Chaos in a Three-Species Food Chain

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Introduction

One of the main aspects of a biological community is its food web. The first models of population dynamics generally considered the interactions between only two species (e.g., Canale [3]; Rosenzweig and MacArthur [8]). However, in nature, food webs of two species only influencing alone the behavior of the ecological network are quite uncommon. Most of the time, they are way more complex and involve more than two species (Hastings and Powell [5]). In that regard, some researchers stated that every food webs study should involve at least three species in order not to lose too much information (Price et al. [7]; Rosenzweig [9]).

At first, the principal interest of food webs researchers was related to equilibrium analysis because they assumed that what was observed in nature was the equilibrium state of dynamics models. Afterwards, different studies declared that chaos played an important role in ecological models. The simplest definition of chaos would be the extreme sensibility of the system to its initial conditions in its resulting behavior (Hastings et al. [6]). This concept has been incorporated in population dynamics during the mid-1970's. Since then, many papers reinforced the importance of chaos in ecology.

Hastings and Powell [5], 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. Considering every aspect of their model, their pioneer study led to a lot of other papers on food webs dynamics and chaos (Brose, Williams, and Martinez [2]; Gakkhar and Singh [4]). Replicating this kind of paper is important for many reasons. For example, we can compare our results, obtained using current technologies, with theirs and make available the code written to recreate the model. In the current paper, we used the same equations and parameters values as Hastings & Powell to replicate their model. We were able to reproduce all the figures in their paper using *Julia v1.1.0*.

Methods

The model formulation used in this paper is the same as the one in the original publication. Hastings & Powell used a 14 parameters model 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 & Powell's paper for more details on the original dimensional parameters. Our model's formulation is given as:

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

with

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

as the functional response.

The parameter values used in this paper are the same as the ones in the original paper (Table 1). However, the 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 element to mention, as the initial conditions strongly affect the simulations, particularly in the context of examining chaotic behavior. We knew from figure 3 of the original paper that $x \approx 0.75$, and we tried to approximate y and z by trial and errors. In order to replicate the original figures as closely as possible, we used different initial conditions in all of our representations to present the closest matching graphical result. The conditions used are specified in each figure. We believe that the use of such different conditions do not alter the results' interpretation.

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

Nondimensional parameters	Values
a_1	5.0
b_1	varied from 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 & Powell, numerical integration is the only way to investigate the global dynamical behavior of the system. We used *Julia version 1.1.0* (Bezanson et al. [1]), along with packages "DifferentialEquations.jl" to compute the numerical integrations, "ParameterizedFunctions.jl" to simplify the parameterized function call, and "Plot.jl" to represent our results. We let the `solve` function select the appropriate algorithm to solve our differential equations, as we believe such a function to be more precise at determining the correct algorithm. In our implementation, it selected a composite algorithm combining, amongst others, algorithms Tsit5 and Rosenbrock23.

In order to replicate figure 2 of the original paper, we followed Hastings & Powell's method and let our system run for 10 000 time steps. We then represented the system's behavior by plotting the species nondimensional variables against time (between time steps 5000 and 6500, which eliminates transient behavior), 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 $1e-14$; if not, the representation was unexpectedly different from the original paper. 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 (in supplement of this paper).

To replicate figure 3 and illustrate the effect of a small change in initial conditions, 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 graph.

To replicate figure 4, 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 had to be slightly different. Hastings & Powell constructed what we consider 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 behavior, as in a typical logistic bifurcation diagram for example. This raised the problem of correctly identifying the maxima values in the cycling dynamic. Moreover, Hastings & Powell mentioned that, in order to clarify their figure, they eliminated points resulting from the appearance of secondary local maxima in the cycling dynamics of species z, but they did not provide details on how they identified such points. Hence, we adopted the following method: 1) we selected the 1000 last solutions for our system between time steps 1 and 10 000, in order to eliminate transient behavior; 2) we selected the values 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 errors 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 behavior 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 & Powell mentioned in their original paper that they also examined the system's behavior when varying b_2 instead of b_1, although they did not present the results. We examined the same behavior 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 fixed $b_1 = 3.0$, as it is the example used to illustrate chaotic behavior throughout Hastings & Powell's paper.

