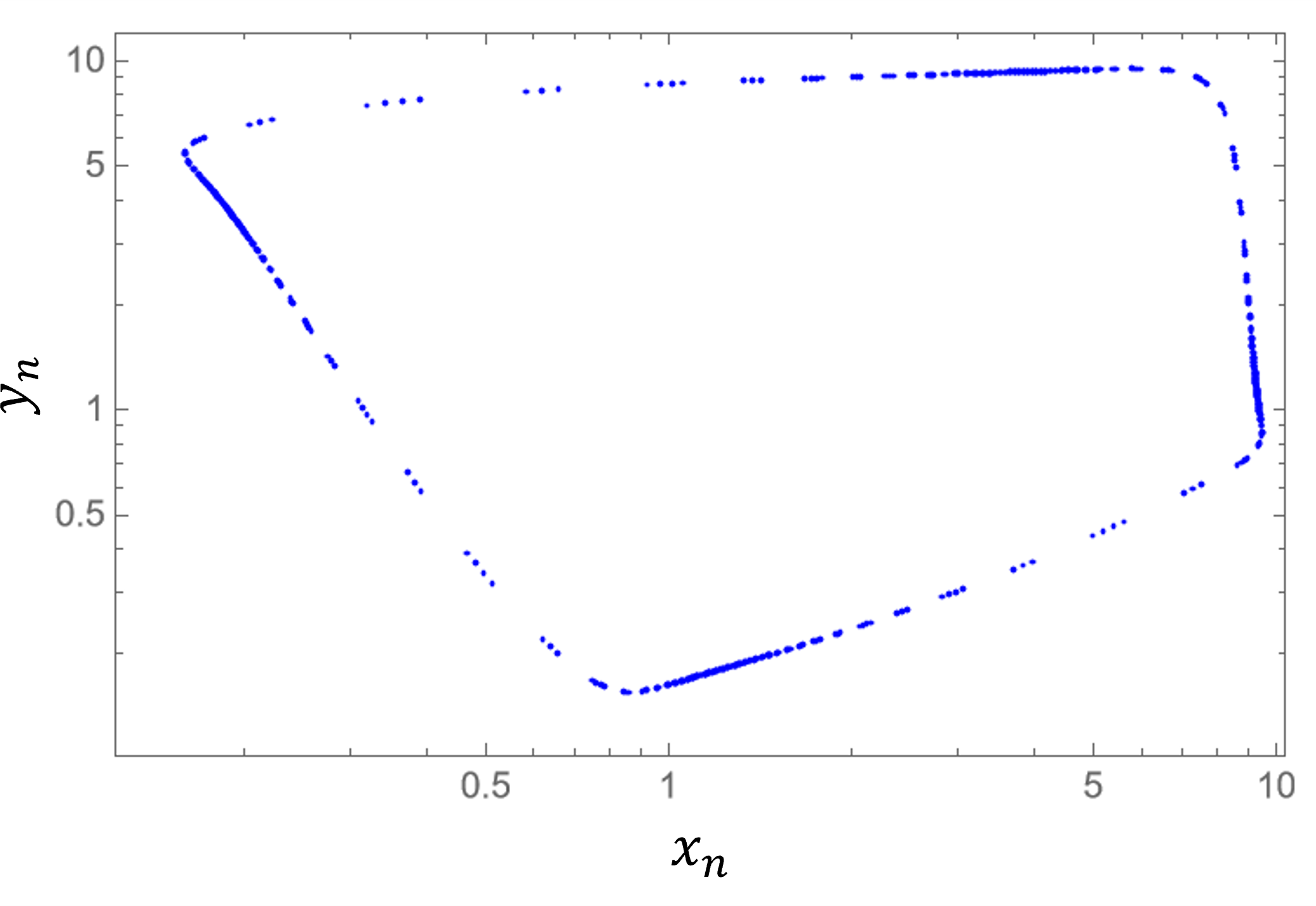
τ = 12 and (b) τ = 20. Since γ = 55 = 18*.*333 *. . .* for *m* = 2 and *b* = 10, (*xn, yn*) converges to (*x*¯*, y*¯) for τ = 12 as shown in Fig.2(a). On the other hand, a cyclic solution is obtained around (*x*¯*, y*¯) for τ = 20 as shown in Fig.2(b).

