

# Teaching dynamical systems modeling, analysis and simulation using a Lotka-Volterra Predation Narrative and a Numerus WebKit App

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## ABSTRACT

The Lotka-Volterra prey-predator (LVPP) equations are among the few ecological models that have become a standard part of the undergraduate mathematics curriculum. Rather than looking elsewhere for fresh examples, we use this familiar story as a single narrative thread along which the toolkit of dynamical systems analysis *and* simulation is introduced, one modeling assumption at a time. Five linked teaching modules progress from the classical model (equilibria, isoclines, linearization, a conserved quantity and the failure of Euler's method on a neutral center), through logistic prey growth (structural stability, Lyapunov functions), a prey Allee effect (bistability, separatrices, basins of attraction) and Holling functional responses (Hopf bifurcations, limit cycles, the paradox of enrichment), to a culminating model with predator interference and ratio dependence, whose non-differentiable origin is attracting but not Lyapunov stable. Multispecies extensions then lead to Gause-Lotka-Volterra competition, May-Leonard heteroclinic cycles, chaos in the Hastings-Powell food chain, May's stability-complexity criterion, and metaphysiological consumer-resource "trophic stacks" in which food-chain length depends non-monotonically on predator self-interference and in which alternative stable states and emergent Allee effects arise. Nine worked examples pair analytical results with simulations in a Numerus WebKit app, a browser-based simulator whose presets require no programming and whose AI window lets students modify the models or build their own. We discuss how the narrative serves students in the biological, social and applied sciences, and argue that comparing alternative narratives of predation teaches students that models are arguments to be tested, refined and sometimes replaced.

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## 1. Introduction

Narratives are among the oldest and most durable instruments of human knowing: they select from the overwhelming detail of experience, impose an order of cause and consequence, and in doing so turn isolated observations into understanding that can be remembered, communicated and contested. Science, for all its formal machinery, is no exception. In mathematics, a proof is a carefully plotted story using notational expressions that are highly compact and generally unambiguous. In the physical sciences, quantitative narratives—that is, narratives supported by the formulation of mathematical equations—have shaped not only what physicists believe but which questions they think worth asking. This is well demonstrated in the competing Heisenberg matrix and Schrödinger wave equation narratives of quantum theory that present very different views of reality—the first involving an infinite number of granular states, the second involving a smooth all-encompassing wave function. Both narratives were later shown to be mathematically equivalent in terms of the predictions they make—a sobering lesson on how two seemingly opposite quantitative narratives can reveal the same reality and embrace the same knowledge.

It is in the biological sciences, however, that quantitative narratives carry the heaviest epistemic loads. Living systems are historically contingent, hierarchically organized and irreducibly variable, so biological explanation rarely takes the form of universal laws. Instead it relies on accounts of how particular structures, populations and interactions came to be and how they persist. Darwin himself described his great opus *On the Origin of Species* as “one long argument.” Injecting mathematical rigor into these biological narratives has produced quantitative biological narratives and, with them, the field of mathematical biology. These quantitative biological narratives have been pivotal in providing insights into the behavior of biological systems at every scale—from biochemistry, through population ecology, to whole-Earth system dynamics.

Dynamical systems theory provides one of the most important quantitative narrative devices for generating an understanding of biological systems at all the levels scoped above. Dynamical systems theory can be introduced to the student in a purely mathematical setting, or its general principles can be elucidated through systems that one may have a passion to better understand. In this paper, we throw back the curtain on the relationship between dynamical systems theory and a particular quantitative narrative thread that has been woven into our understanding of aspects of theoretical ecology that pertain to the interaction of populations. This story begins with a mathematician’s quest to understand why the proportion of predatory fish in the catch rose when fishing was curtailed during World War I.

In the 1920s, the eminent Italian mathematician Vito Volterra (1860-1940) decided that the answer to this conundrum might well lie in the mechanisms of the interactions of prey and predator species of fish in the Adriatic Sea (Volterra, 1926a, 1926b). In a separate but contemporaneous investigation many thousands of miles from Italy, the US mathematician and chemist Alfred James Lotka (1880-1949) proposed a general system of differential equations as a model for interacting species that depend on their mutual densities and various environmental and genetic parameters to describe rates of growth or change over time. He then argued (Lotka, 1925) that a two-dimensional quadratic version of this system, expressed in terms of the prey and predator densities  $x(t)$  and  $y(t)$  (numbers per unit area) respectively, provided an insightful model for exploring oscillatory aspects of prey-predator dynamics.

