User Manual for the LPA Simulator

Robert A. Desharnais

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Contents

1 Overview

The LPA Simulator is a web site, https://LPAsim.org/, that allows you to run ecological simulations for the discrete-time larva-pupa-adult (LPA) population model. One can look at time series, state space, and bifurcation plots of the model output. The user can vary model parameter values and initial values and examine the effects on the model predictions. Options exist for adding stochasticity, lattice effects, and alternating habitat sizes. Simulation data can be saved to a CSV data file.

Section 2 introduces the LPA mathematical model. Section 3 describes the home, times series, state space, and bifurcation views. Optional elaborations on the LPA model are summarized in section 4. Ways to interactively manipulate the figures are explained in section 5. Section 6 covers exporting simulation data. How to use examples inspired by the book *Complex Population Dynamics: Theory and Data* is covered in section 7. The last two sections are the copyright notice and references.

2 LPA Model

Flour beetles of the genus *Tribolium* have a tradition of use in ecology dating back to 1928 [1]. Populations are cultured in the laboratory and, at regular intervals, the numbers of insects in the various life stages are counted and returned to fresh media. Despite this simple experimental protocol, *Tribolium* have been used to study a variety of phenomena in ecology including species competition and nonlinear population dynamics. Reviews of the ecological research involving *Tribolium* can be found in several papers and books [2, 3, 6, 7, 14, 15].

One of the most compelling reasons for using *Tribolium* in the study of populations is that it provides a fascinating example of nonlinear demographic dynamics. Laboratory populations maintained under constant environmental conditions usually exhibit dramatic fluctuations in density and age structure. These fluctuations are the result of strong behavioral interactions among the life stages—the most important being cannibalism.

The life-stage interactions that drive the dynamics of *Tribolium* populations are summarized in Figure 1. The open arrows represent the life cycle, which, for *T. castaneum* at 34°C, has a duration of approximately 28 days. The single arrows represent the interactions. The arrows labeled c_{ea} and c_{pa}

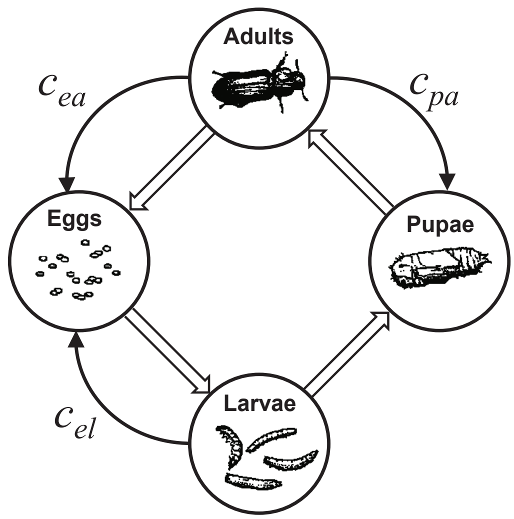


Figure 1: Life cycle and life stage interactions in *Tribolium*. The wide arrows represent the developmental cycle and the narrow arrows represent cannibalism.

represent the cannibalism of eggs and pupae, respectively, by adults. The arrow labeled c_{el} represents the cannibalism of eggs by larvae. The effects of these cannibalistic behaviors on the survival of eggs and pupae can be modeled using negative exponential functions.

The LPA population model describes changes in the numbers of larvae, pupae, and adults as a function of time. The model given by the following three difference equations:

$$\begin{aligned} L_{t+1} &= bA_t \exp\left(-c_{el}L_t - c_{ea}A_t\right) \\ P_{t+1} &= L_t\left(1-\mu_l\right) \\ A_{t+1} &= P_t \exp\left(-c_{pa}A_t\right) + A_t\left(1-\mu_a\right). \end{aligned} \tag{1}$$

The first equation is for the number of feeding larvae, the second is for the number of non-feeding large larvae, pupae and callow adults, and the third is for the number of sexually mature adults. For simplicity, these three stages will be called the larvae, pupae, and adults (LPA). The unit of time is two weeks and is, approximately, the average amount of time spent in the feeding larval stage under experimental conditions. The time unit is also approximately the average duration of the "P-stage." The quantity $b > 0$ is the number of larval recruits per adult per unit of time in the absence of cannibalism. The fractions μ_l and μ_a are the probabilities of mortality for larvae and adults in one time unit. The exponential functions account for the cannibalism of eggs by both larvae and adults and the cannibalism of pupae by adults. The fraction $\exp(-c_{el}L_t - c_{ea}A_t)$ is the probability that an egg is not eaten in the presence of L_t larvae and A_t adults in one time unit. The fraction $\exp(-c_{pa}A_t)$ is the survival probability of a pupa in the presence of A_t adults in one time unit. The model (1) forms the basis of the LPA simulator.

3 LPA Simulator Views

There are four main views in the LPA Simulator (Fig. 2): (a) Home View, (b) Time Series View, (c) State Space View, and (d) Bifurcation Plot View. The time series, state space, and bifurcation plot views have their own parameter values and initial values; however buttons exist to allow you to easily copy and paste values from one view to another. These four views, which are accessible using links on the upper left side of the application, are described in more detail below.

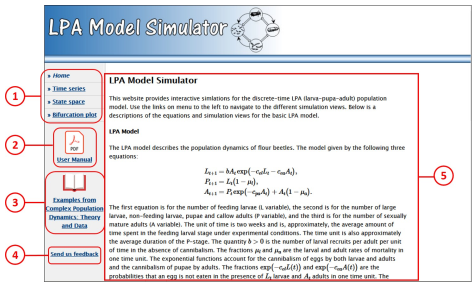
3.1 Home View

The Home View (Fig. 3) provides a brief overview of the LPA model and the LPA Simulator. The different controls and objects in the Home View are described below. The circled numbers in Fig. 3 correspond to the items listed below.

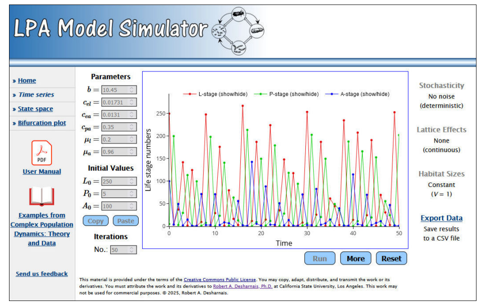
① These links allow you to switch among the main views. The active view is italicized. These links are not specific to the Home View; they always available on the left side of the window.

② This link opens the pdf user manual you are now reading. The manual opens in a new tab in the web browser. This link is available in all four main views.

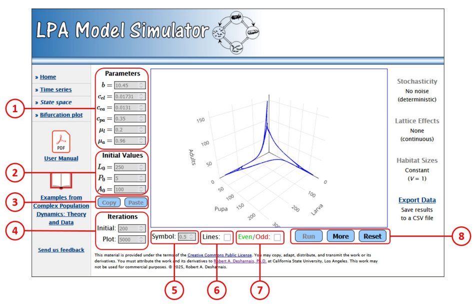
③ This link opens a modal panel within the LPA Simulator that gives users access to the examples tied to the book *Complex Population Dynamics: Theory and Data*. See section 7 for more details. This link is available in all four main views.



