Replication / ecology

[Re] Chaos in a Three-Species Food Chain

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1 Introduction

One of the most important components of an ecological community is its food web. Early models of population dynamics generally only considered interactions between two species (e.g., Canale[1]; Rosenzweig and MacArthur[2]). However, in nature, food webs wherein only two species influence the behaviour of the network are quite uncommon – most networks are far more complex [3]. Therefore, several researchers asserted that every food web study should involve at least three species in order to capture that complexity [4, 5].

At first, the core interest of food web research was in equilibrium analysis, partly based on the assumption that communities observed in nature represent a stable equilibrium state [6]. However, complex dynamics arise in a system with three or more species, and these are better described as chaos rather than stable equilibrium. The simplest definition of chaos is the extreme sensitivity of a system to its initial conditions [6]. Hastings and Powell[3], who studied chaos in a continuous-time model of a food web including three species, contributed considerably to the significance and understanding of this subject. This study led to many others on food webs dynamics and chaos, which reinforced the importance of chaos in ecological modelling [7, 8].

In this article, we provide a replication of the model from Hastings and Powell[3] using the same equations and parameter values. Replicating a classic study and model like this one is important for many reasons: 1) we can compare the original results with ones obtained using current technologies, ensuring that they can still be reproduced; 2) we can provide a publicly available and reproducible version of the codes that recreate the model. We were able to successfully replicate all figures in the original article using *Julia v1.3.1*. All code used to replicate the original model is available alongside this article (https://github.com/BIO6032/2019_replication_HastingsPowell_1991).

2 Methods

The model formulation used in this paper is the same as in the original publication. Hastings and Powell used a continuous-time model with 14 parameters to represent the three-species food chain, with X, Y, and Z as the numbers of the species at the lowest level of the food chain, of the species that preys upon X, and of the species that preys upon Y, respectively. However, all of their analyses are based on a simpler version of the model with nondimensional measures of time and population sizes, hence 10 parameters only, with x, y and z as the standardized abundances of the three species. We

chose to present this simpler nondimensional version only in this paper, and we invite
readers to consult Hastings and Powell's paper for more details on the original dimen-
sional parameters. Our model's formulation is given as:

$$dx/dt = x(1-x) - f_1(x)y$$
$$dy/dt = f_1(x)y - f_2(y)z - d_1 y \tag{1}$$
$$dz/dt = f_2(y)z - d_2 z$$

with

$$f_i(u) = a_i u/(1 + b_i u) \tag{2}$$

as the functional response.

Parameter values used in this paper are the same as in the original paper (Table 1). How-
ever, initial conditions of the simulations (i.e. the values of x, y and z at the start) were
not given in the original paper. This is an important point, as initial conditions strongly
affect the simulations, particularly in the context of chaotic behaviour. We knew from
Fig.3 of the original paper that $x \approx 0.76$. We tried to approximate y and z by trial and
error, and found $x = 0.76$, $y = 0.16$ and $z = 9.9$ to be an appropriate combination for
most cases. We adapted the initial conditions in some simulations to give the closest
matching graphical result to the original figures. The conditions used are specified in
each figure caption. We consider this a successful replication, despite the impossibility
of using precisely the same initial conditions.

Table 1. Nondimensional parameters and the values used in the simulations

	Values
a_1	5.0
b_1	$2.0 \to 6.2$
a_2	0.1
b_2	2.0
d_1	0.4
d_2	0.01

As noted by Hastings and Powell, numerical integration is the only way to investigate
the global dynamical behaviour of the system. We used *Julia v1.3.1* [9], along with pack-
ages `DifferentialEquations.jl` [10] to compute the numerical integrations and
`Plots.jl` to represent our results. Not knowing the exact algorithm used in the orig-
inal article, we let the `solve()` function select the appropriate algorithm to solve our
differential equations. In our implementation, it selected a composite algorithm com-
bining, amongst others, algorithms Tsit5 and Rosenbrock23. We did note, however, that
setting a specific algorithm such as RK4 sometimes resulted in a similar behaviour for
the system.

To fully replicate key findings of the original paper, we focused on replicating original
figures. Here we describe the steps we took for Fig. 2, 3, 4 and 5 from the original paper.
Note that Fig. 5A refers to Hastings and Powell's figure, while Figure 5a refers to our
reproduction.

Original Fig. 2 illustrates the chaotic behaviour of the system in time for each species.
In order to replicate it, we followed Hastings and Powell's method and let our system run
for 10 000 time steps. We then represented the system's behaviour by plotting the species
nondimensional variables against time (between time steps 5000 and 6500, which elimi-
nates transient behaviour), as well as a three-dimensional phase plot of the three species
(for all time steps). Note that in the case of the three-dimensional phase plot, we had
to set RK4 as the solving algorithm, as well as a relative tolerance of $1e-14$; otherwise,
the representation was unexpectedly different from the original paper. This suggests

that the results for this figure in the original article may have been an artifact. In order to illustrate the dynamics of the model, we created a Graphics Interchange Format (GIF) file of the three-dimensional phase plot that showed the trajectories of x, y and z for the selected parameters (https://github.com/BIO6032/2019_replication_HastingsPowell_1991/blob/master/article/figures/figure2D.gif).