In the form we use here, which adds logistic self-limitation of the prey to the quadratic system of Lotka and Volterra, the model involves the two population density variables  $x(t)$  (prey) and  $y(t)$  (predators), measured as numbers of individuals per unit area, as dynamically changing functions of time  $t$ , along with five population parameters  $r$ ,  $K$ ,  $b$ ,  $c$  and  $d$  whose interpretations will be discussed in

detail later:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - bxy \quad \text{and} \quad \frac{dy}{dt} = cxy - dy. \quad (1)$$

(Note: do not be confused by  $dy$  and  $dy$  in the above equation: the first is part of the differential operator symbol  $\frac{d}{dt}$  applied to  $y(t)$  and the second is the parameter  $d$  multiplied by the variable  $y$ ). We keep this dual use of the letter  $d$  for historical reasons. In the limit  $K \rightarrow \infty$ , the pair of equations (1) reduces to what has come to be known as the classical Lotka-Volterra model of predation (Eq. (2) in Module 1). They, together with the so-called Gause-Lotka-Volterra quadratic model that expresses the process of two species competing for a common but implicitly embedded resource, constitute the fundamental paradigm for modeling multispecies interactions (May, 1973).

Some personal details of this history itself make interesting reading. Vito Volterra was a professor of mathematical physics in Rome when his daughter Luisa became engaged to the marine biologist Umberto D’Ancona (Kingsland, 1985). D’Ancona had noticed in fish-market data from the Upper Adriatic that the proportion of predatory fish increased during 1914–18, when fishing effort was greatly reduced by the war. In setting out to explain this observation, Volterra formulated the equations that now bear his and Lotka’s names (Volterra, 1926a, 1926b). Alfred James Lotka, having arrived at the same quadratic system in his own research, published it in his seminal book, *Elements of Physical Biology* (Lotka, 1925). Concerned about his priority over Volterra in developing his prey-predator equations, he wrote to *Nature*; his letter, published back to back with a reply from Volterra, finally established the independent but overlapping contributions of these two early mathematical biologists (Lotka, 1927; Volterra, 1927).

The Lotka-Volterra prey-predator (LVPP) and competition equations are, in the words of Kleshnina et al. (2026), “perhaps one of only a few limited examples of ecology that have ubiquitously made it into undergraduate mathematics classrooms”, and for that reason those authors chose not to review them. We agree with their assessment but not their inclination. Because the LVPP story is familiar, it can carry an unusually large amount of mathematics without overwhelming students with new biology. Each time a single ecological assumption is relaxed—prey no longer grow exponentially, small prey populations struggle to reproduce, predators become satiated—a new and fundamental idea from dynamical systems theory appears: structural stability, multiple attractors, bifurcations, limit cycles. In this sense the LVPP model is less a single example than a *quantitative narrative vehicle* for an entire course on dynamical systems theory (cf. Strogatz, 2024; van der Hoff, 2017).

In theoretical ecology, the Lotka-Volterra system of equations—along with Leslie-Lefkovitch age/stage (Lefkovitch, 1965; Leslie, 1945, 1948), Nicholson-Bailey host-parasitoid (Hassell, 2000; Nicholson & Bailey, 1935), MacArthur consumer-resource (Chesson, 1990; MacArthur, 1972), and Levins metapopulation (Hanski, 1999; Levins, 1969) models—provides a series of quantitative narratives that constitute various chapters of a sacred “Book of Theoretical Ecology.” In particular, the dogma of LVPP is well entrenched, despite well-known weaknesses and inconsistencies that more consistent narratives have since addressed (e.g. Getz, 1984, 2011; Ginzburg & Colyvan, 2004; Murdoch et al., 2003). Yet the imprint of culture on education—even in the sciences—is powerful enough that the LVPP narrative is likely to dominate the teaching of population interactions for the foreseeable future. The LVPP narrative has endured less because of its predictive power than because of its explanatory power: it tells a compelling, tractable story of how organisms depend on and constrain one another, and interact in a complex dance of oscillations, tipping points and regime shifts (Boettiger & Hastings, 2012; May, 1977; Scheffer et al., 2001, 2009).