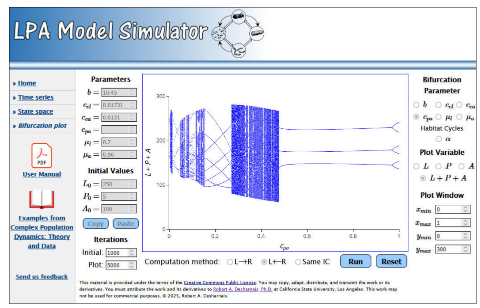
(a) Home View



(b) Time Series View



(c) State Space View



(d) Bifurcation Plot View

Figure 2: The four main views of the LPA Simulator.

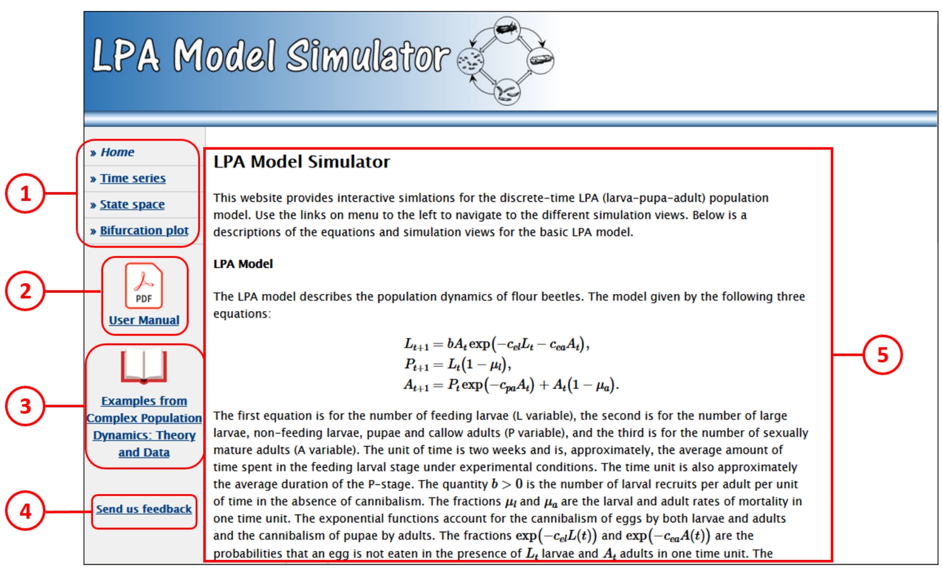


Figure 3: The Home View for the LPA Simulator. See text for an explanation of the numbered items.

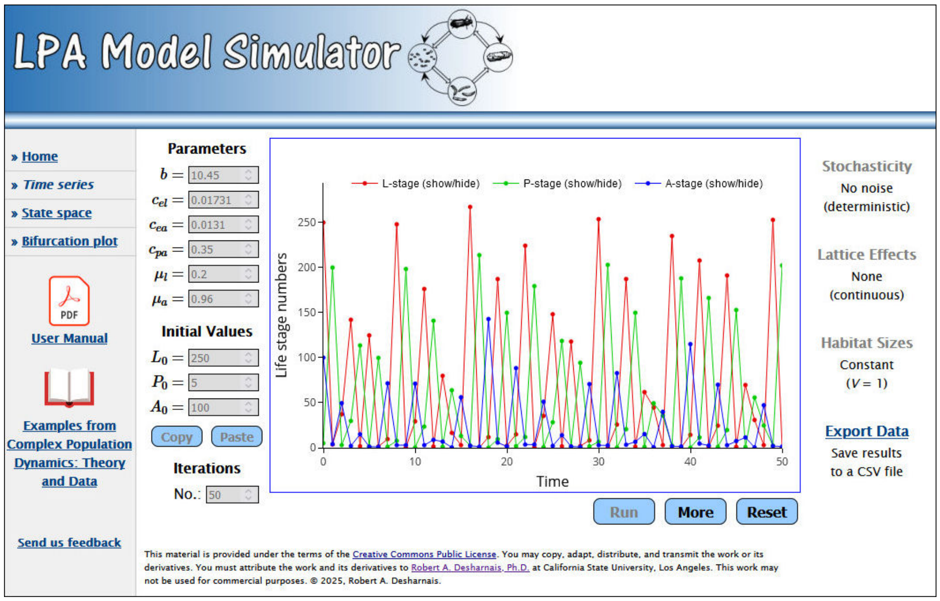


Figure 4: The Time Series View for the LPA Simulator. The default parameter values and initial numbers are from the "hunt for chaos" experiment [4, 10]. See text for an explanation of the numbered items.

④ This link can be used to send feedback on the LPA Simulator via email. This link is available in all four main views.

⑤ This area provides a brief description of the LPA model and the features of the LPA Simulator. The manual you are reading provides more details.

3.2 Time Series View

The Time Series View (Fig. 4) allows the user to run simulations of the LPA model and view the output as time series graphs. The numbers of larvae, pupae, and adults are plotted together. You can set the parameter values and initial values of the simulation. The circled numbers in Fig. 4 correspond to the items listed below.

① These text fields allow you to change the parameter values of the LPA model. Changes only apply to the Time Series View. Each value must be within a specific range; otherwise the parameter value field will be highlighted in red and an error message will appear when you try to run the simulation.

② These text fields allow you to change the initial values of the larva, pupae, and adult life stages. Changes only apply to the Time Series View. Each value must be within a specific range; otherwise the initial value field will be highlighted in red and an error message will appear when you try to run the simulation.

③ These buttons allow you to Copy and Paste the parameter values and initial values among the three simulation views. (Changes made in the any one simulation view do not apply automatically to the other two simulation views.)

④ This text field can be used to change the number of iterations that appear on the x-axis in the time series plot. This number must be an integer in the range from 10 to 200.

⑤ The legend for the time series plot shows the colors of the symbols and lines used to distinguish the plot traces for the three life stages. Clicking on a legend item allows you to hide or show the plot trace.

⑥ These three buttons allow you to control the simulation. The Run button will execute a new simulation and plot the results. The More button will extend the current simulation. The Reset button will clear the plot and allow you to modify the parameter, initial, and iteration values to produce a new simulation.

3.3 State Space View

The State Space View (Fig. 5) allows the user to run simulations of the LPA model and view the output in three-dimensional LPA state space. The axes are the numbers of larvae, pupae, and adults. Each point in state space is produced by one iteration of the LPA model. You can set the parameter values and initial values of the simulation. Options exist for specifying the size of the plotting symbol and connecting the points produced at consecutive times with lines.

State space plots are often used to examine the geometry of the *model attractors*. Attractors are the sets of points that trajectories of the model

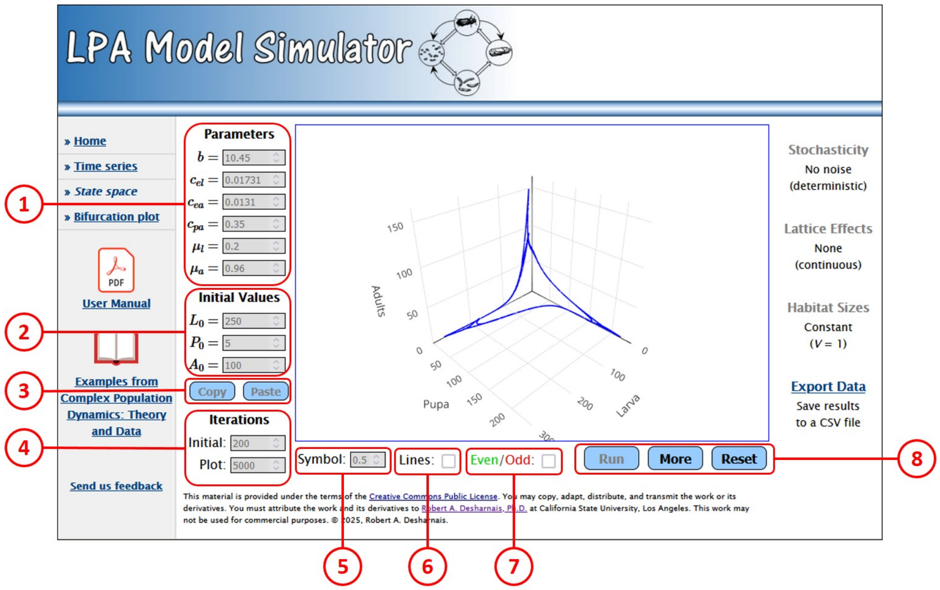


Figure 5: The State Space View for the LPA Simulator. The default parameter values and initial numbers are from the "hunt for chaos" experiment [4, 10]. See text for an explanation of the numbered items.