In order to replicate Hastings & Powell's figure 5, 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 & 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* of 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) and (c)), by plotting y against x coordinates of the retained points, and the Poincaré maps (subfigures (b) and (d)), by plotting x coordinates of the retained points ($x(n)$) against that of their immediate subsequent retained points ($x(n+1)$). Since Hastings and Powell's figure 5 (e) 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 figure 1, which was only a schematic representation of the three-species food chain. All the code used to replicate the original paper is available alongside the article.

Results

We were able to replicate Hastings & Powell's main findings, even without knowing their exact algorithm and sets of initial conditions. First, our time series of the nondimensional variables (Fig. 1) present similar patterns as those identified by Hastings and Powell. We observed that the standardized population densities of x, y, and z (Eq. 1, Eq. 2) oscillate in 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 (Fig. 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 & 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 (Fig. 1), as seen in the original paper.

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

Third, our bifurcation diagrams (Fig. 4) have the same general shapes as the ones of Hastings & 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 & Powell had only found a dichotomy of values. The differences are even more apparent in Fig. 4 (c), which represents a detailed portion of Fig. 4 (a). 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 (Fig. 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 & 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 crash 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 $b_1 = 3.0$ (Fig. 4 (a, b)). The main discordance lies in the number of points that cross the plane, and consequently on the apparent smoothness of the graphs. On the contrary, it was harder to precisely replicate the Poincaré map for $b_1 = 6.0$ (Fig. 4 (d)), even though the corresponding reproduced Poincaré section (Fig. 4 (c)) was similar to the one in Hastings & Powell's paper.

Discussion

We were able to replicate the chaotic behaviour displayed by Hastings & Powell's model. The resulting behavior is indeed very sensible to the initial conditions, showing increasingly diverging trajectories (fig 2.) for slightly different parameters, as well as unending oscillations (Fig. 1). The bifurcation diagrams (Fig. 4) further confirm the existence of chaos by illustrating the presence of cyclic behavior for some values and chaotic intervals for others, hence the extreme sensibility of the system to b_1 values. As for the Poincaré sections (Fig. 4 (a, c)), Hastings & 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 (Fig. 4 (b, d)). The slopes of these latter graphs therefore also denoted chaos, as specified by Hastings & Powell.

For Fig. 1 and Fig. 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 surely did not use the exact same initial conditions as the original authors. Such difference is to be expected with a system exhibiting chaotic behavior and do not alter the results interpretation.

The difference between our Fig. 4 and Hastings & Powell's bifurcation diagram is more intriguing. Admittedly, we could not figure out exactly what Hastings & 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 be either missing some lower values or having 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 behavior, such as ours for certain values past $b_1 = 5.01$, but that Hastings & Powell's method selected some values anyways, explaining the behavior 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 & Powell that "chaos is more likely for larger values of b_2". As Fig. 6, 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 behavior 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 & 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 Fig. 4 came from the algorithm we used to identify the points that coincided with the plane. For instance, we had to specify a tolerance value (*epsilon*), which defined a region under and above the plane. Although we were able to precisely replicate the Poincaré sections for $b_1 = 3.0$ (Fig. 4 (a)) and 6.0 (Fig. 4 (c)), the Poincaré maps need some refinement. For $b_1 = 3.0$ (Fig. 4 (b)), it lacked some points of the phase plots and included others that were closed yet non-coincident with the plane. For $b_1 = 6.0$ (Fig. 4 (d)), the discrepancy was more obvious, and might be due to the more chaotic behavior of the system under this parameter, observed for example from the larger width of its "handle" (compare axis intervals of Fig. 4 (a, c)). We are still working on improving our algorithms to adequately replicate Hastings & Powell's Poincaré maps.