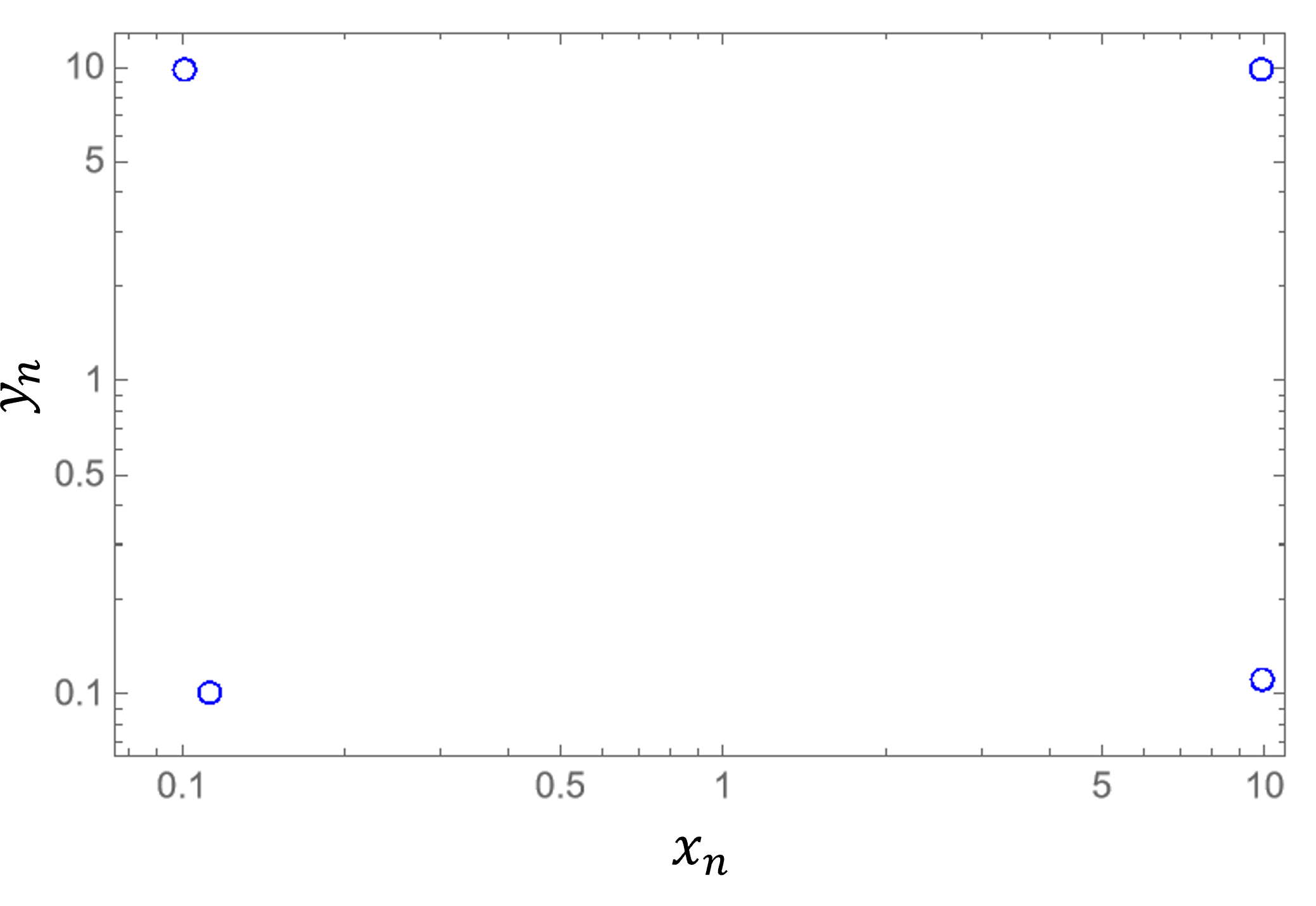
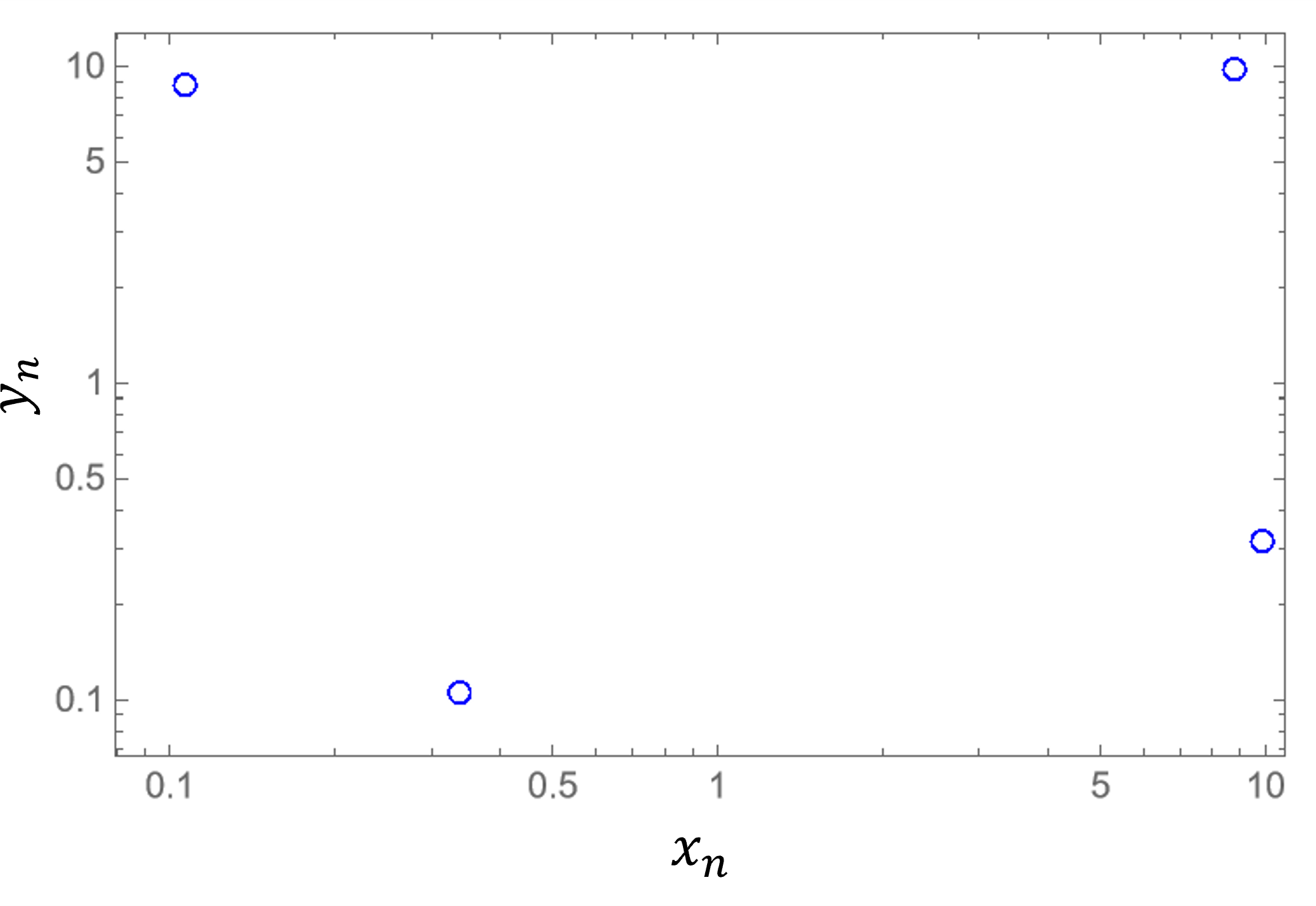
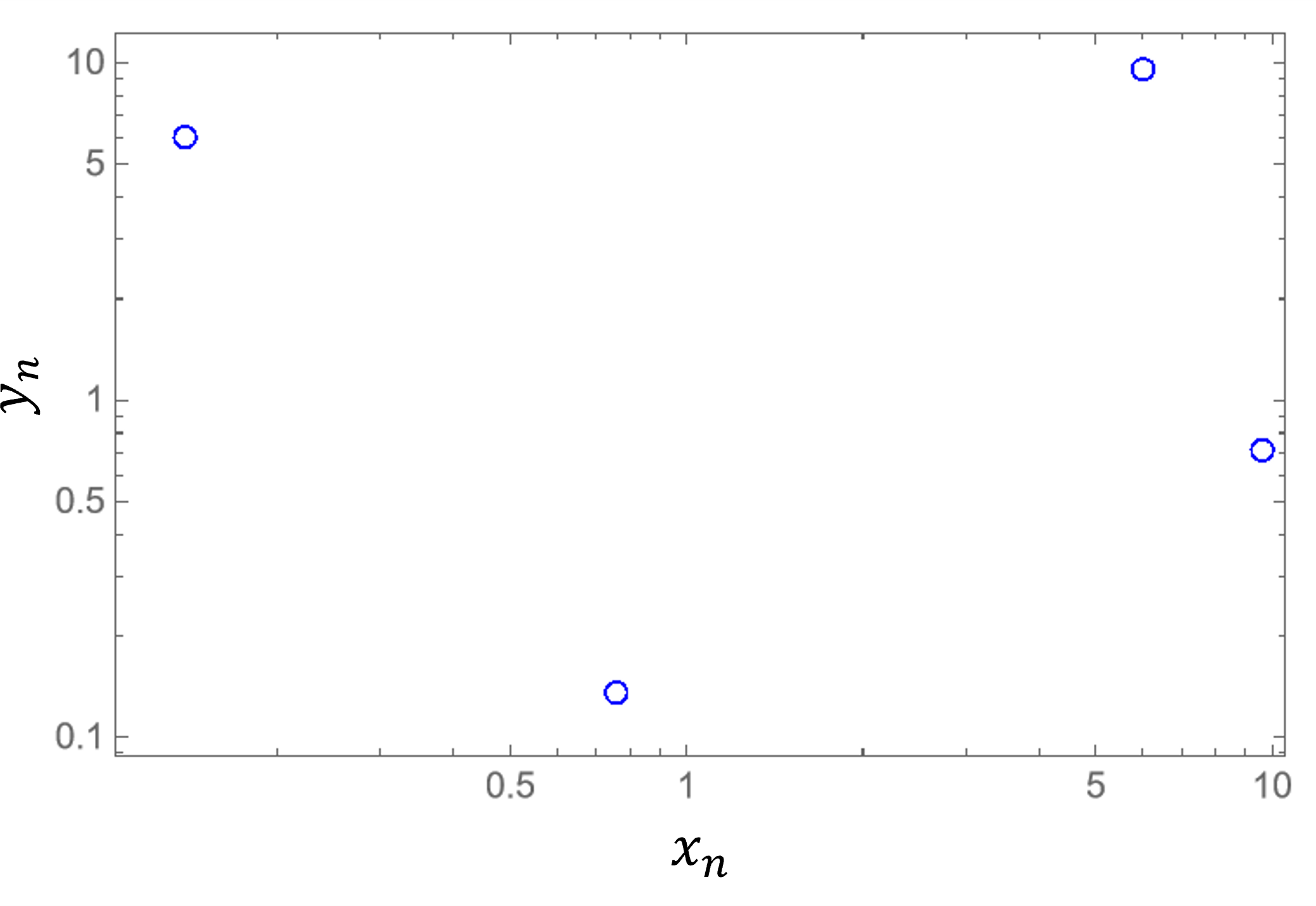
3