approach as $t \to \infty$. For discrete-time models they can be single fixed points (equilibria), a finite number of two or more fixed points (cycles), or an infinite number of points (invariant loops or chaotic attractors). To see the attractors in state space, one must either initiate the simulation on or very near the attractor or discard some number of initial iterations (transients) until the simulation is in a close neighborhood of the attractor. A plot of subsequent points will reveal the geometry of the attractor. The State Space View allows you to specify the number of initial iterations to be discarded and the number of subsequent points to plot.

There are situations where it is informative to examine the output of the LPA model as a *composite time series*, where the values of L_{t+2}, P_{t+2}, and A_{t+2} are considered as functions of the values of L_t, P_t, and A_t. Graphically, one looks at the output at every other unit of time. An option exists for using different colors (green and red) for the LPA points produced at even and odd times. If the Lines option is also selected, output produced at even and odd time points will be connected by lines as separate traces using the their corresponding colors. A legend will be added to the plot that allows you to show or hide each of the two traces.

The circled numbers in Fig. 5 correspond to the items listed below.

① These text fields allow you to change the parameter values of the LPA model. Changes only apply to the State Space View. Each value must be within a specific range; otherwise the parameter value field will be highlighted in red and an error message will appear when you try to run the simulation.

② These text fields allow you to change the initial values of the larva, pupae, and adult life stages. Changes only apply to the State Space View. Each value must be within a specific range; otherwise the initial value field will be highlighted in red and an error message will appear when you try to run the simulation.

③ These buttons allow you to Copy and Paste the parameter values and initial values among the three simulation views. (Changes made in the any one simulation view do not apply automatically to the other two simulation views.)

④ These text fields can be used to change the number of initial iterations to be discarded and the number of iterations that are plotted.

⑤ This text field can be used to change the size of the plotting symbol in pixels. Values can range from 0.1 to 10.

⑥ This check box gives you the option of connecting consecutive time points with lines. If the Even/Odd option is also selected, then points produced at even and odd times are connected with lines separately.

⑦ This check box gives you the option of plotting points produced at even and odd times using different colors (green and red, respectively). If the Lines option is also selected, then points produced at even and odd times are connected separately with lines. A legend will be added to the plot that allows you to show or hide each of the two series.

⑧ These three buttons allow you to control the simulation. The Run button will execute a new simulation and plot the results. The More button will add more plot points to the current simulation. The Reset button will clear the plot and allow you to modify the parameter and initial values and change the other options to produce a new simulation.

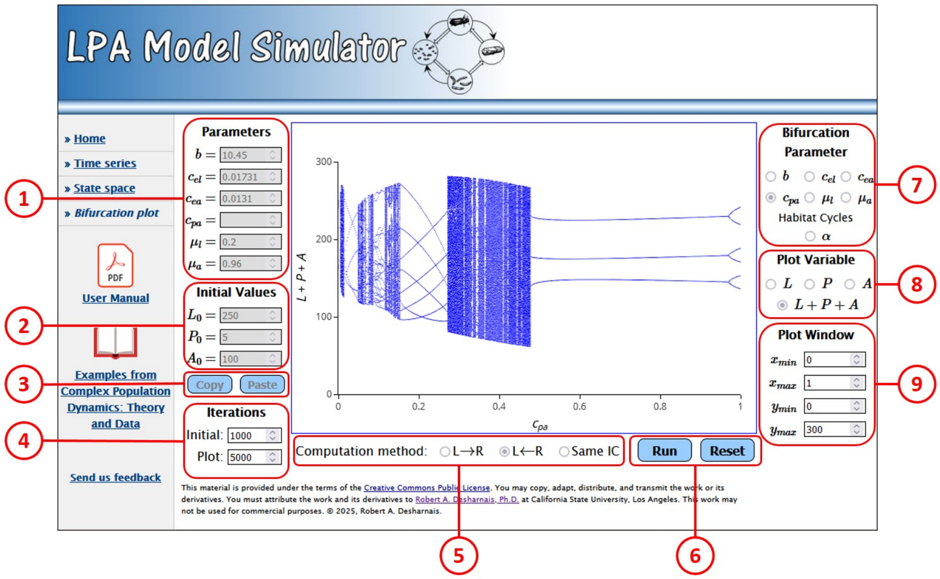


Figure 6: The Bifurcation Plot View for the LPA Simulator. The default parameter values and initial numbers are from the "hunt for chaos" experiment [4, 10]. See text for an explanation of the numbered items.

3.4 Bifurcation Plot View

Bifurcation plots allow you to examine how the attractors of a dynamic system change as one of the model parameters is altered. The value of the *bifurcation parameter* is plotted on x-axis and the attractor points of one or a combination of the state variables is plotted on the y-axis. For each value of the bifurcation parameter, the model is iterated until it approaches a close neighborhood of the attractor and these transients are discarded. The model is then iterated further to get a reasonable sample of the values of the state variables near attractor which are then plotted against the bifurcation parameter value. Equilibria appear as single points, cycles as two or more discrete points, and acyclic attractors (invariant loops or chaotic attractors) appear as vertical lines where the attractor points are dense. One can then visualize the parameter intervals where these different attractors reside. Figure 6 provides an example.

The Bifurcation Plot View (Fig. 6) allows you to create a bifurcation plot of the deterministic LPA model as any one of the model parameters are varied. You can set the parameter values and initial values of the simulation.

Options exist for choosing the bifurcation parameter, the state variable to be plotted, and the ranges of the two axes. The circled numbers in Fig. 6 correspond to the items listed below.

① These text fields allow you to change the parameter values of the LPA model. Changes only apply to the Bifurcation Plot View. Each value must be within a specific range; otherwise the parameter value field will be highlighted in red and an error message will appear when you try to run the simulation.

② These text fields allow you to change the initial values of the larva, pupae, and adult life stages. Changes only apply to the Bifurcation Plot View. Each value must be within a specific range; otherwise the initial value field will be highlighted in red and an error message will appear when you try to run the simulation.

③ These buttons allow you to Copy and Paste the parameter values and initial values among the three simulation views. (Changes made in the any one simulation view do not apply automatically to the other two simulation views.)

④ These text fields can be used to change the number of initial iterations to be discarded and the number of iterations that are plotted for each value of the bifurcation parameter.

⑤ These radio buttons allow you to choose the computation method for the bifurcation plot. The L→R option follows the attractors from left to right. The L←R option follows the attractors from right to left. The Same IC option uses the user-specified initial values (initial condition) for each value of the bifurcation parameter. See below for a further explanation.