We have succeeded in replicating Hastings & 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 flaws of Hastings & Powell's paper in terms of replication were the absence of the values of the initial conditions, which have a huge impact on a chaotic system, and the insufficient description of certain 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 Poincaré sections and maps boundaries). Hence, our replication is somewhat not very flexible 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 behavior and its boundaries, in order to obtain an even better performing implementation.

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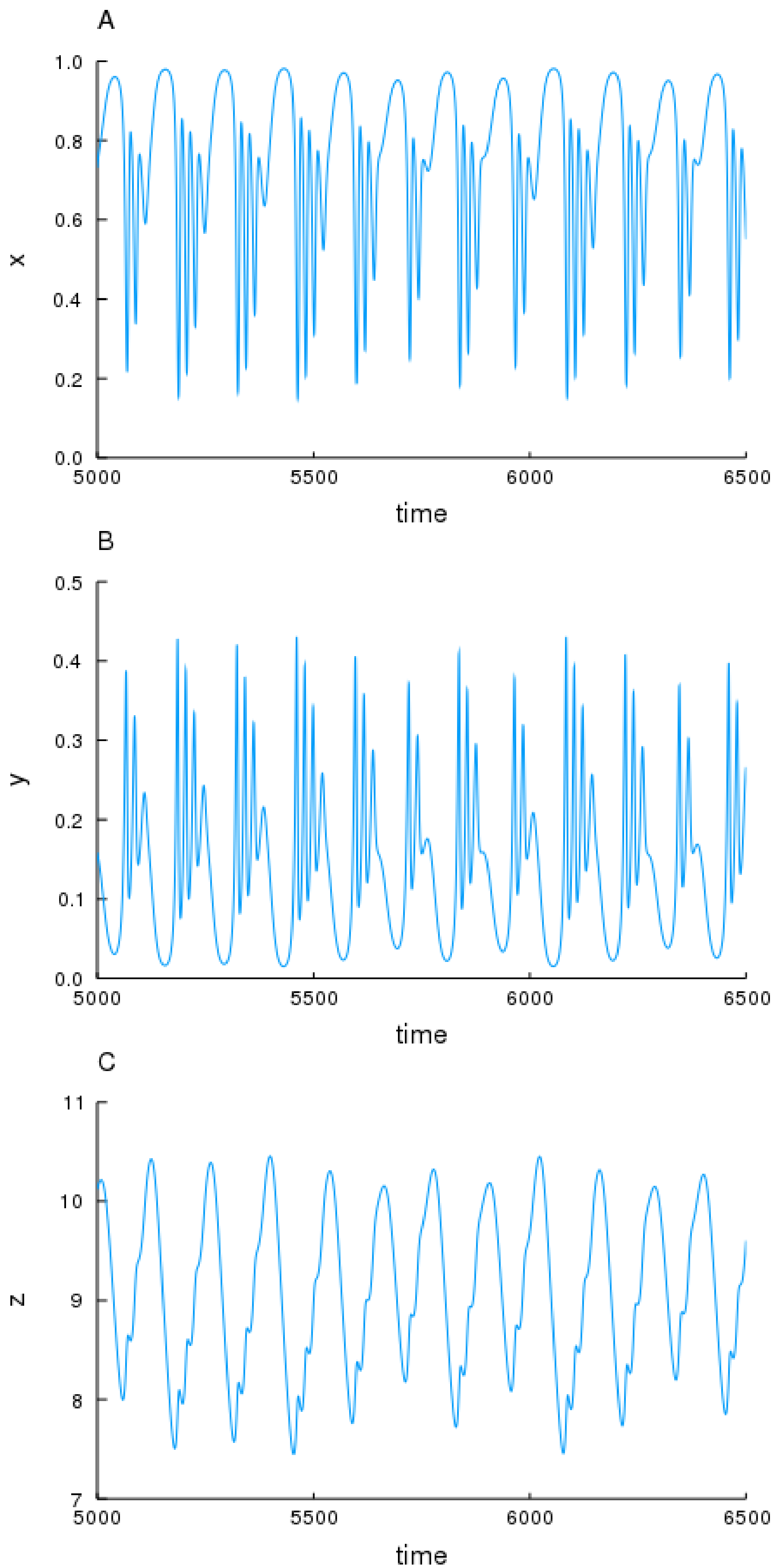