For the states in the limit cycle solutions, Fig.3 shows the plot of (*xn, yn*) as a function of τ. From this ﬁgure, we conﬁrm the following features. (i) When τ = 20, the states (*xn, yn*) are broadly distributed as shown in Fig.3(a). (ii) From Fig.3(b)-(c), as τ increases the states tend to become sparsely distributed. (iii) When τ is larger than 200, only

four states exist in the limit cycles as shown in Fig.3(d)-(f). We can consider the limit cycles with the four discrete states as the ultradiscrete limit cycles. Then our result shows that the ultradiscrete limit cycle emerges at a ﬁnite value of τ. Also, it is found that the ultradiscrete limit cycle with only four states is realized for large τ even in the case of τ ∞. Similar emergence of ultradiscrete limit cycles for a large value of τ has already been found in the case of the ultradiscrete Sel’kov model [9].

*→*

(a) τ = 20 (b) τ = 100 (c) τ = 150

(d) τ = 200 (e) τ = 500 (f) τ = 104

**FIGURE 3.** τ-dependence of the states (*xn, yn*) in the limit cycles obtained from eq. (2) for *m* = 2 and *b* = 10.

# MAX-PLUS MODELLING

Here we discuss dynamical properties of the ultradiscrete limit cycle when τ is inﬁnity. In the case of τ ∞, eq.(2) becomes

*→*

*xn*+1 = *yn,*

 1 + *x*

*y*

*b*

(8)

*n*+1 = *m .*

*n*

Performing the variable transformations, *xn* = *eXn/*ε , *yn* = *eYn/*ε , *b* = *eB/*ε , and taking the ultradiscrete limit [7]

lim ε log(*eA/*ε + *eB/*ε + *· · ·*) = max(*A, B,· · ·*)*,*

ε*→*+0

we obtain the max-plus equation,

*Xn*+1 = *Yn,*

{

*Yn*+1 = *B−* max(0*, mXn*)*.*

(9)

Gibo and Ito have derived essentially the same equation as eq.(9) and reported existence of the ultradiscrete limit cycle [4]. Here we report the results of further investigation for the dynamical properties of eq.(9).

When *Xn >* 0, eq.(9) can be rewritten as

(*Xn*+1) = ( 0 1)(*Xn*)+ (0) *,* (10)

*Yn*+1

*−m* 0

*Yn*

*B*

and eq.(10) has the ﬁxed point ***x*¯**I = ( *B ,*  *B* ). The trace and the determinant of the matrix ***A***I = ( 0 1 ) are given

I

I

as Tr***A***

= 0 and det***A***

= *m*

1+*m*

1+*m*

*−m* 0

, respectively. Therefore, the discrete trajectory given by eq.(10) is characterized as spiral

sink (0 *< m <* 1), center (*m* = 1), and spiral source (1 *< m*), respectively [10]. (In all cases, rotations are in the

clockwise direction.) When *Xn <* 0, eq.(9) has the matrix form

(*Xn*+1) = (0 1)(*Xn*)+ (0) *.* (11)

*Yn*+1

0 0

*Yn*

*B*

**TABLE 1.** The time evolution of ***x****n* = (*Xn,Yn*) from the initial condition ***x***0 = (*X*0*,Y*0) for *B <* 0. The signs “+” and “ ” in the table represent the signs of *Xn* and *Yn*.