⑥ These two buttons allow you to control the simulation. The Run button will execute a new simulation and plot the results. You can change the iteration numbers and plot window to recompute a modified version of the plot. The Reset button will clear the plot and allow you to modify the parameter and initial values and change the other options to produce a new bifurcation plot.

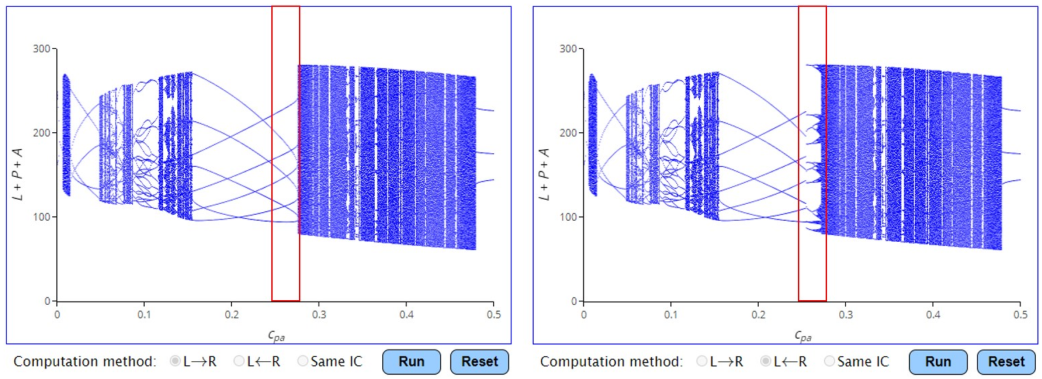


Figure 7: Two bifurcation plots created using different computation methods. The plot on the left used the L→R method to follow attractors from the left to the right. The plot on the right used the L←R method to follow attractors from the right to the left. The red lines highlight a region of multiple attractors.

⑦ These radio buttons allow you to choose the bifurcation parameter. The parameter α is the magnitude of the habitat two-cycles (see section 4.3).

⑧ These radio buttons allow you to choose the state variable that is plotted on the y-axis. The option $L + P + A$ is the total population size.

⑨ These text fields allow you to specify the values for the Plot Window. The fields x_{min} and x_{max} determine the range for the x-axis and y_{min} and y_{max} determine the y-axis range.

A dynamic model may have *multiple attractors*. Given the same parameter values, but different initial values, the system may approach a different set of points in state space. In this case, for any value of a bifurcation parameter, only one set of attractor points will be plotted. To help mitigate this issue, the Bifurcation Plot View provides three options for how the initial values are chosen as the bifurcation parameter changes. The first option, L→R, applies the specified initial values to the smallest value of the bifurcation parameter and then computes the attractor points. For the next value of the bifurcation parameter, the final LPA attractor values from the previous computation are used as the initial values for the next computation. This process is repeated for all subsequent values of the bifurcation parameter, so, in effect, the computation method follows the attractors from left to right.

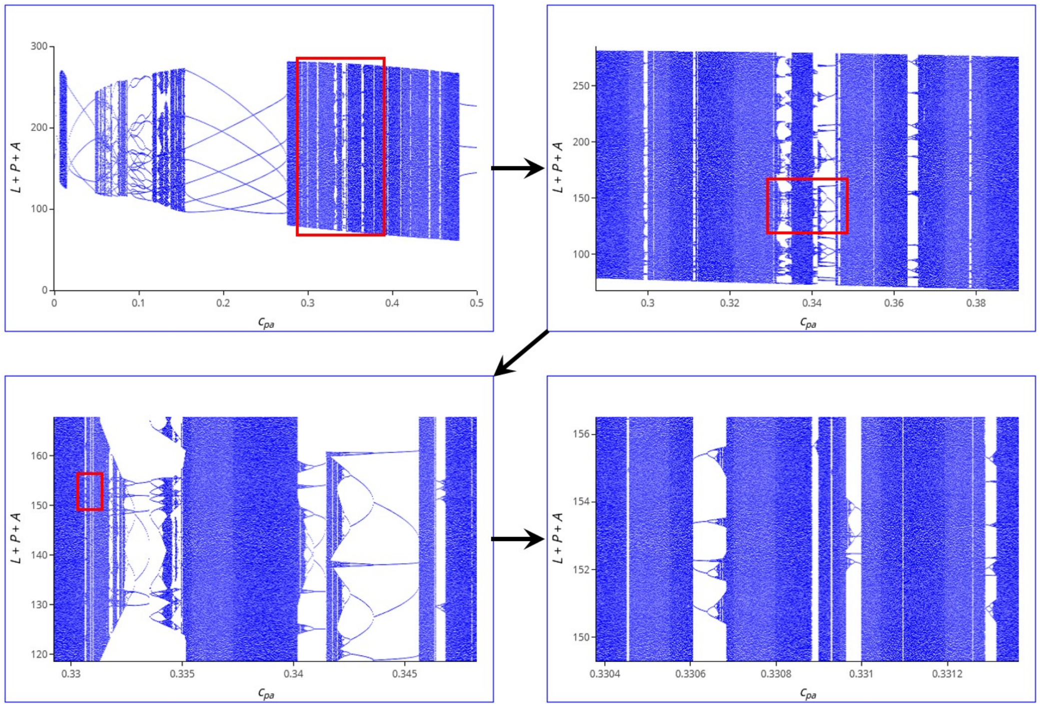


Figure 8: Examples of zooming into bifurcation plots. The red rectangles delineate three successive zooms of the original bifurcation plot in the upper left. As indicated by the arrows, the zooms proceed from top left to top right to bottom left to bottom right.

The second option, L←R, is similar, except that it starts with largest value of the bifurcation parameter and follows the attractors from right to left. The third option uses the same user-specified initial values of the LPA state variables for all values of the bifurcation parameter (labeled Same IC for same initial condition). If any of these computation methods shows regions where the attractors are different, this suggests the presence of multiple attractors in those regions. An example appears in Figure 7.

It is sometimes helpful (and fun!) to zoom into a bifurcation plot in order to see details at a higher resolution. There are two ways this can be accomplished using the Bifurcation Plot View of the LPA Simulator. First, you can alter the values of the axes ranges for the Plot Window (Fig. 6). Alternatively, you can use the mouse pointer to drag out a rectangle on an existing bifurcation plot to determine the zoomed region. The new axes