Figure 1: Time series of the nondimensional variables (a) x, (b) y and (c) z, for t ranging from 5000 to 6500 ($x = 1.0$, $y = 1.0$, and $z = 1.0$ as initial conditions). The parameter values used in the simulations are given in Table 1 ($b_1 = 3.0$). This figure replicates fig. 2 (a-b-c) of Hastings & Powell.

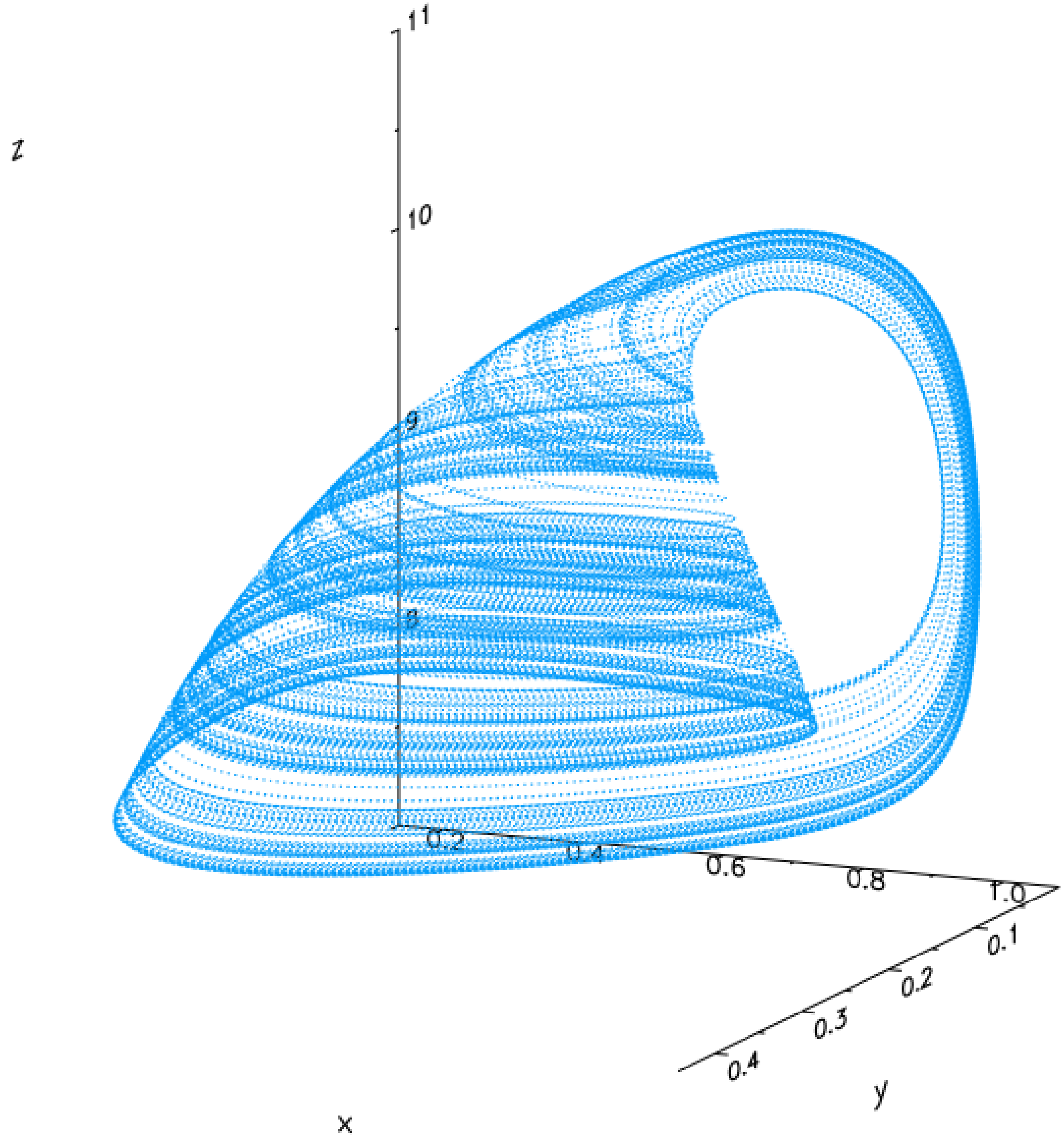

Figure 2: Three-dimensional phase plot of species x, y and z for t ranging from 1 to 10 000 ($x = 0.7$, $y = 0.2$, and $z = 8.0$ as initial conditions). The