Original Fig. 3 shows the divergence of trajectories caused by a small change in initial conditions when the system exhibits chaotic behaviour. To replicate the figure, we plotted the trajectory for species x between time steps 0 and 500 starting at $x = 0.77$, then changed the initial x value by 0.01 (to $x = 0.78$) and plotted the new trajectory for the same interval on the same figure.

Original Fig. 4 illustrates the appearance of chaotic behaviour as a function of changes in b_1. To replicate it, we constructed a bifurcation diagram for species z where we varied values of b_1 from 2.2 to 6.2 in steps of 0.01. However, our approach was slightly different from the original one. Hastings and Powell's figure is a special type of bifurcation diagram representing only the maxima of z as a function of b_1, rather than all possible values in the system's behaviour as in a typical logistic bifurcation diagram. This raises the problem of correctly identifying the maximum values in the cycling dynamics. Moreover, Hastings and Powell mention removing points resulting from secondary local maxima, but do not provide details on how to identify these points. Hence, we adopted the following method: 1) we let the system run for continuous time steps between 0 and 10 000, then kept the last 1000 solutions to the numerical integration to eliminate transient behaviour (note that these do not occur at time steps between 9000 and 10 000, as the system doesn't necessarily reach a stable solution, and that the exact time steps vary for all values of b_1); 2) we selected the values of z that were greater than both their preceding and following values, which identified local maxima only; and 3) we only kept values that were greater than a given threshold of the cycle's maximal amplitude, in order to remove secondary local maxima. We determined by trial and error that the best threshold was 66%, as it best removed values in apparent second branches of b_1 while keeping the values in the primary branch. We note however that for some values of b_1, the true solutions of the system were unstable and that the system did not reach a cycling behaviour within 10 000 steps. For these values of b_1 (37 values, all between 5.01 and 6.2), we could not present any values of z in our bifurcation diagram.

Hastings and Powell mention in their original paper that they also examined the system's behaviour when varying b_2 instead of b_1, although they do not present the results. We examined the same behaviour by constructing another bifurcation diagram of z for values of b_2 varying from 1.5 to 3.2, using the same method as described above. We set $b_1 = 3.0$, as it is the example used to illustrate chaotic behaviour throughout Hastings and Powell's paper.

Original Fig. 5 illustrates another diagnostic feature of chaos, slopes of high magnitude on a Poincaré map, for values of b_1 where the bifurcation diagram suggests chaotic behaviour. In order to replicate this figure, we solved the system of differential equations using the abovementioned algorithm RK4, as well as a relative tolerance of $1e - 14$. We used $b_1 = 3.0$ and $b_1 = 6.0$, as in the original paper, to replicate its subfigures A-B and C-D, respectively. We defined planes of equation $z = 9.0$ and $z = 3.0$ for those subfigures, respectively, as these intercepted the "handles" of their respective three-dimensional phase plot. We defined those "handles" as in Hastings and Powell, that is as the region in the phase plots where z declines from its maxima to its minima. However, we had to use a tolerance value $\epsilon = 0.05$ in order to identify the points whose distance from the plane was negligible (i.e. their z values ranging between 8.95-9.05 and 2.95-3.05, respectively), since we were not able to find the phase plots' exact interception points. We specified the planes' x and y coordinates to retain only the points that were in the "handles" (subfigures A,B: x and y ranging between 0.95-0.98 and 0.015-0.040, respectively; subfigures C,D: x and y ranging between 0.93-1.00 and 0.00-0.09, respectively). As in the original paper, we recreated the Poincaré sections (subfigures A,C), by plotting y against x coordinates of the retained points, and the Poincaré maps (subfigures B,D), by plotting

[margin note: we use the same ic every time does that make sense?]

[margin note: maybe we can do this for reproduction and then also try the Matlab code that identifies the number of intersections with a plane]

[margin note: i am still not fully sure about the meaning of the branches so point of attention]

[margin note: unstable in what way precisely?]

x coordinates of the retained points $x(n)$ against that of their immediate subsequent retained points $x(n + 1)$. Since Hastings and Powell's Fig. 5E only schematized the plane in the three-dimensional phase plot, we did not reproduce it.

The objective of this paper being to reproduce the main results of the original paper, we did not reproduce its Fig. 1, which was only a schematic representation of the three-species food chain.

3 Results

We were able to replicate Hastings and Powell's main findings, even without knowing their exact algorithm and initial values. First, our time series of the nondimensional variables (Figure 1) presents similar qualitative results as those identified by Hastings and Powell. We observed that the standardized population densities of x, y, and z (Equation 1, Equation 2) oscillate with a period of around 125 time steps. Within a cycle, the population densities of species x and y oscillate while that of species z grows until it reaches its primary local maximum (see definition in methods), at which y and x respectively reach their local minimum and maximum values. z then declines until it reaches its local minimum, forming the "handle" of the teacup (Figure 2), and subsequently beginning a new cycle. The animated figure we produced illustrates this dynamic (see supp. online material). Although slight discrepancies exist between our results and those of Hastings and Powell, they did not seem to strongly influence the abovementioned period length, nor the values of the local maxima and minima of the dimensionless variables. Indeed, x varies approximately from 0.2 to 1.0, y from 0.0 to 0.4, and z from 7.5 to 10.5 (Figure 1), as seen in the original paper.