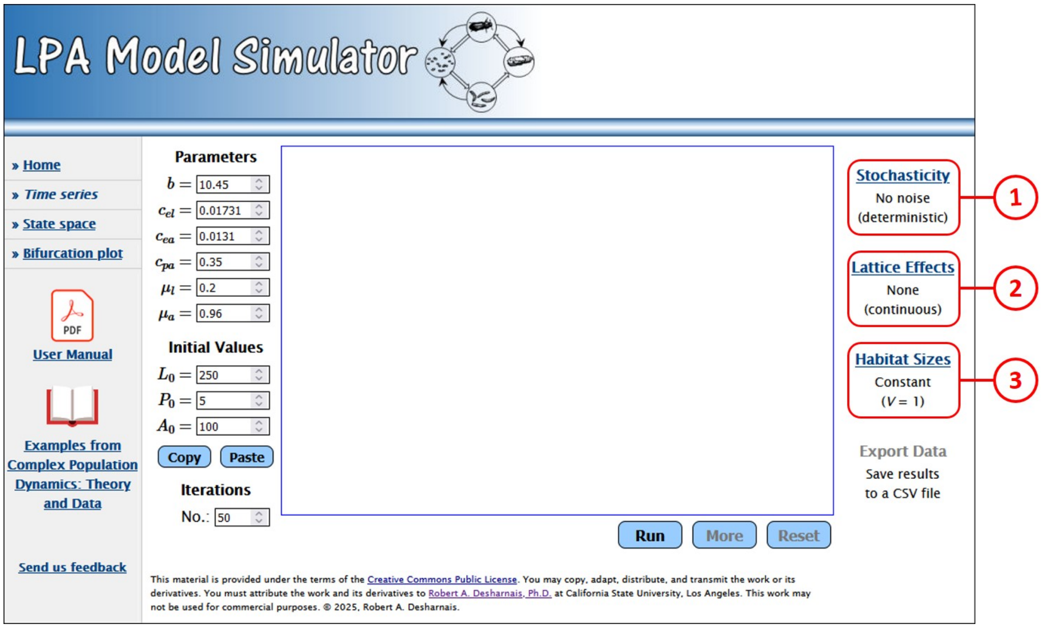


Figure 9: Three links on the right side of the Time Series and State Space Views allows the addition of ① stochasticity, ② lattice effects, and ③ habitat size changes to the LPA model.

ranges will be entered automatically for the Plot Window. Clicking the Run button will produce higher resolution plot of the zoomed region. This process can be repeated to see the details of progressively smaller regions of the bifurcation plot. For zoomed plots, it is helpful to increase both the Initial and Plot numbers for the Iteration values (item ④ in Fig. 6). Figure 8 demonstrates an example of three successive zooms.

4 LPA Model Elaborations

The LPA Simulator allows for elaborations of the basic model (1). You can add stochasticity, lattice effects, and changes in habitat size using the links shown in Fig. 9. These features can be added separately or in any combination. There are several options for each which are detailed below.

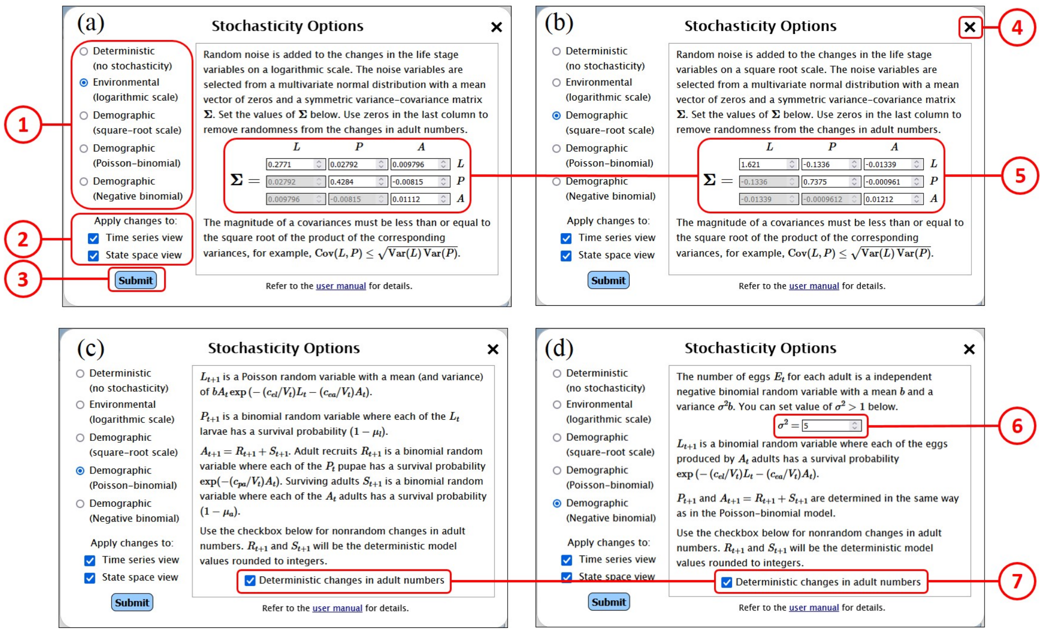


Figure 10: The four options for adding stochasticity to the LPA model: (a) environmental (logarithmic scale) noise, (b) demographic (square-root scale) noise, (c) the Poisson-binomial model for demographic variability, and (d) the negative binomial model for demographic variability. See text for an explanation of the numbered items.

4.1 Stochasticity

Stochastic models add randomness to the fluctuations in population numbers. There are two general sources of randomness. The first is *environmental stochasticity* which is caused by extrinsic forces that affect the entire population as a whole such as variation in temperature or rainfall. The second is *demographic stochasticity* which is caused by factors intrinsic to the population such as such variation in the numbers of offspring produced by individuals or the timing of deaths. Both types of stochasticity are available in the LPA Simulator.

The LPA Simulator provides four options for adding stochasticity to the deterministic LPA model: (1) environmental stochasticity, where random noise variables are added to the model on a logarithmic scale, (2) demographic stochasticity, where random noise variables are added to the model on a square-root scale, (3) a Poisson-binomial model of demographic stochasticity, and (4) a negative binomial model of demographic stochasticity. Each of these models is described in more detail below.

To add stochasticity to the LPA model, click the Stochasticity link on the left side of either the Time Series or State Space Views (item ① in Fig. 9). This opens the Stochasticity Options modal panel (Fig. 10). This panel allows you to choose one of the four available stochastic models and set the options for each model. There are four common controls (Fig. 10):

① These radio buttons allow you the select the stochastic model to be used in the simulations. Each choice changes the options on the right side of the panel so that they are appropriate to the chosen model. Choosing Deterministic implements the LPA model with no stochasticity.

② The Time Series and State Space Views have can have their stochasticity options. These check boxes allow you to choose the view to which the current options will be applied. The stochasticity options can be applied to one or both of the LPA Simulator views. If one or both views are checked, the Stochasticity panel will close once the Submit button is clicked. If neither view is selected, the Submit button will have no effect and the Stochasticity panel will remain open.

③ Use this button to apply the stochasticity options to the selected views.

④ Use this button to close the Stochasticity Options Panel without making any changes.

The subsections below describe in detail the four different stochastic models and their options.

4.1.1 Environmental stochasticity (logarithmic scale noise)

Environmental stochasticity is caused by factors external to the population such as temperature or rainfall. One way to model this type of randomness is to add noise variables to the equations on a logarithmic scale [8, 9]. For the LPA model (1), the stochastic difference equations are

$$\begin{aligned} L_{t+1} &= bA_t \exp\left(-c_{el}L_t - c_{ea}A_t\right)\exp\left(E_{1t}\right) \\ P_{t+1} &= L_t\left(1-\mu_l\right)\exp\left(E_{2t}\right) \\ A_{t+1} &= \left(P_t \exp\left(-c_{pa}A_t\right) + A_t\left(1-\mu_a\right)\right)\exp\left(E_{3t}\right), \end{aligned} \tag{2}$$

where $\mathbf{E}_t = (E_{1t}, E_{2t}, E_{3t})^\top$ is a column vector of random variables that has a trivariate normal distribution with a mean vector of zeros and a 3×3 variance-covariance matrix $\mathbf{\Sigma}$. The diagonal elements of $\mathbf{\Sigma}$ are the three variances for the elements of $\mathbf{E}_t$ and the off-diagonal elements are the covariances between the elements of $\mathbf{E}_t$. The matrix $\mathbf{\Sigma}$ is symmetric. It is assumed that there are no serial autocorrelations in the elements of $\mathbf{E}_t$.