*−*

* + 1. (b)

*n Xn Yn Xn Yn*

0 + + +

*−*

1 + + *B*

*−*

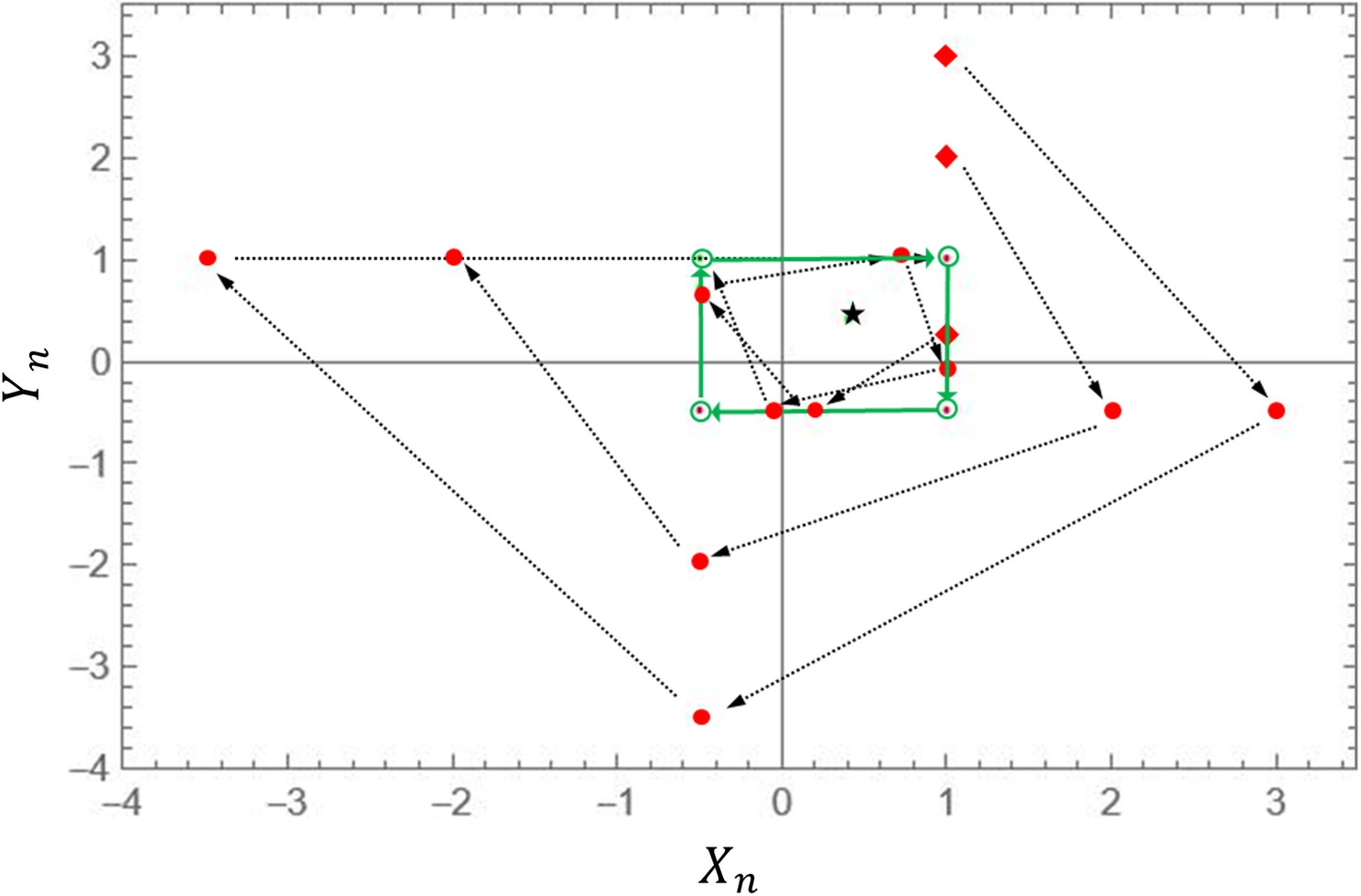
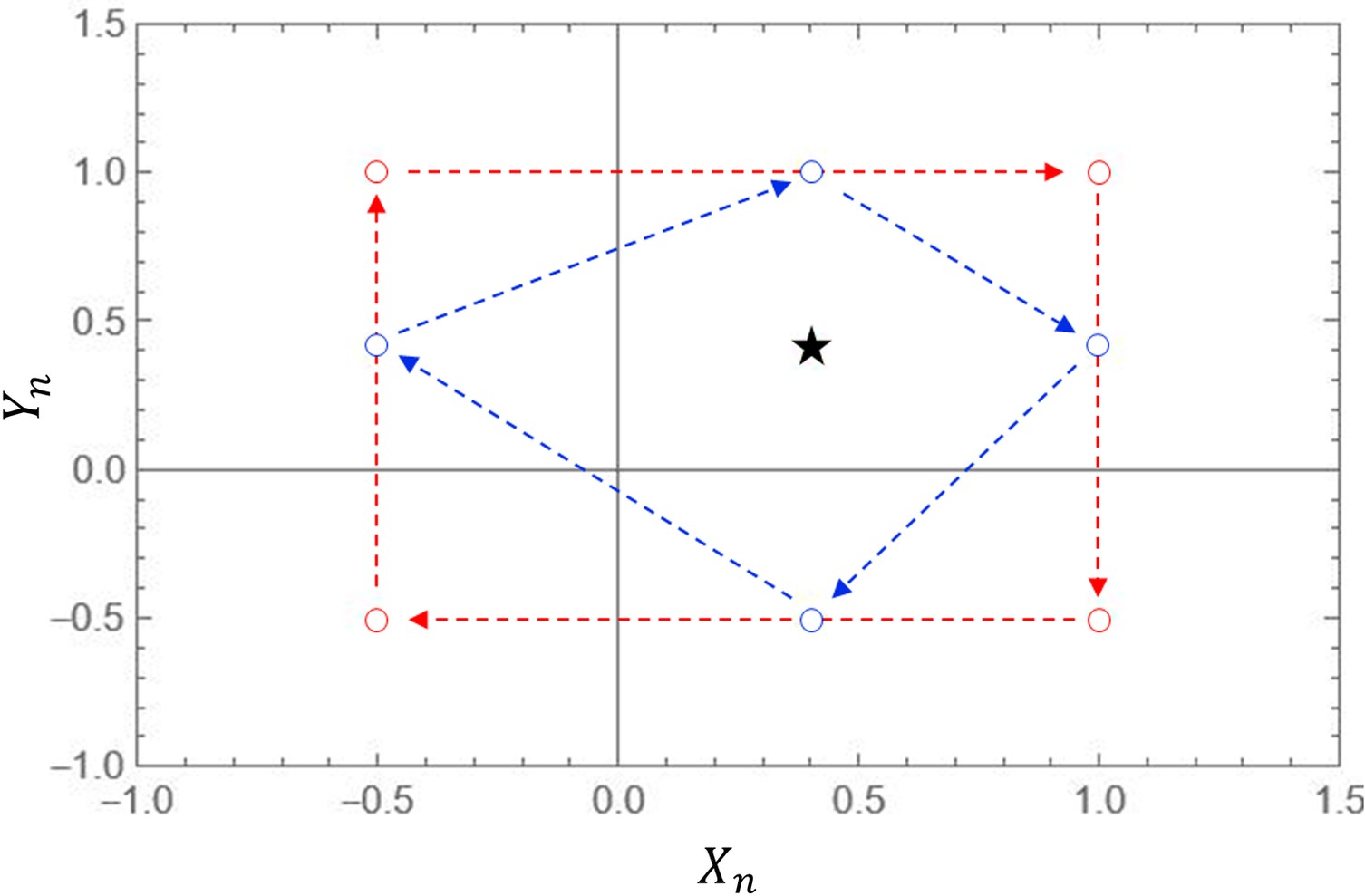
1. *B*