Second, the time series of x from $t = 0$ to 500 supports the chaotic behaviour of the system, with slightly different initial conditions leading to increasingly different trajectories (Figure 3). The values themselves are almost identical to Hastings and Powell's until $t \approx 250$, at which point they start to diverge, but this behaviour was to be expected without the exact same initial conditions.

Third, our bifurcation diagrams (Figure 4) have the same general shapes as the ones of Hastings and Powell, and are in the same range of z_{max}. We identified most of the local maxima of z found in the original paper for b_1 ranging from 2.2 to 6.2. However, we missed some of them and we found others that were absent in their paper. For instance, for $b_1 = 3.1$, we found multiple local maxima of z, whereas Hastings and Powell had only found a dichotomy of values. The differences are even more apparent in Figure 4c, which represents a detailed portion of Figure 4a. For example, contrary to their findings, we did identify local maxima values for b_1 ranging from 2.30 and 2.35. In other words, we did not observe the significant gap in the bifurcation diagram that they had found.

Our additional bifurcation diagrams, where we varied b_2 instead of b_1 (Figure 6), confirm that chaos occurs for values other than $b_2 = 2.0$. Chaos is apparent for both smaller or greater values. However, while Hastings and Powell reported that chaos was more likely for greater values of b_2, our results highlight that z instead converges to a single value and starts to rapidly approach zero past $b_2 = 2.35$.

Lastly, although Hastings and Powell did not specify the equation of the plane that crosses the trajectories of the phase plot at its "handle", we were able to accurately replicate their Poincaré section and map for $b_1 = 3.0$ (Figure 6 a,b). The main discordance lies in the number of points that cross the plane, and consequently on the apparent smoothness of the plots. On the other hand, it was harder to precisely replicate the Poincaré map for $b_1 = 6.0$ (Figure 6d), even though the corresponding reproduced Poincaré section (Figure 6c) was similar to the one in Hastings and Powell's paper.

4 Discussion

We were able to replicate the chaotic behaviour displayed by Hastings and Powell's model. The resulting behaviour is indeed very sensitive to the initial conditions, showing increasingly diverging trajectories (Figure 3) for slightly different parameters, as well as unending oscillations (Figure 1). The bifurcation diagrams (Figure 4) further confirm the existence of chaos by illustrating the presence of cyclic behaviour for some values and chaotic intervals for others, hence the extreme sensitivity of the system to b_1 values. As for the Poincaré sections (Figure 6 a,c), Hastings and Powell plotted (x,y) coordinates of points of the phase plots that theoretically coincided with the plane in the "handle" of the teacup-shaped diagrams. The Poincaré sections being almost unidimensional, we considered, as explained in the original paper, a single variable within our Poincaré maps (Figure 6 b,d). The slopes of these latter graphs therefore also denoted chaos, as specified by Hastings and Powell.

For Figure 1 and Figure 3, the shape of the cycles and oscillations are similar to Hastings and Powell's. As mentioned earlier, the slight differences are due to the fact that we could not use the exact same initial conditions as the original authors. Such difference is to be expected with a system exhibiting chaotic behaviour and do not alter the conclusions. The difference between our Figure 4 and Hastings and Powell's bifurcation diagram is more intriguing. Admittedly, we could not figure out exactly what Hastings and Powell's method was, and some elements such as identifying maxima values by increasing b_1 first, then by decreasing it, did not make sense to us. Our method should be appropriate, theoretically, to select only values that are primary local maxima, and it did seem to work very well for most b_2 values; yet, the broad range of values that we observed at b_1 = 3.1 instead of a dichotomy is hard to explain. It seems unlikely that the problem could be related to our arbitrary threshold of 66% or to our identification of a local maximum, because we would then either miss some lower values or have too many, not having more in between. The timeseries of all values of z (not presented here) for b_1 = 3.1 confirms that there are "intermediate" maxima values, which should be selected by any proper method. We suggest that the difference might be due to the algorithms used for the numerical integration in our two studies. It is possible that the relationship between the parameters at this point is such that a small difference in algorithm might have an important impact. It is also possible that their algorithm came up with an unstable solution and a system that did not reach cycling behaviour, such as ours for certain values past b_1 = 5.01, but that Hastings and Powell's method selected some values anyways, explaining the behaviour at b_1 = 3.1.

While we also found chaos for values of b_2 other than the default one of 2.0, both smaller or greater, we do not totally agree with Hastings and Powell that "chaos is more likely for larger values of b_2". As Figure 6 shows, chaos can be quite likely for both smaller or larger values. We find important to note, however, that at a certain value of b_2, z converges and starts to crash, thus exhibiting non-chaotic behaviour within a given range of b_1 values. This crash is to be expected when looking at the original dimensional parameters, so it is possible that Hastings and Powell simply chose not to reach this limit in their analyses, as they were only interested in biologically reasonable parameters likely to occur with the three species present.