The elements of the matrix $\mathbf{\Sigma}$ can be specified using the Stochasticity Options panel of the LPA Simulator (item ⑤ in Fig. 10a). The default values were estimated from experimental data [8]. Enter the desired variances for E_{1t}, E_{2t}, and E_{3t} into the diagonal fields for rows 1, 2, and 3, respectively. Enter the covariances in the upper off-diagonal fields. Since the matrix is symmetric, the lower off-diagonal elements will update automatically.

The correlation between two random variables x and y is defined as $\rho = \mathrm{Cov}\,(x, y)/\sqrt{\mathrm{Var}\,(x)\,\mathrm{Var}\,(y)}$. Correlations must in the range $-1 \leq \rho \leq +1$. This means that the magnitude of the covariance is bounded: $|\mathrm{Cov}\,(x, y)| \leq \sqrt{\mathrm{Var}\,(x)\,\mathrm{Var}\,(y)}$. This constraint must be observed when specifying the elements of the variance-covariance matrix $\mathbf{\Sigma}$. The LPA Simulator will highlight invalid entries in red.

In the "hunt for chaos" experiment [4, 10], adult mortality and recruitment into the adult stage were controlled experimentally to fix the values of the parameters μ_a and c_{pa}. To remove stochasticity from the transitions for the adult life stage, enter values of zeros in the fields for the last column of the matrix $\mathbf{\Sigma}$.

4.1.2 Demographic stochasticity (square-root scale noise)

Demographic stochasticity is caused by differences in life history attributes among individuals such as numbers of offspring or the timing of deaths. There are two approaches to modeling demographic stochasticity. One involves the use mechanistic models where the vital rates themselves are random variables, for example, using a binomial distribution to describe the number of individuals surviving during a fixed time interval. Another approach is to use a phenomenological stochastic model, where random variables representing variation due to demographic stochasticity are added to the transition equations on a square-root scale [10]. Applying the latter methodology to the LPA model (1), the stochastic difference equations are

$$\begin{aligned} L_{t+1} &= \left[\sqrt{bA_t \exp\left(-c_{el}L_t - c_{ea}A_t\right)} + E_{1t}\right]^2 \\ P_{t+1} &= \left[\sqrt{L_t\left(1-\mu_l\right)} + E_{2t}\right]^2 \\ A_{t+1} &= \left[\sqrt{P_t \exp\left(-c_{pa}A_t\right) + A_t\left(1-\mu_a\right)} + E_{3t}\right]^2, \end{aligned} \tag{3}$$

where $[x] = \max(x, 0)$. Like the model (2), $\mathbf{E}_t = \left(E_{1t}, E_{2t}, E_{3t}\right)^\top$ is a column vector of random variables that has a trivariate normal distribution with a mean vector of zeros and a 3×3 variance-covariance matrix $\mathbf{\Sigma}$. The diagonal elements of $\mathbf{\Sigma}$ are the three variances for the elements of $\mathbf{E}_t$ and the off-diagonal elements are the covariances between the elements of $\mathbf{E}_t$. The matrix $\mathbf{\Sigma}$ is symmetric. It is assumed that there are no serial autocorrelations in the elements of $\mathbf{E}_t$.

The elements of the matrix $\mathbf{\Sigma}$ can be specified using the Stochasticity Options panel of the LPA Simulator (item ⑤ in Fig. 10b). The default values were estimated from the control cultures of the "hunt for chaos" experiment [10]. Enter the desired variances for E_{1t}, E_{2t}, and E_{3t} into the diagonal fields for rows 1, 2, and 3, respectively. Enter the covariances in the upper off-diagonal fields. Since the matrix is symmetric, the lower off-diagonal elements will update automatically. As explained in section 4.1.1, the elements of $\mathbf{\Sigma}$ must confrom to the inequality $\left|\mathrm{Cov}\left(E_i, E_j\right)\right| \leq \sqrt{\mathrm{Var}\left(E_i\right)\mathrm{Var}\left(E_j\right)}$. The LPA Simulator will highlight invalid entries in red.

In the "hunt for chaos" experiment [4, 10], adult mortality and recruitment into the adult stage were controlled experimentally to fix the values of the parameters μ_a and c_{pa}. To remove stochasticity from the transitions for the adult life stage, enter values of zero in the fields for the last column of the matrix $\mathbf{\Sigma}$.

4.1.3 Demographic stochasticity (Poisson-binomial model)

The Poisson-binomial model of demographic stochasticity is based on the assumption that the number of eggs produced per adult female follows a Poisson distribution and that the mortality events of each age class are Bernoulli trials. The stochastic difference equations are

$$\begin{aligned} L_{t+1} &= \mathrm{Pois}\left(bA_t \exp\left(-c_{el}L_t - c_{ea}A_t\right)\right) \\ P_{t+1} &= \mathrm{bin}\left(L_t, (1-\mu_l)\right) \\ A_{t+1} &= \mathrm{bin}\left(P_t, \exp\left(-c_{el}A_t\right)\right) + \mathrm{bin}\left(A_t, (1-\mu_a)\right), \end{aligned} \tag{4}$$

where $\mathrm{Pois}\,(x)$ represents a Poisson random variable with mean (and variance) x, and $\mathrm{bin}\,(n, p)$ represents a binomial random variable for n Bernoulli trials, each with probability p. The Poisson and binomial are discrete probability distributions, so the life stage numbers are integers.

In the "hunt for chaos" experiment [4, 10], adult mortality and recruitment into the adult stage were controlled experimentally to fix the values of the parameters μ_a and c_{pa}. To remove stochasticity from the transitions for the adult life stage, we replace the binomial random variables for adult numbers with deterministic integer values:

$$A_{t+1} = \mathrm{int}\left(P_t \exp\left(-c_{el}A_t\right)\right) + \mathrm{int}\left(A_t\left(1-\mu_a\right)\right), \tag{5}$$

where $\mathrm{int}\,(x)$ means rounding x to the nearest integer. (If the "floor" option is selected for lattice effects, the integer portion of the argument will be used. See section 4.2.) Use the check box (item ⑦ in Fig. 10c) to select this option.

4.1.4 Demographic stochasticity (negative binomial model)

The negative binomial model of demographic stochasticity is based on the assumption that the number of eggs produced per adult follows a negative binomial distribution and, like the Poisson-binomial model (4), the numbers of surviving individuals follows a binomial distribution. The use of the negative binomial distribution is appropriate if females differ with respect to their inherent rates of fecundity. The stochastic difference equations are

$$\begin{aligned} L_{t+1} &= \mathrm{bin}\left(X_t, \exp\left(-c_{el}L_t - c_{ea}A_t\right)\right) \\ P_{t+1} &= \mathrm{bin}\left(L_t, (1-\mu_l)\right) \\ A_{t+1} &= \mathrm{bin}\left(P_t, \exp\left(-c_{el}A_t\right)\right) + \mathrm{bin}\left(A_t, (1-\mu_a)\right), \end{aligned} \tag{6}$$

where $X_t = \mathrm{Nbin}\left(A_t b, A_t \sigma^2\right)$ is a random variable with a negative binomial distribution with mean $A_t b$ and variance $A_t \sigma^2$. The value $\sigma^2 > 1$ is the variance among adults in the number of eggs produced. Like the Poisson,