parameter values used in the simulations are given in Table 1 ($b_1 = 3.0$). This figure replicates fig. 2 (d) of Hastings & Powell.

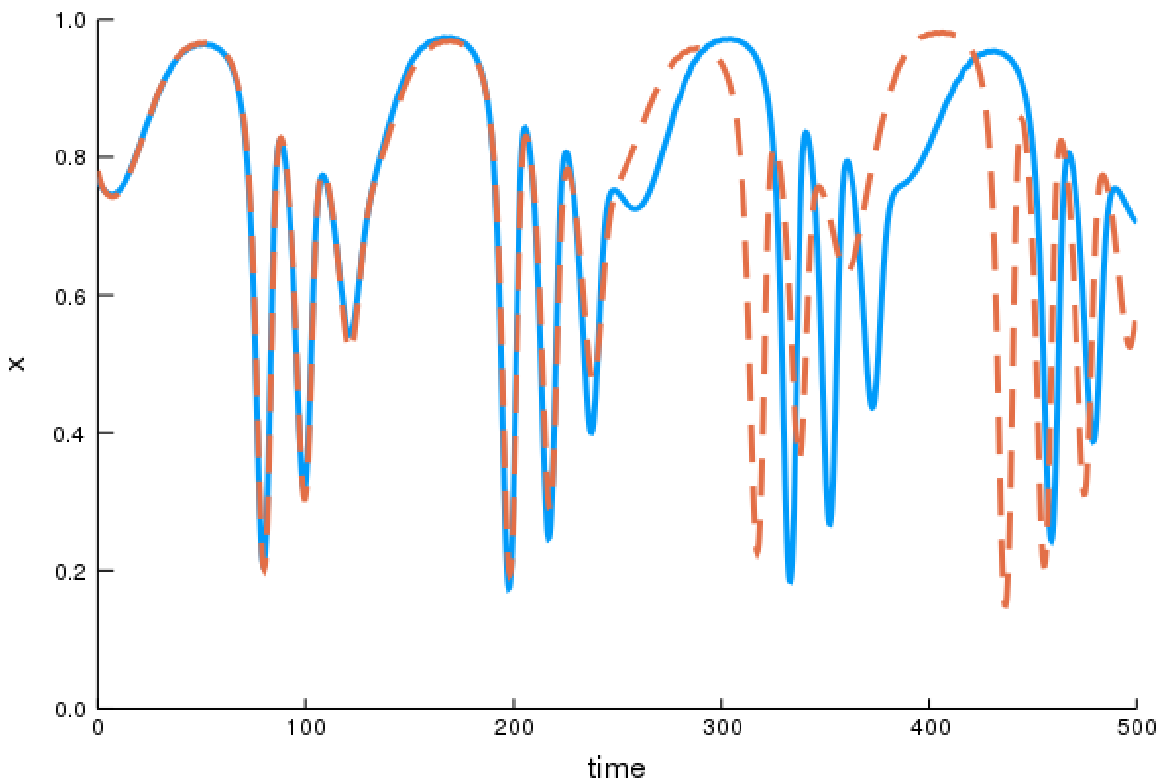

Figure 3: Time series of x, for t ranging from 0 to 500. The solid and dash lines have $x = 0.77$ and $x = 0.78$ as initial conditions respectively ($y = 0.16$ and $z = 9.9$ as initial conditions are unchanged). The parameter values used in the simulations are given in Table 1 ($b_1 = 3.0$). This figure replicates fig. 3 of Hastings & Powell.