We believe that our mixed results in attempting to replicate Figure 6 came from the algorithm we used to identify the points that coincided with the plane. For instance, we had to specify a tolerance value (ϵ = 0.05), which defined a region under and above the plane. Although we were able to precisely replicate the Poincaré sections for b_1 = 3.0 (Figure 6a) and 6.0 (Figure 6c), the Poincaré maps need some refinement. For b_1 = 3.0 (Figure 6b), it lacked some points of the phase plots and included others that were closed yet non-coincident with the plane. For b_1 = 6.0 (Figure 6d), the discrepancy was more obvious, and might be due to the more chaotic behaviour of the system under this parameter value, observed for example from the larger width of its "handle" (compare

axis intervals of Figure 6 a,c).

We have succeeded in replicating Hastings and Powell's model and its main findings, as our results confirm chaos arising in a three-species food chain in continuous time. In general, the model, including its equations and parameters, was well described by the authors. The most significant obstacles to reproducibility in Hastings and Powell's paper were the absence of the values of the initial conditions, which have a huge impact on a chaotic system, and the insufficient description of the numerical integration methods. Consequently, there are slight differences between our results and theirs. Furthermore, since we tried to keep our implementation as close as possible to the original one, some steps did rely on arbitrary thresholds (for instance for the primary local maxima or the boundaries of the Poincaré sections and maps). Hence, our replication is somewhat inflexible and possibly could not be applied to a broader range of parameter values. We suggest that an interesting step forward would be to train machine-learning algorithms, such as neural networks, to identify chaotic behaviour and its boundaries, in order to obtain an even better performing implementation.

5 Author Contributions

GD, FB and EB performed the first version of the reproduction and wrote the first version of the manuscript. AMD and TP provided guidance and comments during the reproduction, and revised the manuscript. GD performed the final revisions.