*− − −*

1. *B B*

*− −*

1. *B B B B*



(a) (b)

**FIGURE 4.** (a) The two limit cycles *C* (red circles) and *Cs* (blue circles). We set *B* = 1 and *m* = 1*.*5. (b) Examples of trajectories

starting from three different ﬁlled squares. The trajectories ﬁnally converge into *C* consisting of the four green open circles. The

).

star in each ﬁgure stands for the ﬁxed point ***x*¯***I* = ( 1 *B B*

+*m*

*,* 1

+*m*

Equation (11) has the ﬁxed point ***x*¯**II = (*B, B*), which is a stable node. Then the dynamics of eq.(9) can be characterized by eqs.(10) and (11).

For eqs.(10)-(11), we ﬁrst consider *B <* 0. The time evolution of (*Xn,Yn*) ***x****n* from the initial condition (*X*0*,Y*0)

*≡ ≡*

***x***0 can be summarized dependent on the signs of *X*0 and *Y*0 as shown in Table 1. Thus, ***x*¯**II = (*B, B*) is stable and every

initial state converges to ***x*¯**II at most four iteration steps, for any *m >* 0.

Next we set *B >* 0, where ***x*¯**I = ( 1 *B B* ) is a unique unstable ﬁxed point. When *m >* 1, it is found that there exist

+*m*

*,* 1

+*m*

the two clockwise periodic solutions around ***x*¯**I, *C* and *Cs*, as shown in Fig. 4 (a); they are composed of the following four points:

*C* :(*B, B*)[*≡* ***x****C* ] *→* (*B,* (1 *−m*)*B*) *→* ((1 *−m*)*B,* (1 *−m*)*B*)

0

*→* ((1 *−m*)*B, B*)[*→* ***x****C* ]*,*

0

*Cs* :(*B/*(*m* + 1)*, B*)[*≡* ***x****Cs* ] *→* (*B, B/*(*m* + 1)) *→* (*B/*(*m* + 1)*,* (1 *−m*)*B*)