Over time, of course, the Lotka-Volterra prey-predator models have been extended and refined to make them more realistic. A critical extension to the LVPP narrative was the work of C.S. “Buzz”

Holling (Holling, 1959a, 1959b; Holling, 1965, 1966), later extended to include interference among predators (Beddington, 1975; DeAngelis et al., 1975). In the late 1950s, Holling split a predator's time between two distinct activities: searching for prey and handling (capturing, eating, and digesting) prey. He famously demonstrated this using experiments with human subjects picking up sandpaper discs. As prey density rises, predators spend less time searching and more time handling prey, which eventually creates a consumption ceiling.

Although the Lotka-Volterra models and the subsequent modifications of Holling provide models that can be understood using various analytical methods to determine the existence and stability properties of equilibria associated with Lotka-Volterra-Holling (LVH) prey-predator systems, the advent of modern computers has made it possible for mathematical ecologists to explore the behavior of multispecies prey-predator systems (or food webs) in spatially heterogeneous environments through the medium of numerical simulation. Thus, it has become important for ecologically oriented students of population dynamics to gain skills in formulating equations underlying algorithms that describe the behavior of growing populations, as well as the interactions of populations consisting of individuals of different types. Skills in writing code to numerically solve such equations or simulate such algorithms and interpret numerical output, whether visually from graphical construction or statistically from reams of output data, have also gained importance, though current advances in AI make the honing of such skills less critical than they used to be.

Beyond the analytics of dynamical systems, a second theme of this Classroom Note is the topic of simulation itself. Students today rarely meet differential equations without also meeting a computer, yet the relationship between the analytical and the numerical is seldom examined explicitly. The LVPP narrative provides striking opportunities to do so: the classical model has closed orbits that a naïve numerical method converts into outward spirals; adding an Allee effect makes the outcome depend on initial conditions in ways that are easiest to map by simulation; and a Holling Type II response with logistic prey growth produces, once the carrying capacity is large enough, limit cycles whose existence is guaranteed analytically but whose shape and amplitude are only accessible numerically. All modules are supported by presets of the browser-based Dynamical Systems Simulation (DynSS) LVPP app built on the Numerus WebKit™ (NWK) platform (see Getz, Salter, et al., 2018; Salter & Getz, 2026, for the underlying Numerus approach), so instructors can demonstrate and students can explore without writing code. Table 1 summarizes the modules and extensions, together with the worked examples and app presets that support them.

## 2. Mathematical Background

Few quantitatively oriented courses draw a more heterogeneous audience than mathematical ecology. In a typical upper-division undergraduate or first-year graduate class, biology and environmental science majors who have taken one or two semesters of calculus may sit alongside students who have studied differential equations and linear algebra. Data science students often arrive with strong programming skills but little experience of analytical reasoning in dynamical systems. Some students in the same room will have met dynamics only through discrete-time models of the kind used in population biology and fisheries; others will know continuous-time theory well but have never seen a model parameter that had to be estimated from data. These gaps run in both directions: biologists may struggle with eigenvalues, whereas students with strong quantitative backgrounds may need help to see that  $r$ ,  $b$ ,  $c$  and  $d$  in Eq. (2) are measurable rates, with units, whose values constrain what a model can credibly predict (cf. National Research Council, 2003; Thompson et al., 2013).

A shared narrative helps here. Every student, whatever their background, can follow the LVPP story at the level of ‘more prey means more food for predators, and more predators means fewer prey’.

**Table 1.** Summary of the teaching modules (Section 4) and multispecies extensions (Section 5) built on the Lotka-Volterra prey-predator (LVPP) narrative, with the worked examples (WE) and NWK DynSS LVPP presets (P) that accompany them.