6 Acknowledgments

References

1. R. P. Canale. "An analysis of models describing predator-prey interaction." en. In: **Biotechnology and Bioengineering** 12.3 (May 1970), pp. 353–378.
2. M. L. Rosenzweig and R. H. MacArthur. "Graphical Representation and Stability Conditions of Predator-Prey Interactions." en. In: **The American Naturalist** 97.895 (July 1963), pp. 209–223.
3. A. Hastings and T. Powell. "Chaos in a Three-Species Food Chain." en. In: **Ecology** 72.3 (June 1991), pp. 896–903.
4. P. W. Price, C. E. Bouton, P. Gross, B. A. McPheron, J. N. Thompson, and A. E. Weis. "Interactions Among Three Trophic Levels: Influence of Plants on Interactions Between Insect Herbivores and Natural Enemies." en. In: **Annual Review of Ecology and Systematics** 11.1 (Nov. 1980), pp. 41–65.
5. M. L. Rosenzweig. "Exploitation in Three Trophic Levels." en. In: **The American Naturalist** 107.954 (Mar. 1973), pp. 275–294.
6. A. Hastings, C. L. Hom, S. Ellner, P. Turchin, and H. C. J. Godfray. "Chaos in Ecology: Is Mother Nature a Strange Attractor?" In: **Annual Review of Ecology and Systematics** 24.1 (1993), pp. 1–33.