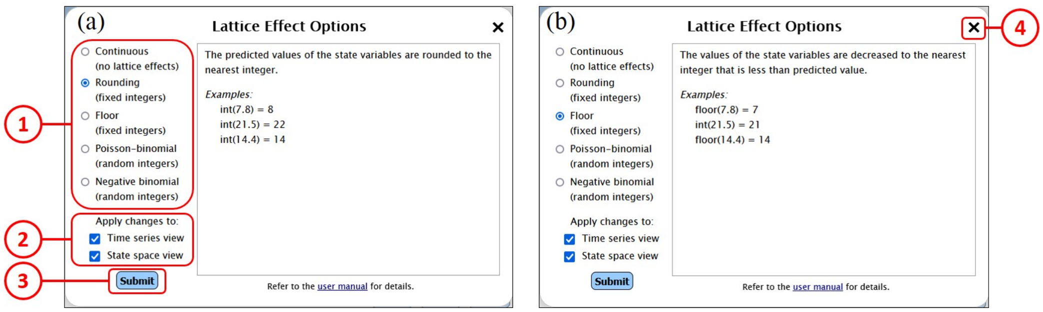


Figure 11: The two options for adding lattice effects to the LPA model: (a) rounding population size to the nearest integer, (b) decreasing population size to the nearest integer less than the predicted value (floor option). See text for an explanation of the numbered items.

the negative binomial is a discrete probability distributions, so the life stage numbers are integers.

In the "hunt for chaos" experiment [4, 10], adult mortality and recruitment into the adult stage were controlled experimentally to fix the values of the parameters μ_a and c_{pa}. Click the check box (item ⑦ in Fig. 10d) to make the transitions for the adult life stage deterministic (5).

4.2 Lattice Effects

Since the number of individuals in a population takes on integer values, population size is constrained to a *lattice*. This discretization of population numbers can have unexpected consequences, especially if population fluctuations are influenced by nonlinear dynamics [13].

There are two general approaches for the incorporation of lattice effects into a population model. For deterministic or stochastic models, one can simply replace the predicted continuous values with integers. This method applied to the LPA model gives the following equations:

$$\begin{aligned} L_{t+1} &= \mathrm{int}\left(X_t, \exp\left(-c_{el}L_t - c_{ea}A_t\right)\right) \\ P_{t+1} &= \mathrm{int}\left(L_t, (1-\mu_l)\right) \\ A_{t+1} &= \mathrm{int}\left(P_t, \exp\left(-c_{el}A_t\right)\right) + \mathrm{int}\left(A_t, (1-\mu_a)\right), \end{aligned} \tag{7}$$

where int (x) can mean rounding x to the nearest integer (rounding option) or only using the integer portion of x (flooring option). A second approach is to use discrete probability functions, such as the Poisson, binomial, and negative binomial distributions, in a stochastic model of the population's dynamics. Examples of the latter approach for the LPA model were presented above in sections 4.1.3 and 4.1.4.

The LPA Simulator allows for the incorporation of lattice effects into the LPA model. Click the Lattice Effects link on the left side of either the Time Series or State Space Views (item ② in Fig. 9). This opens the Lattice Effects Options modal panel (Fig. 11) which allows you to choose one of the four available lattice models. There are four common controls (Fig. 11):

① These radio buttons allow you the select the lattice model to be used in the simulations. Choosing the Poisson-binomial or Negative binomial options and clicking the Submit button will take you to the corresponding model in the Stochasticity Options panel (Fig. 10c,d).

② The Time Series and State Space Views have can have their own lattice options. These check boxes allow you to choose the view to which the selected option will be applied. The lattice effect options can be applied to one or both of the LPA Simulator views. If neither view is selected, the Submit button will have no effect and the Lattice Effect Options panel will remain open.

③ Use this button to apply the lattice options to the selected views. If either the Poisson-binomial or Negative binomial options are selected, the Stochasticity Options panel will open.

④ Use this button to close the Lattice Effect Options panel without making any changes.

4.3 Habitat Size

In *Tribolium* laboratory experiments, rates of cannibalism by larvae and adults are inversely proportional size of the habitat (amount of flour medium). This can be used to control the overall population size [11] or to investigate the effects of changes in habitat size on population dynamics [5, 12]. The

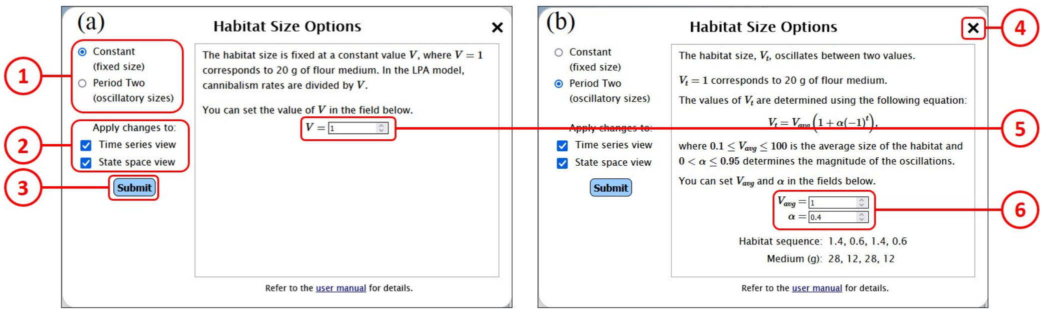


Figure 12: The two options for adding changes in habitat size to the LPA model: (a) specifying a constant value for the habitat size, (b) choosing habitat size cycles of period two). See text for an explanation of the numbered items.

LPA model (1) can be modified to include habitat size explicitly:

$$\begin{aligned} L_{t+1} &= bA_t \exp\left(\frac{-c_{el}L_t}{V_t} - \frac{c_{ea}A_t}{V_t}\right) \\ P_{t+1} &= L_t\left(1-\mu_l\right) \\ A_{t+1} &= P_t \exp\left(\frac{-c_{pa}A_t}{V_t}\right) + A_t\left(1-\mu_a\right). \end{aligned} \tag{8}$$

Here, V_t represents the habitat size in units of 20 g of medium ($V = 1$), the standard used in most of experiments designed around the LPA model. One option is to alter the size of the habitat, but keep it at a fixed value, that is, $V_t = V$. Another option is to introduce habitat cycles of period two with varying average sizes and amplitudes:

$$V_t = V_{avg}\left(1 + \alpha\left(-1\right)^t\right), \tag{9}$$

where V_{avg} is the average size of the habitat over time and $0 \leq \alpha \leq 1$ is the cycle amplitude. Both of these options are available in the LPA Simulator.

To incorporate changes in habitat size, click the Habitat Sizes link on the left side of either the Time Series or State Space Views (item ③ in Fig. 9). This opens the Habitat Size Options modal panel (Fig. 12). This panel allows you to choose one of the two available options. There are four common controls on the panel (Fig. 12):

① These radio buttons allow you the select the habitat size option to be used in the simulations, a constant habitat size or habitat cycles.

② The Time Series and State Space Views have can have their own habitat size options. These check boxes allow you to choose the view to which the selected option will be applied. The habitat size options can be applied to one or both of the LPA Simulator views. If neither view is selected, the Submit button will have no effect and the Habitat Size Options panel will remain open.

③ Use this button to apply the habitat size options to the selected views.

④ Use this button to close the Habitat Size Options panel without making any changes.

⑤ This text field applies to the option for a constant habitat size, $V_t = V$. You can enter a value for V between 0.1 and 100.

⑥ These text fields apply to the option for habitat cycles of period two. You can enter values of $0.1 \leq V_{avg} \leq 100$ and $0.001 \leq \alpha \leq 0.95$. The sequences for V_t and the amounts of medium in grams will be displayed at the bottom of the panel.