0

*→* ((1 *−m*)*B, B/*(*m* + 1))[*→* ***x****Cs* ]*.*

0

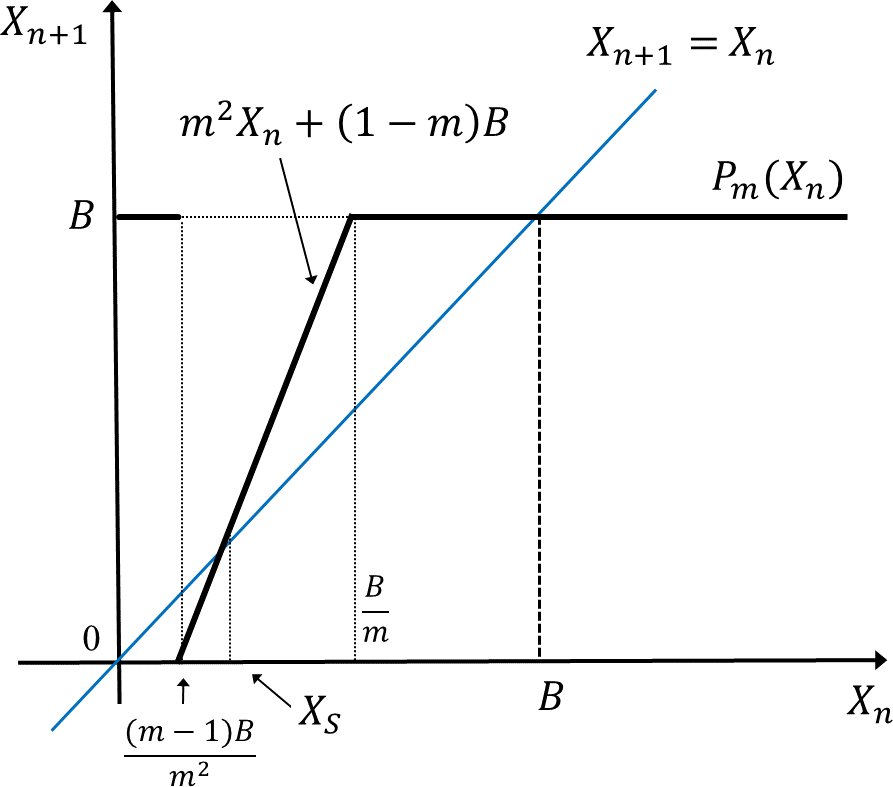
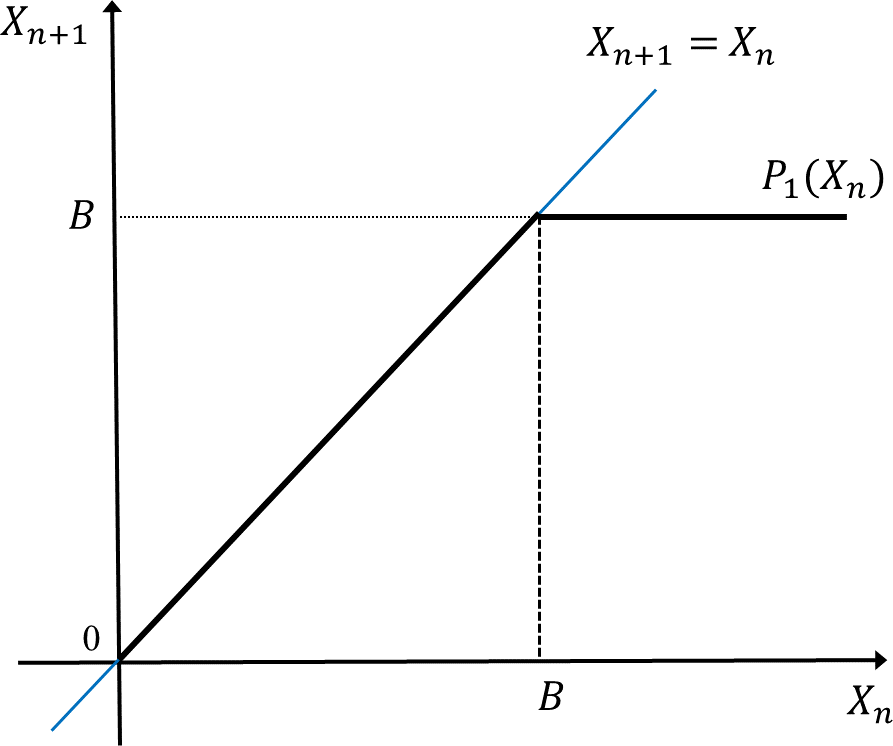
Figure 4 (b) shows trajectories from three different initial conditions; they all ﬁnally converge to *C* .

To grasp the dynamical properties of *C* and *Cs*, we introduce the Poincaré section *L ≡ {*(*X, B*)*, X >* 0*}* [11]. Note that every trajectory possesses a point on the line *L*. In particular, ***x****C* and ***x****Cs* are on *L* and return to themselves. The

0 0

Poincaré map *Pm* on *L* is constructed by considering the next return point *Xn*+1 on *L* for the trajectory from the point

*Xn* on *L*. Actually when *m >* 1, *Pm* is obtained as the one-dimensional piecewise linear discrete dynamical system,

(a) (b)

**FIGURE 5.** The graphs of the Poincaré map *Xn*+1 = *Pm*(*Xn*), eq.(12), for (a) *m >* 1 and (b) *m* = 1. The blue lines show *Xn*+1 = *Xn*.

*Xn*+1 = *Pm*(*Xn*), where

*B* 0 *< Xn* (*m−*1)*B ,*

*m*2

 ( *≤* )

*Pm*(*Xn*) = *m*2*Xn* + (1 *−m*)*B* ((*m−*1)*B < Xn < B* ) *,*

 ( )*B ≤ X .n*

*m*2

*B*

*m*

*m*

(12)

Figure 5 (a) shows the graph of *Xn*+1 = *Pm*(*Xn*) for *m >* 1. This graph intersects the line *Xn*+1 = *Xn* at the two points *Xn* = *Xs B* and *Xn* = *B*, which are found to be unstable and stable, respectively. Therefore, we conclude that *C* (*Cs*) is an attracting (repelling) limit cycle. From the graph of *Pm*, it is also found that the slope of *Pm* tends to 1 when *m* 1 as shown in Fig. 5 (b). Then, a trajectory starting from a point outside of *C* (*m* = 1) converges to *C* (*m* = 1). On the other hand, a trajectory starting from inside of *C* (*m* = 1) becomes a different cycle dependent on the initial states around the ﬁxed point *B , B* as shown in Fig. 6 (a). Therefore, *C* (*m* = 1) is the half-stable limit cycle.

*→*

( )

*m*+1

*≡*

2

2

When *m <* 1, the time evolution of *Yn* for eq.(9) can(be written) as *Yn*+2 = *B −* max(0*, mYn*). It is found from this

*m*+1

*m*+1

time evolution that any initial state ﬁnally converges to

*B , B*

, which is the spiral sink. Therefore, in eq.(9) with

*B >* 0, *m* = 1 becomes the bifurcation point for the Neimark-Sacker bifurcation and the two limit cycles *C* and *Cs*

emerge when *B >* 0 and *m >* 1.