7. B. Blasius, A. Huppert, and L. Stone. "Complex dynamics and phase synchronization in spatially extended ecological systems." en. In: **Nature** 399.6734 (May 1999), pp. 354–359.
8. S. Gakkhar and A. Singh. "Control of chaos due to additional predator in the Hastings–Powell food chain model." en. In: **Journal of Mathematical Analysis and Applications** 385.1 (Jan. 2012), pp. 423–438.
9. J. Bezanson, A. Edelman, S. Karpinski, and V. B. Shah. "Julia: A Fresh Approach to Numerical Computing." en. In: **SIAM Review** 59.1 (Jan. 2017), pp. 65–98.
10. C. Rackauckas and Q. Nie. "DifferentialEquations.jl – A Performant and Feature-Rich Ecosystem for Solving Differential Equations in Julia." In: **The Journal of Open Research Software** 5.1 (2017). Exported from https://app.dimensions.ai on 2019/05/05.
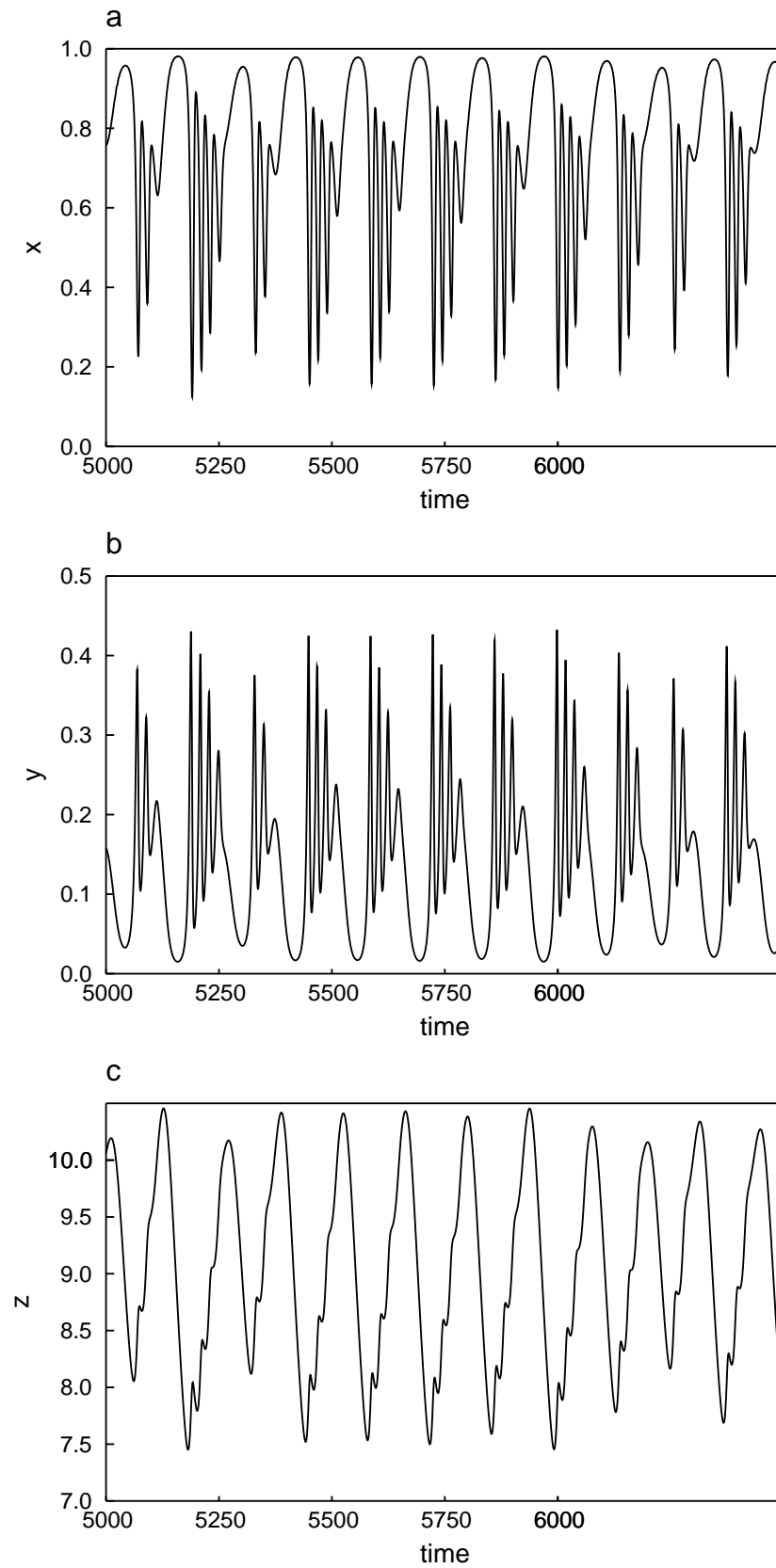