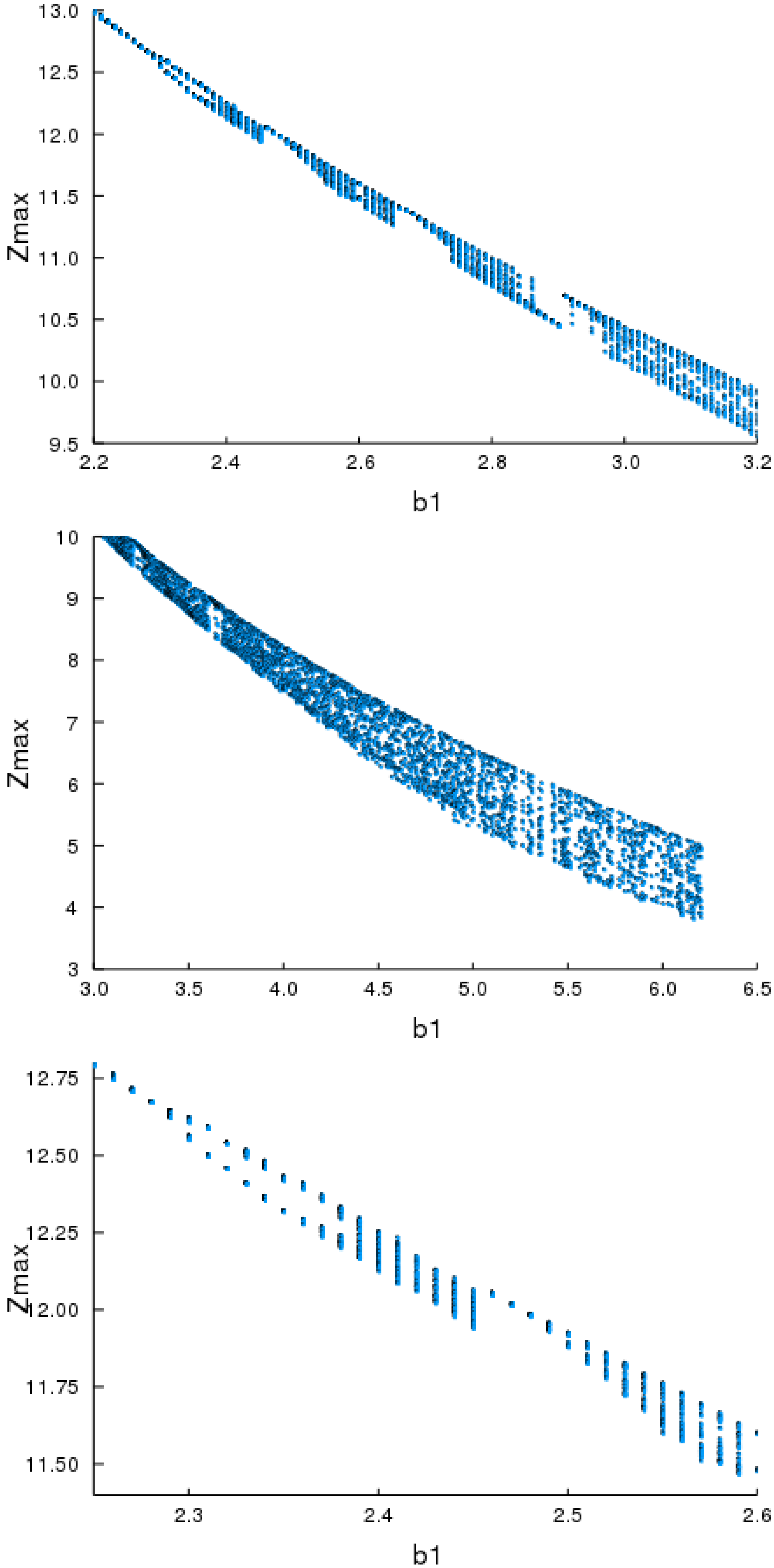

Figure 4: Bifurcation diagrams of the local maxima of z plotted against b_1 ranging from (a) 2.2 to 3.2, (b) 3.0 to 6.2, and (c) 2.25 to 2.6. The other parameter values used in the simulations are given in Table 1 ($x = 1.0$, $y = 1.0$, and $z = 1.0$ as initial conditions). This figure replicates fig. 4 of Hastings & Powell.