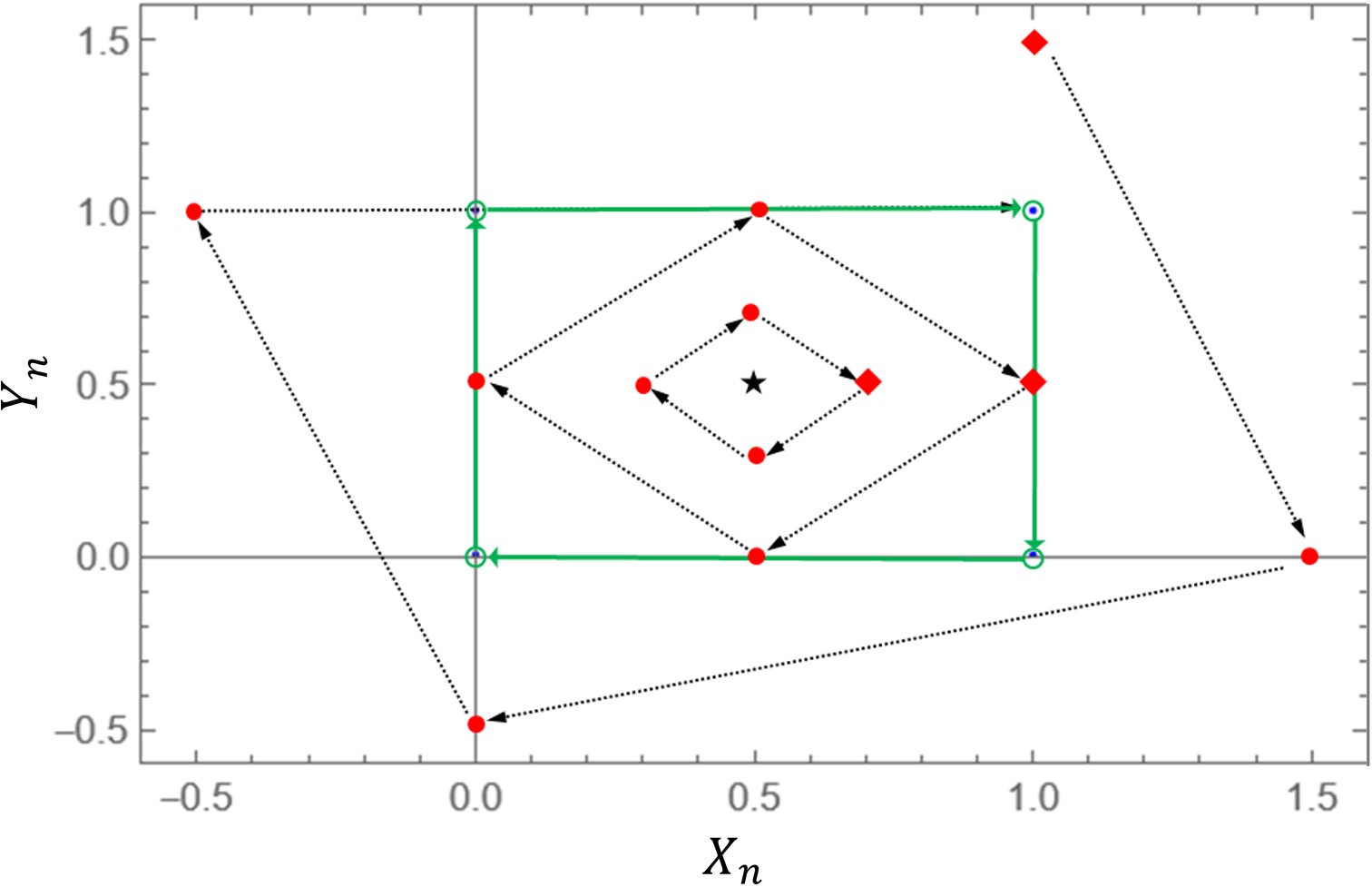
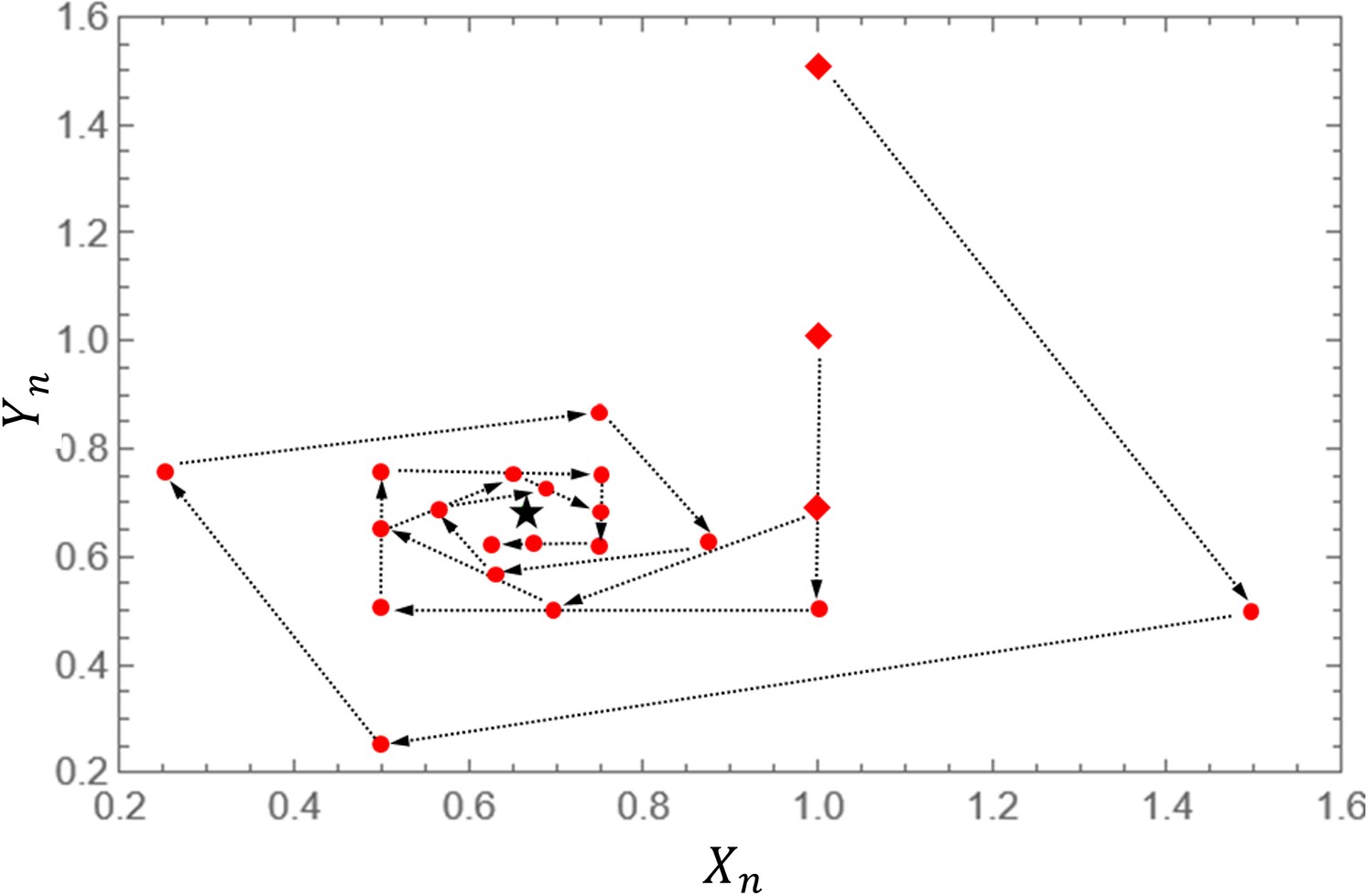
Finally, we brieﬂy comment on the relationship between limit cycle solutions of eqs.(2), (8) and that of eq.(9). Figure 7 shows a comparison of the four limit cycles with different values of τ in eq.(2) and the limit cycle of eq.(8) with that of the max-plus equation, eq.(9). It is found that as τ increases the limit cycle states of the tropically discretized equation approach those of the max-plus equation.