Figure 1. Time series of the nondimensional variables (a) x, (b) y and (c) z, for t ranging from 5000 to 6500 ($x = 0.76$, $y = 0.16$, and $z = 9.9$ as initial conditions). The parameter values used in the simulations are given in Table 1 ($b_1 = 3.0$). This figure replicates Fig. 2 A,B,C of Hastings and Powell[3].
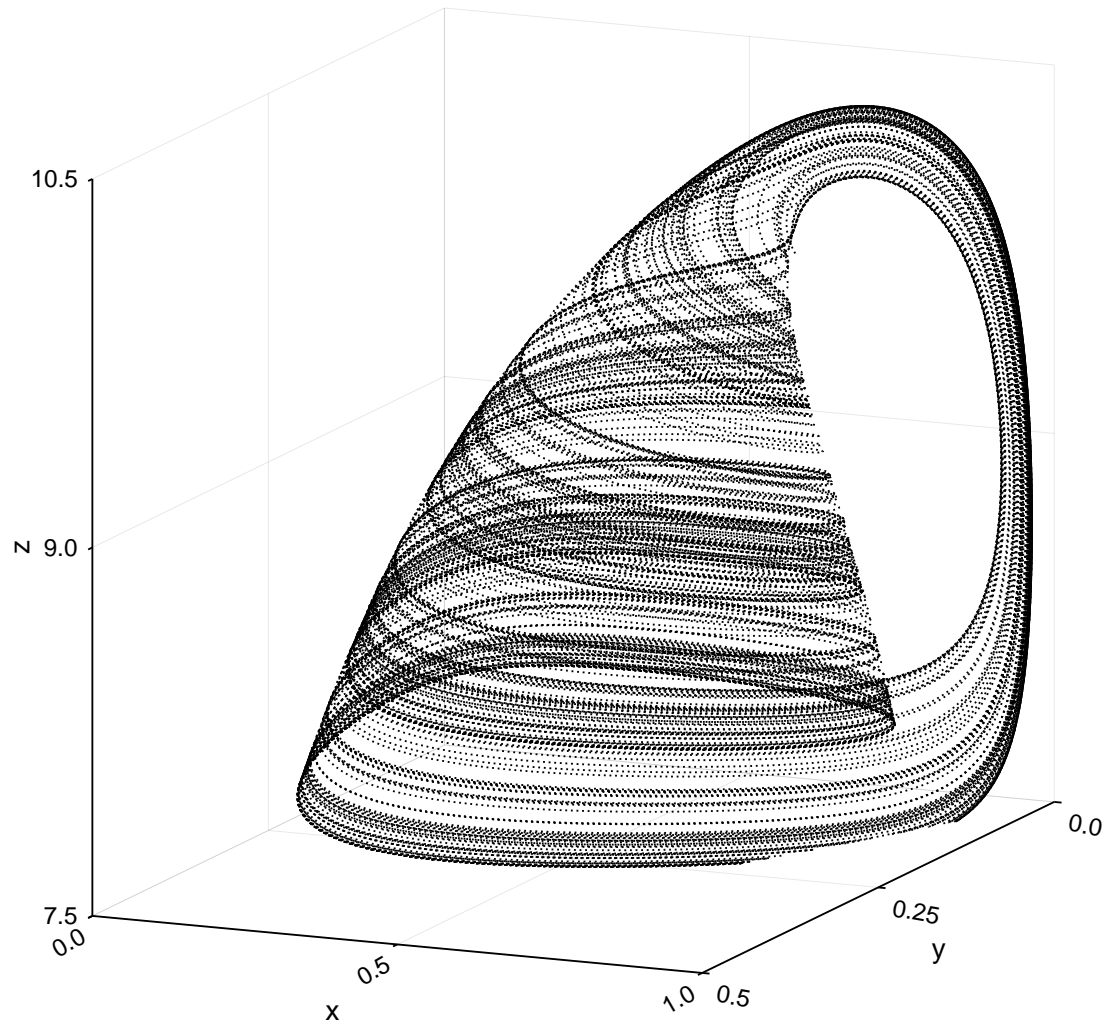
Figure 2. Three-dimensional phase plot of species x, y and z for t ranging from 1 to 10 000 ($x = 0.76$, $y = 0.16$, and $z = 9.9$ as initial conditions). The parameter values used in the simulations are given in Table 1 ($b_1 = 3.0$). This figure replicates Fig. 2D of Hastings and Powell[3].
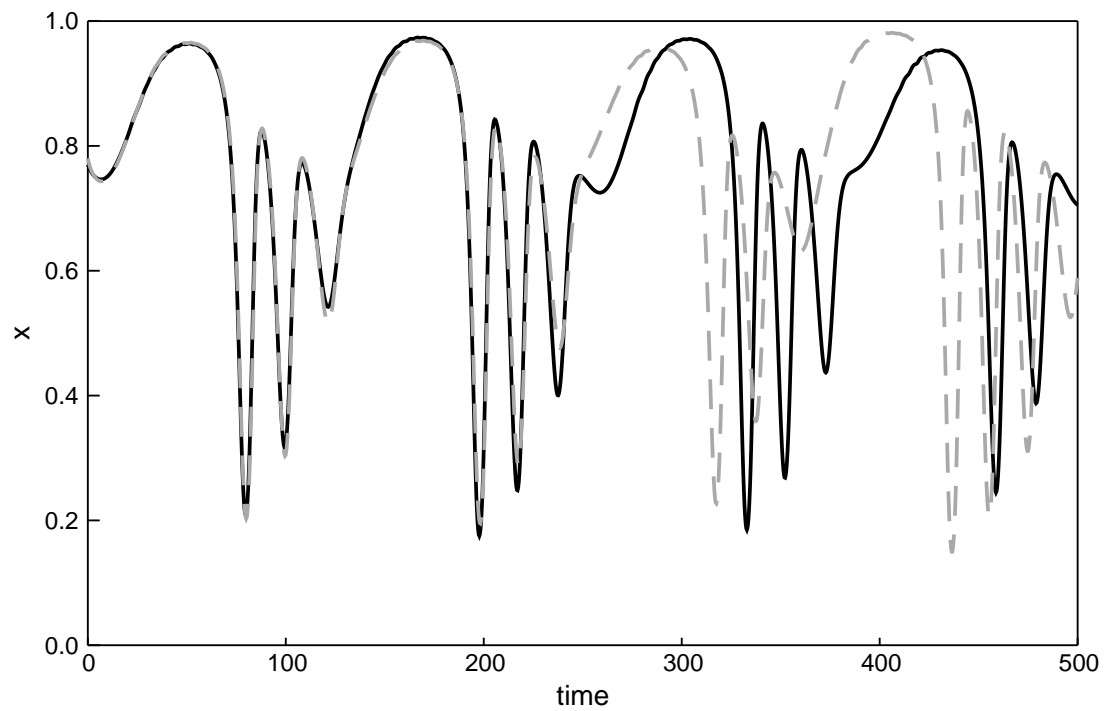
Figure 3. Time series of x, for t ranging from 0 to 500. The solid and dashed lines have $x = 0.77$ and $x = 0.78$ as initial conditions respectively ($y = 0.16$ and $z = 9.9$ as initial conditions are unchanged). The parameter values used in the simulations are given in Table 1 ($b_1 = 3.0$). This figure replicates Fig. 3 of Hastings and Powell[3].
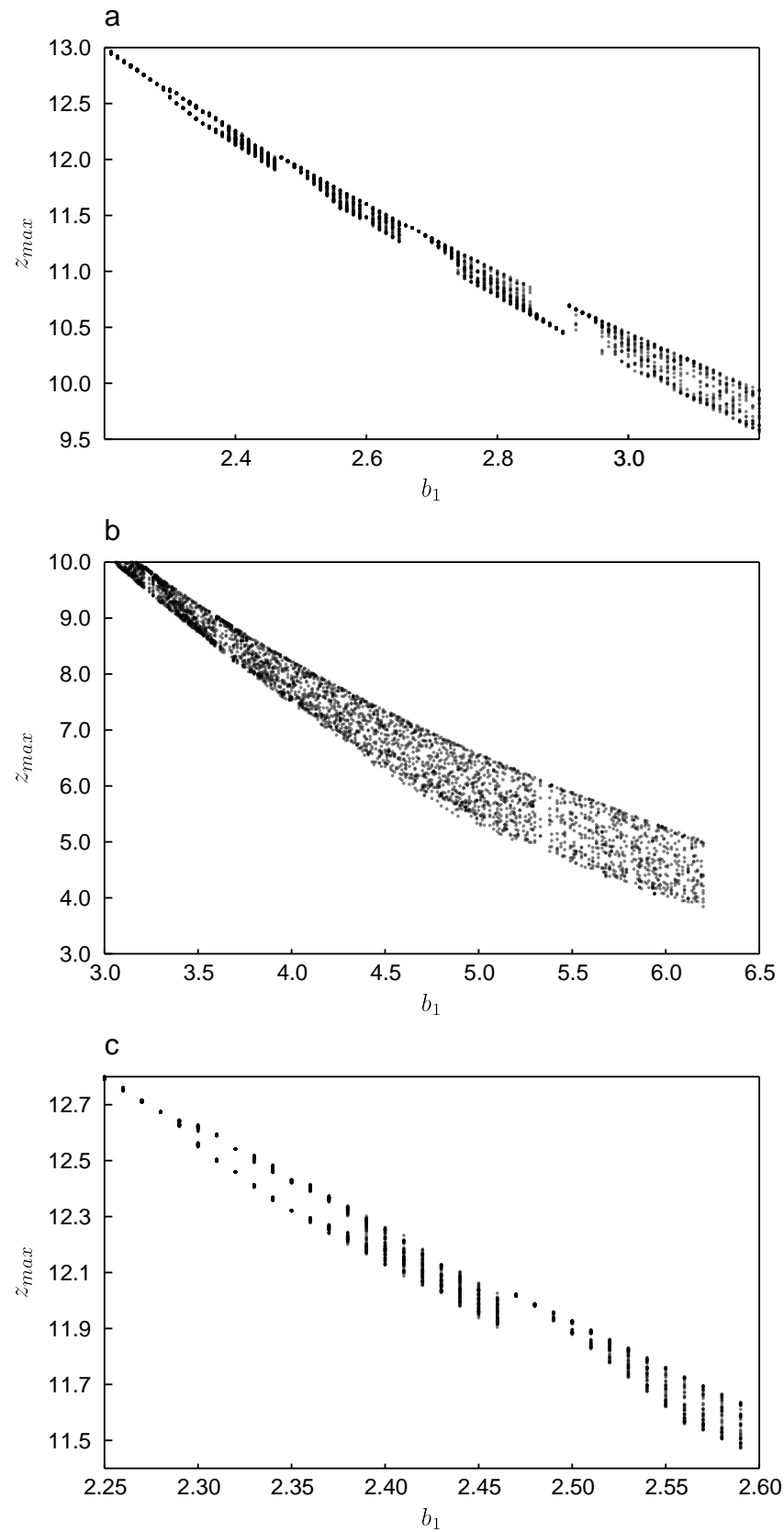