| Section                        | Model                                                          | Dynamical systems concepts                                                                                         | Simulation focus                                                        | WE; P   |
|--------------------------------|----------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------|---------|
| <i>Teaching modules</i>        |                                                                |                                                                                                                    |                                                                         |         |
| 4.1                            | Classical model (exponential prey, mass action)                | Equilibria, null-isoclines, Jacobian, centers, conserved quantities                                                | Euler vs. Runge-Kutta on a neutral center                               | 1; 1    |
| 4.2                            | Logistic prey growth                                           | Structural stability, trace-determinant plane, Lyapunov functions and global stability, transcritical bifurcation  | Damped spirals; transient vs. asymptotic behavior                       | 2; 1    |
| 4.3                            | Allee effect in prey                                           | Multiple attractors, saddles, separatrices, basins of attraction                                                   | Mapping basins by sweeping initial conditions                           | 3; 3    |
| 4.4                            | Holling Type II/III functional response                        | Hopf bifurcation, limit cycles, Poincaré-Bendixson, critical slowing down, paradox of enrichment                   | Runs either side of a bifurcation; numerical artifacts near it          | 4; 2, 4 |
| 4.5                            | Culminating system; predator interference and ratio dependence | Model comparison, structural sensitivity, non-differentiable equilibria, attraction vs. stability                  | Switch-based comparison of variants; enrichment without destabilization | 5; 0, 5 |
| <i>Multispecies extensions</i> |                                                                |                                                                                                                    |                                                                         |         |
| 5.1                            | Gause-Lotka-Volterra competition                               | Real eigenvalues, invasion criteria, saddles and separatrices                                                      | Coexistence, exclusion and bistability                                  | 6; 6    |
| 5.2                            | Three competitors (May-Leonard)                                | Circulant matrices, Lyapunov functions, neutral and heteroclinic cycles                                            | Ever-lengthening transients; Euler vs. RK4 near saddles                 | 7; 7    |
| 5.2                            | Three-species food chain (Hastings-Powell)                     | Period doubling, chaos, Lyapunov exponents                                                                         | Sensitivity to initial conditions and step size                         | 8; 8    |
| 5.3, 5.4                       | Metaphysiological consumer-resource systems and trophic stacks | Emergent logistic growth, $n$ -dimensional equilibria, alternative stable states, coexisting equilibria and cycles | Self-interference, outbreaks and food-chain length                      | 9; 9    |
| 5.5                            | Many species (May)                                             | Community matrices, random-matrix stability criteria, the elliptic law                                             | Random-matrix trials; user-coded multispecies models                    | –; –    |

The modules in Section 4 then invite each student to deepen their engagement from wherever they start through the NWK DynSS LVPP app. For example, biology students can begin with simulation and phase-plane diagrams in the NWK DynSS LVPP presets before formalizing what they see, while mathematics students can begin with the analysis and use simulation to test, extend and sometimes correct their conclusions. In our experience, mixed-background teams in which students are explicitly responsible for explaining their ‘home’ perspective to one another work particularly well.

Nonetheless, all students need at least a rudimentary working knowledge of a common core. Beyond differential calculus (derivatives, the chain rule, partial derivatives and first-order Taylor expansion) and comfort with exponential and logarithmic functions, this core comprises six areas: (i) complex numbers, because the eigenvalues that govern oscillations come in complex-conjugate pairs; (ii) elementary matrix theory, in particular determinants, traces and the eigenvalues of  $2 \times 2$  matrices; (iii) elementary solution theory for ordinary differential equations, including separable and linear equations and the

meaning of existence and uniqueness; (iv) linearization and the stability theory of equilibria, including the Jacobian matrix, the classification of planar equilibria, and the basic ideas of Lyapunov functions, limit cycles and bifurcations; (v) simulation algorithms and elementary numerical analysis, sufficient to understand why the choice of method and step size matters; and (vi) sensitivity analysis, which connects model predictions back to uncertain parameter values. None of these requires a full course. Appendix A gives a self-contained summary of what students should know in each area. Each summary is framed around the LVPP models used in this note and ends with self-check exercises, so that instructors can assign it as preparatory reading, use it as a diagnostic at the start of a course, or point individual students to the sections where they are weakest.

### 3. The NWK DynSS LVPP App

The modules in Section 4 are designed to be worked through with paper, pencil and a simulator side by side. The simulator we use is the NWK DynSS LVPP app, a configuration of the general-purpose Numerus WebKit™ DynSS (Dynamical Systems Simulation) app described by Salter and Getz (2026), preloaded with a bank of population-biology presets. In this section we explain why we chose a browser-based app over the more familiar alternatives, outline how the app works, and describe the features that the modules rely on, including an AI facility that generates model code from a plain-language request.

#### 3.1. Why a browser-based simulator?

Platforms such as MATLAB, Mathematica and R are powerful, but each requires dedicated training before a student can simulate even a two-equation model, and lighter-weight systems-modeling tools such as Stella or NetLogo also take concentrated effort to master (Salter & Getz, 2026). In a class of mixed backgrounds (Section 2), time spent learning a programming environment is time not spent on dynamics, and it falls unevenly: the computer science student is fluent within minutes, while the biology student may still be fighting syntax at the end of the first laboratory. The Numerus WebKit™ apps run directly in a web browser, are free, and require no installation, so the same model is available to every student on the first day of a course, on a laptop, a tablet or a library computer.