5 Plotly Graph Controls

The LPA Simulator uses the Plotly javascript graphics library. Graphs generated using this library can be manipulated. When the mouse pointer is placed inside the graph area a horizontal menu appears at the top of the view. Table 1 below summarizes the various options provided by Plotly.

The following features are also supported:

- When your mouse cursor hovers near a data point in any plot, a box pops up with the coordinate values of that point.
- When your mouse cursor hovers near a data point in the State Space plot, perpendicular lines also appear at the coordinate values in the three axis planes.
- On the Time Series plot, you can click on a life stage in the legend at the top of the graph to hide or show that life stage. Double-clicking on a life stage will show only that life stage.

Table 1: Plotly graph controls.

Icon	Option	Description
Options below are available in all plots.		
	Download plot	Plot is downloaded as a PNG graphics file.
	Zoom	Use mouse to zoom in on an area of the plot.
	Pan	Use mouse to pan plot after zooming.
Options below are only available in time series and bifurcation plots.		
	Zoom in	Zooms in on the center of plot.
	Zoom out	Zooms out from the center of the plot.
	Autoscale	Rescales the plot.
	Reset axes	Reset plot axes.
Options below are only available in state space plot.		
	Orbital rotation	Use mouse to orbitally rotate the 3D plot.
	Turntable rotation	Use mouse to turntable rotate the 3D plot.
	Reset camera	Resets camera viewpoint of the 3D plot.

- On the State Space plot, when the Even/Odd option is used, you can click the legend entries to hide or show the even or odd data series.
- On both the Time Series and Bifurcation plots, dragging out a rectangular area will modify the axes limits to zoom in to that area.
- Dragging your mouse in the State Space plot will rotate the plot in the direction of your mouse movements.
- Using your mouse wheel in the State Space plot will zoom the plot inwards or outwards.

All of these features are implemented by the Plotly javascript library.

6 Exporting Data

Simulation data from the Time Series and State Space plots can be exported to a comma-separated-values (CSV) file. The CSV files can be used to import

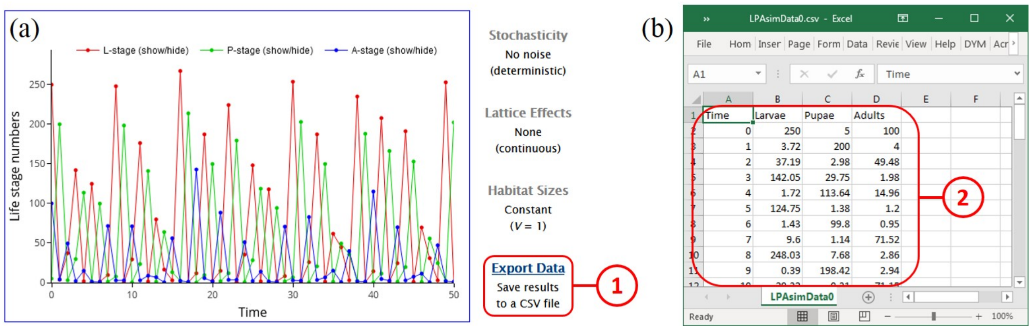


Figure 13: Data from the Time Series and State Space plots can be exported to a comma-separated-values (CSV) file: (a) the button ① for exporting data and (b) the exported data ② after being opened as a spreadsheet in Microsoft Excel.

the data into a variety of software programs for applications like spreadsheets, statistical analyses, or graphical plotting. Click on the Export Data link (item ① in Fig. 13). Your web browser will present the downloaded file or you may need to retrieve it from your downloads folder. The downloaded files will be named LPAsimData0.csv, LPAsimData1.csv, LPAsimData2.csv, etc., for multiple exports from a single session.

The exported simulation data will be organized into four columns: time and the life stage numbers for larvae, pupae, and adults. The first row will contain the headers and each of the subsequent rows will hold the sequential time values (item ② in Fig.13). If you have extended the simulation using the More button (item ④ in Fig. 4 or item ⑧ in Fig. 5), the exported file will contain all the data from the start of the simulation. For State Space plots, the exported data will exclude the initial iterations; only the plotted values will be exported.

7 Book Examples

The book *Complex Population Dynamics: Theory and Data* is a comprehensive examination of the how the LPA model has been used to make predictions and design experiments to study various aspects of nonlinear population dynamics. The LPA Simulator can be used to explore many of the topics covered in the book. To assist in this endeavor, the LPA Simulator includes examples from several sections in the book.

The book examples can accessed by using the link on the lower left side on

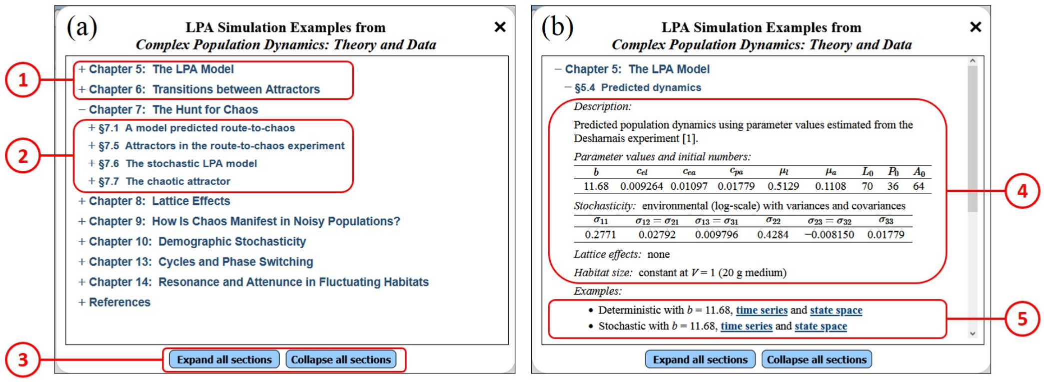


Figure 14: The book examples panel from the LPA Simulator are (a) organized by chapters and sections and (b) include brief descriptions and links to set up each example in the simulator views.

the web page (item ③ in Fig. 3). This brings up a modal panel of examples organized by the chapters and sections where the examples are located (Fig. 14). The chapters and sections can be expanded or contracted. Each section contains several links that load the examples into the appropriate simulator views. The highlighted items in Fig. 14 are described below:

① Each chapter can be expanded or contracted by clicking on its title. Expanded chapters will show the sections nested within it.

② Below each chapter are one or more sections which contain examples from the book. Each section can be expanded or contracted by clicking on its title.

③ Use these buttons to expand or collapse the groups. The expand button will open all the chapters and sections. The collapse button will close all groups resulting in a list of chapters.

④ Expanded sections contain a brief description of the examples, a table of parameter values and initial conditions, and the settings for the stochasticity, lattice, and habitat size options.

⑤ Each section contains links to two or more simulation examples. These links will load the parameter values, initial numbers, and all other options into the appropriate simulation view. When clicked, the panel for the book examples will close, and the application will switch to the appropriate simulation view. All you need to do is to click the Run button.

The book *Complex Population Dynamics: Theory and Data* contains links at the end of the sections corresponding to the LPA Simulator book examples. Each URL is of the form https://lpasim.org/?c=X&s=Y, where X is the chapter number and Y is the section number. For example, https://lpasim.org/?c=5&s=4 will open section 4 of chapter 5 (item 4 in Fig. 14).

8 Copyright Notice

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