# SUMMARY AND CONCLUSION

We have investigated the dynamical properties of the tropically discretized and the max-plus negative feedback mod- els. For the tropically discretized model, we analytically identify conditions under which the Neimark-Sacker bifur- cation occurs and the limit cycle solutions emerge, in a systematic manner. We ﬁnd the ultradiscrete limit cycle with four states emerges when τ is large even for τ ∞. Furthermore for the ultradiscrete max-plus model, the two limit cycles, *C* and *Cs*, emerge when *B >* 0 and *m >* 1. These limit cycles have been analyzed by using the Poincaré map method, and we ﬁnd that *C* is stable and *Cs* is unstable. We have also conﬁrmed that the limit cycle solutions by the tropically discretized model become close to those by the max-plus model when τ ∞. The dynamical behavior of the limit cycles for the tropically discretized equations as τ increases and the approach to the limit cycle for the max-plus model when τ tends to inﬁnity are also observed in Sel’kov model [11, 12], suggesting that they are general characteristics.

*→*

*→*

(a) (b)

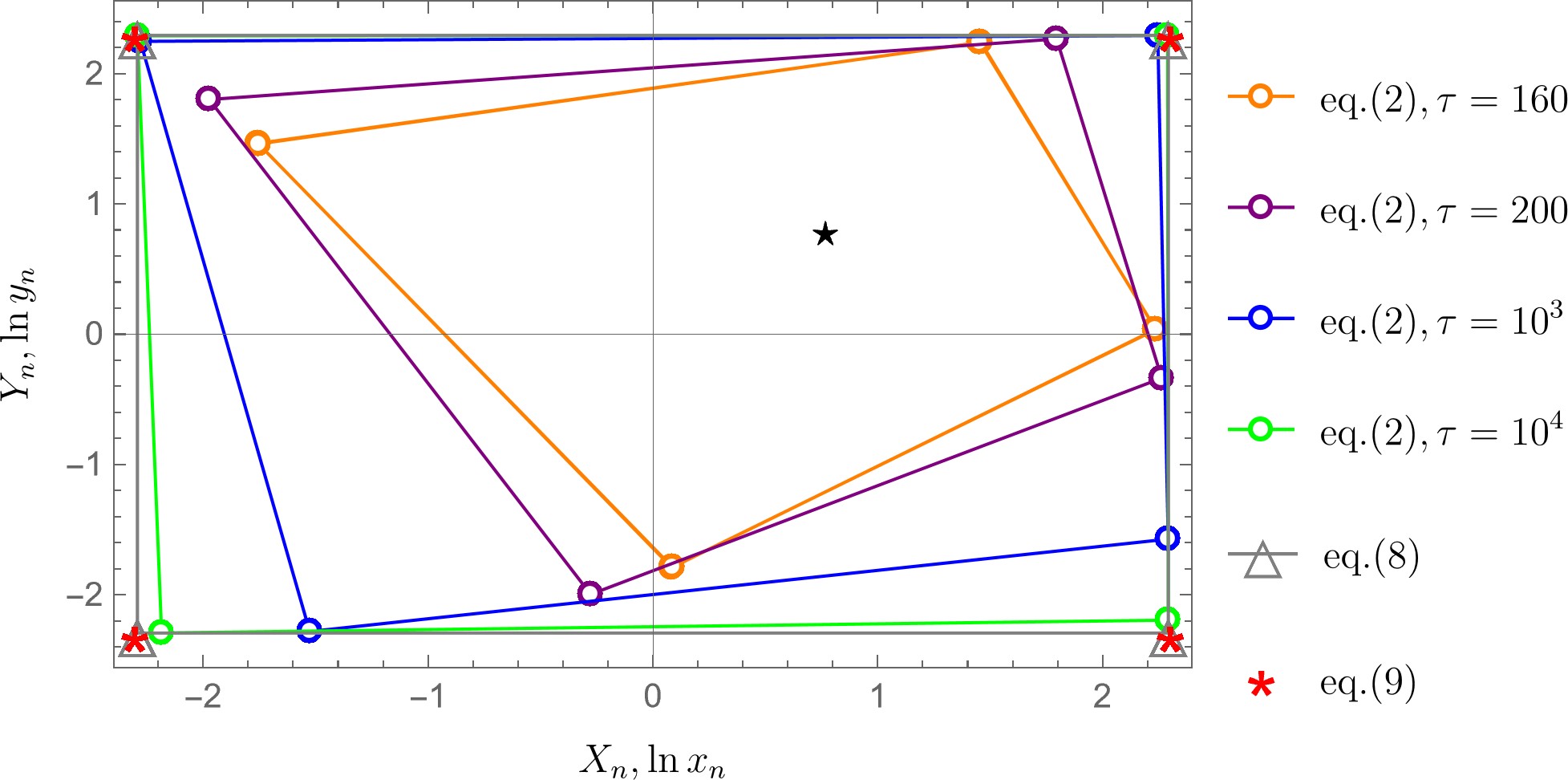
**FIGURE 6.** Trajectories starting from three different ﬁlled squares for (a) *m* = 1 and (b) *m* = 0*.*5. Now we set *B* = 1. The star in

each ﬁgure shows the ﬁxed point ***x*¯***I* = ( 1 *B B* ). The four green open circles in (a) show the ultradiscrete states in *C* (*m* = 1).

+*m*

*,* 1

+*m*



**FIGURE 7.** Circles show limit cycle states with four different values of τ in eq.(2). Triangles show the case of eq.(8). Red asterisks and the black star show the limit cycle states and the ﬁxed point obtained from the max-plus equations, respectively. We set *b* = 10 (*B* = ln *b*).

# ACKNOWLEDGMENTS

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