Figure 4. Bifurcation diagrams of the local maxima of z plotted against b_1 ranging from (a) 2.2 to 3.2, (b) 3.0 to 6.2, and (c) 2.25 to 2.6. The other parameter values used in the simulations are given in Table 1 ($x = 0.76$, $y = 0.16$, and $z = 9.9$ as initial conditions). This figure replicates Fig. 4 of Hastings and Powell[3].
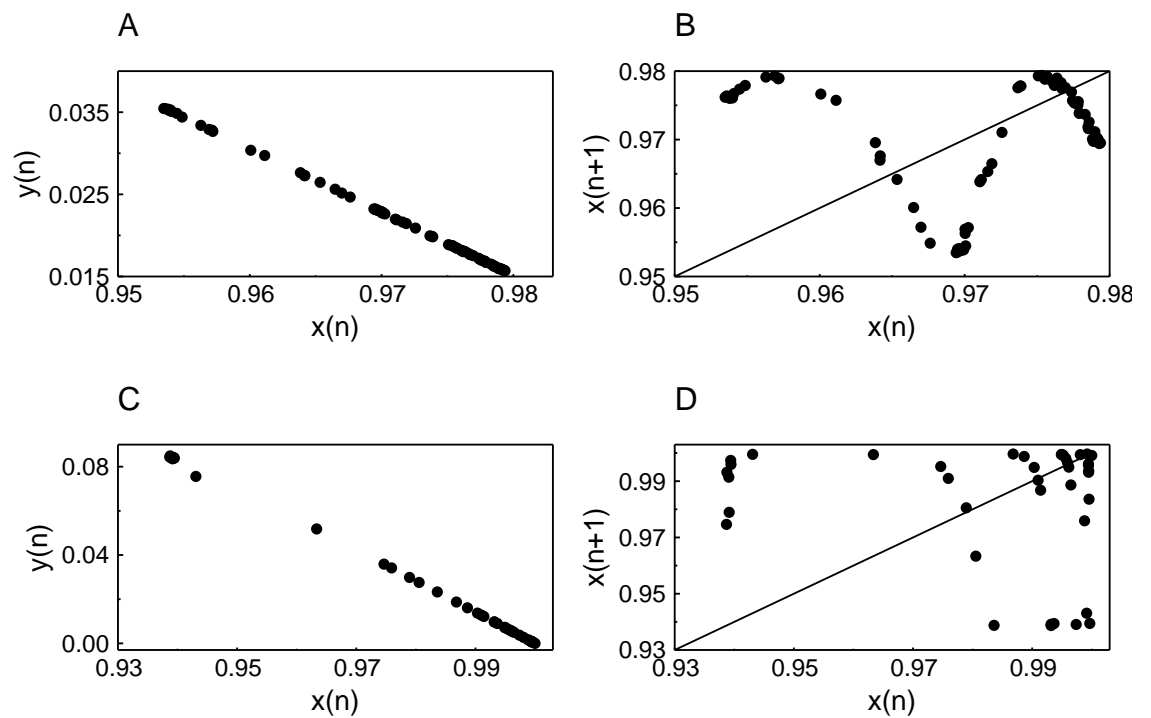
Figure 5. (a) and (b) Poincaré section and map, respectively, for the parameter values given in Table 1 ($b_1 = 3.0$). (c) and (d) Poincaré section and map for the same parameter values except $b_1 = 6.0$. All sets of initial values are unchanged ($x = 0.76$, $y = 0.16$, $z = 9.9$). The solid lines of equation $x(n + 1) = x(n)$ are shown in (b) and (d). This figure replicates Fig. 5 of Hastings and Powell[3], except their Fig. 5E, which is partly reproduced in Figure 2.
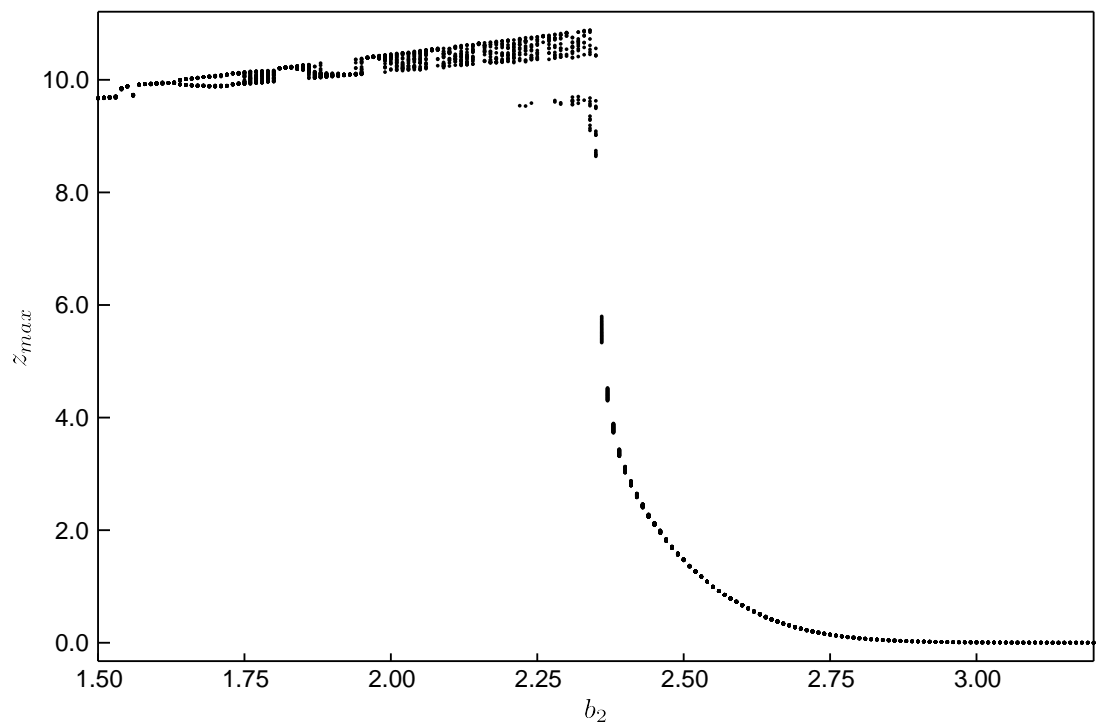
Figure 6. Bifurcation diagrams of the local maxima of z plotted against b_2 ranging from 1.5 to 3.2. The other parameter values used in the simulations are given in Table 1 ($x = 1.0$, $y = 1.0$, and $z = 1.0$ as initial conditions, $b_1 = 3.0$).