There is also a deeper reason. As calculators, automation and now AI take over routine computation, people's intuition for how dynamical systems behave—how drug concentrations rise and fall over a course of pills, how time delays shape commodity prices, how a harvested population responds to fishing pressure—is likely to erode. Our view is that the best counter to this erosion is to give students direct, hands-on experience of systems behavior through simulation, coupled with enough analysis to understand *why* the simulation does what it does. The LVPP narrative supplies the analysis, and the app supplies the experience. The same app can also be used to introduce elementary dynamical systems simulation in the high school mathematics classroom in the form of simple growth models in biology and economics (e.g., compound interest), elementary physical processes (e.g., Newton's Law of Cooling), and mathematical curiosities (e.g., the Collatz conjecture, Fibonacci's rabbits), so the approach scales from secondary school to graduate level.

#### 3.2. How the app works

Numerus WebKit™ grew out of the Numerus Designer and Studio platforms and their runtime alterable modeling platform (RAMP) technology (Getz, Salter, et al., 2018; Salter & Getz, 2026). Its central design choice is to separate the simulation engine from the user interface: a single, shared interface code base is customized for each project by a configuration file, the project's 'DNA', which specifies the controls, displays and, for DynSS, the model itself. The interface has two parts. The *dashboard* (Fig. 1)

holds parameter sliders (each paired with an editable text field), switches, run controls and `plotly.js` graphs. A pull-out *drawer* (Fig. 2) holds the model documentation, the code window and the preset manager. Simulation output can be downloaded as a comma-separated values (CSV) file for further analysis, for example in a spreadsheet or in R.



**Figure 1.** The NWK DynSS LVPP dashboard (to the left of the vertical light purple line) running the Lotka-Volterra prey-predator preset (Preset 1). Sliders set parameter values and initial conditions; the run ribbon shows the integration method and step size; and the time and phase-plane graphs update as the simulation runs. The sliders show the factory settings of the preset, except that initial prey density is set to 60 for the last of the three runs, and the right-hand graph shows the prey-predator phase space for three runs of the classical model with exponential prey growth (Module 1), started from  $(x_0, y_0) = (100, 10)$  (outer green; factory setting),  $(80, 10)$  (red) and  $(60, 10)$  (inner green). The drawer icon ( $\equiv$ , upper right of the dashboard) opens the windows to the right of the purple line, here partly cut off: documentation above, and the bank of presets (0-9 factory, 10-25 user) with buttons for saving presets to, and restoring them from, a local file below. Selecting the Model Definition radio button at the top of the drawer opens two further windows, one describing the model and the other holding its NuML code (Fig. 2).

### 3.3. Specifying a model in NuML

In most Numerus WebKit<sup>TM</sup> apps the model is fixed when the app is built. In NWK DynSS LVPP the first ten presets (0-9) are fixed: their code and parameter settings revert to their ‘factory settings’ whenever the Restore button (in the run ribbon immediately below the sliders in Fig. 1) is clicked. Changes made to these presets are remembered until the factory settings are restored. The remaining presets (10-25) are open for users to insert their own models into the code window (Fig. 2) using NuML (Fig. 3), a compact, mathematics-like language that the app compiles at run time (Salter & Getz, 2026). As discussed in Section 3.5 below, AI can also be prompted to generate NuML code for a desired model. NuML extends JavaScript syntax with two operators. The operator `@=` defines the model: `deriv(x) @= ...` declares the right-hand side of a differential equation, `next(x) @= ...` the update of a difference equation, `initial(x) @= ...` an initial value, and `update(...)` `@= ...` the variables