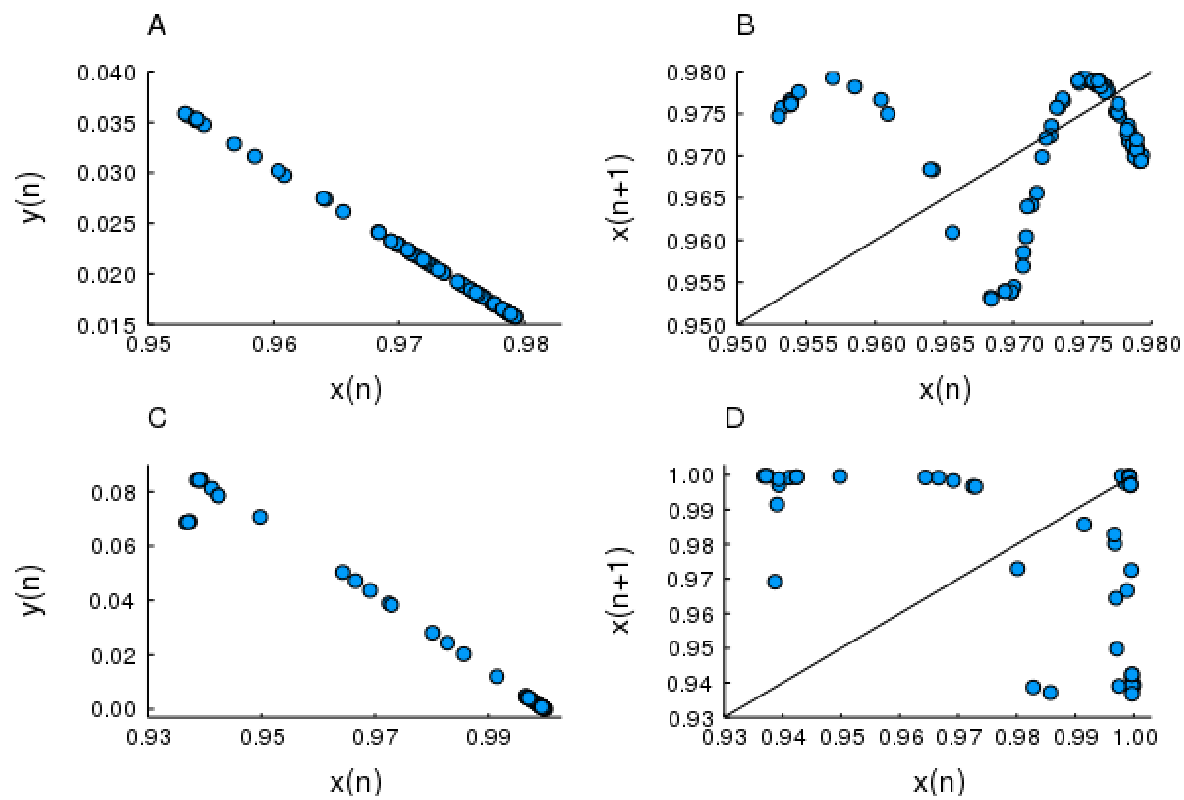

Figure 5: (a) and (b) Poincaré section and map, respectively, for the parameter values given in Table 1 ($b_1 = 3.0$). (c) and (d) Poincaré section and map for the same parameter values except $b_1 = 6.0$. All sets of initial values are unchanged ($x = 0.7$, $y = 0.2$, $z = 8.0$). The solid lines of equation $x(n+1) = x(n)$ are shown in (b) and (d). This