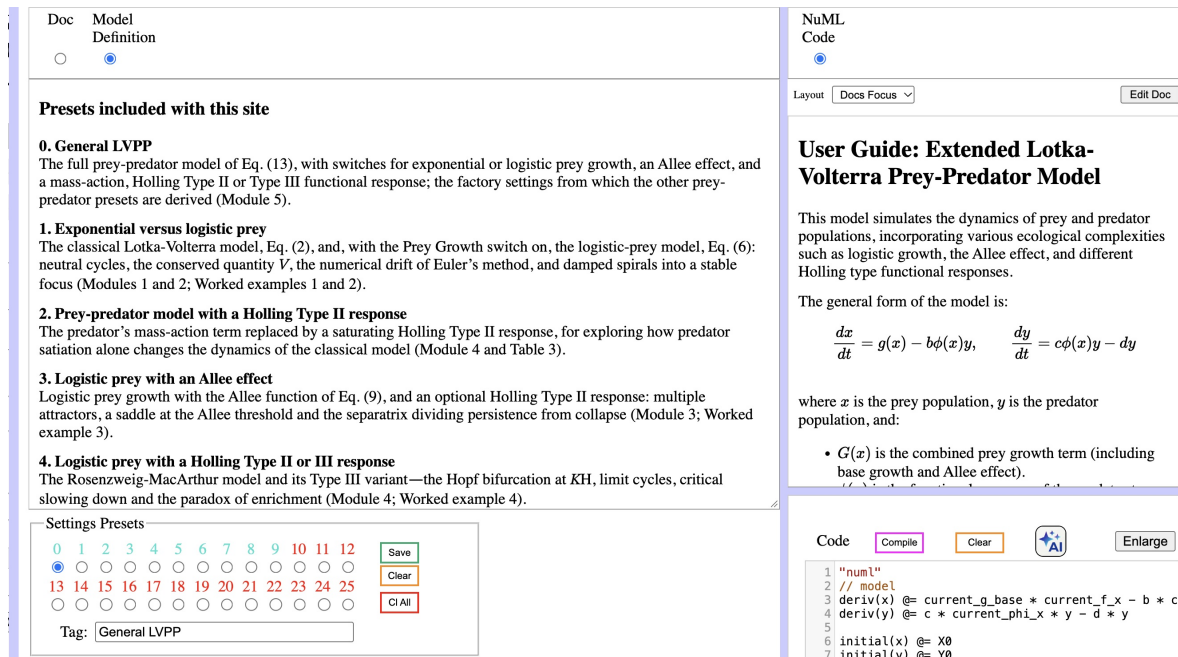


**Figure 2.** The NWK DynSS LVPP drawer (Fig. 1) with Model Definition selected. Left: documentation describing the presets included with the app, above the bank of presets (here Preset 0, ‘General LVPP’, is selected). Upper right: the user guide to the model of the selected preset. Lower right: the code window, which holds the model’s NuML code and has Compile, Clear and Enlarge buttons, together with an AI button that opens a window in which the user can ask a large language model to build a simulation model in NuML (Section 3.5).

sent to a graph. The operator `#=` configures the dashboard: slider ranges and labels, graph titles and axes, and the integration settings. Figure 3 shows an abridged NuML specification of the logistic-prey model, Eq. (6), adapted from the factory Lotka-Volterra preset; setting the slider for  $K$  to a very large value approaches the classical LV model with exponential prey growth, Eq. (2).

Pedagogically, NuML has two virtues. First, the code is transparent: it reads almost line for line like the equations in Section 4, so students can see that the program *is* the model, and can move between the two without a translation step. Second, it is modifiable: replacing Prey by a Holling Type II term in Predation and Ingestion, or multiplying Births by the Allee function of Eq. (9), takes a line or two, so each step of the LVPP narrative becomes a small, deliberate edit to working code. Salter and Getz (2026) illustrate exactly this, modifying the factory Lotka-Volterra preset to include an Allee effect and a Holling Type III response and showing that the resulting model supports coexistence, predator extinction and limit cycles depending on a single parameter.

### 3.4. Features used in the teaching modules

The following four features of the app are used in the teaching modules and extensions of Sections 4 and 5.