figure replicates fig. 5 of Hastings & Powell, except their fig. 5 (e), which is partly reproduced in our fig. 2 (d).

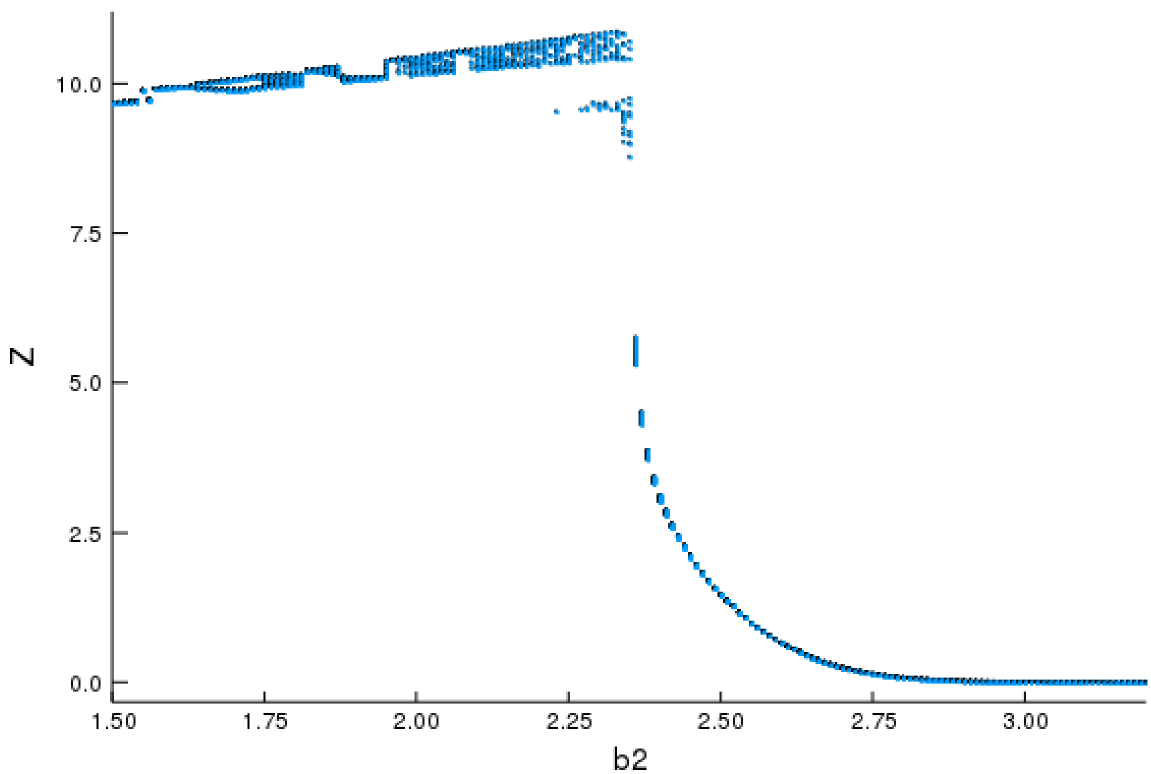

Figure 6: Bifurcation diagrams of the local maxima of z plotted against b_2 ranging from 1.5 to 3.2. The other parameter values used in the simulations are given in Table 1 (x = 1.0, y = 1.0, and z = 1.0 as initial conditions, b_1 = 3.0).