*Integration method and step size.* NWK DynSS LVPP offers two methods, forward Euler (intended for difference equations, run with  $\Delta t = 1$ ) and classical fourth-order Runge-Kutta (RK4, the default for differential equations), together with a user-set step size,  $\Delta t$  (dt in the app; default 0.5). Being able to switch from RK4 to Euler on a running model is what makes the numerical lesson of Module 1 so direct: students watch the closed orbit of the classical model turn into an outward spiral, then shrink  $\Delta t$  and watch the spiral tighten, with no code to write. Because NWK DynSS LVPP does not include specialized solvers for stiff systems (Salter & Getz, 2026), it also provides a natural point for a discussion about

```

// model
deriv(Prey) @= Births - Predation
deriv(Pred) @= Ingestion - Death
// initial conditions
initial(Prey) @= Init_Prey
initial(Pred) @= Init_Pred
// terms
Births    @= r * Prey * (1 - Prey/K)
Predation @= b * Prey * Pred
Ingestion @= c * Prey * Pred
Death     @= d * Pred
// send solutions to the graphs
update(Prey, Pred) @= mainGraph
update(Prey, Pred) @= phaseGraph
// link parameters to sliders
Init_Prey @= Slider1
Init_Pred @= Slider2
r @= Slider3
b @= Slider4
c @= Slider5
d @= Slider6
K @= Slider7
// dashboard configuration
Slider3 #= [legend("Growth Rate (r)"), min(0.0), max(2), value(0.4), step(0.01)]
...
Slider7 #= [legend("Carrying Capacity (K)"), min(100), max(1000), value(100), step(10)]
TimeGraph0 #= [legend("Prey Population", "Predator Population"),
  title("Prey-Predator Dynamics"), ylabel("Population"), xlabel("Time") ]
PhaseGraph01 #= [legend("Prey vs Predator"), title("Prey-Predator Phase Space"),
  xlabel("Prey Population"), ylabel("Predator Population")]
// simulation control
integration #= [maxTime(200), dt(0.1), method("RK4")]

```

**Figure 3.** An example of NuML code for the logistic-prey Lotka-Volterra model, Eq. (6), in the notation of this paper. The @= statements define the model; the #= statements configure the dashboard (only two of the seven slider definitions are shown). To see the actual code of the NWK DynSS LVPP app, click on the drawer icon (see Fig. 1) and then on the Model Definition radio button at the top of the window that opens to the right of the dashboard (Fig. 2; see Salter & Getz, 2026, for more details).

numerical methods that can be employed to generate accurate solutions that do not diverge from true solutions as a result of accumulated numerical errors (Appendix A.6).

*Phase-plane and time-series displays.* Every preset displays both  $x(t)$  and  $y(t)$  against time and the trajectory in the  $(x, y)$  phase plane. Seeing the two views side by side helps students connect the abstract phase portraits of the analysis to the oscillating time series that ecologists actually observe. With *autorun* switched on, the simulation reruns whenever a slider is moved, so students can drag  $K$  through the transcritical point of Module 2 or the Hopf point of Module 4 and watch the phase portrait change in real time. If *batch mode* is switched on, solutions are graphed only once the run is complete.

*Sensitivity mode.* A sensitivity platform reruns the model while stepping a chosen parameter between user-set limits, overlaying the runs and plotting their mean  $\pm$  one standard deviation (Salter & Getz, 2026). Stepping  $K$  in Module 4 yields a crude bifurcation diagram, and stepping an initial predator density in Module 3 traces out the boundary between the coexistence and extinction basins. In both cases the simulation produces in seconds what would take a full laboratory session to code from scratch, leaving time to discuss what the results mean. The mode lets students experiment with how solutions change as a parameter changes. The sensitivity analysis of Appendix A.7 is based on linearization and so applies to *local sensitivities* (small perturbations in parameter values). The runs made in this

NWK DynSS LVPP mode, by contrast, are full nonlinear solutions, and because of nonlinear effects nothing general can be said about them without carrying out the simulations themselves: bifurcations and boundaries between basins of attraction can make solutions change dramatically as a parameter crosses a threshold value.

*Presets.* A preset stores the complete state of the app—model code, parameter values, integration settings—and can be recalled with a single click. Presets 0-9 hold the factory settings; the remaining presets can be overwritten by the user, persist in the browser between sessions, and can be saved to and restored from a file (Salter & Getz, 2026). The links to presets 0-9 are listed in the Data Availability Statement at the end of this paper along with a description of each.

### 3.5. AI-assisted model building

NWK DynSS LVPP also includes an AI window in which the user describes a model in plain language (or in structured markdown, with equations in  $\text{\LaTeX}$  notation) and a large language model (currently Gemini, ChatGPT or DeepSeek) returns two things: NuML code, and a documentation page that states the model's equations in standard mathematical notation (Salter & Getz, 2026). The code and documentation can be saved into the app, run immediately, edited by hand, or refined through further prompts. For well-known models a short prompt suffices: asking for “the Lotka-Volterra prey-predator model” reliably produces a working model.

We regard this facility as a teaching opportunity rather than a shortcut, because AI-generated models have to be checked, and checking them requires exactly the understanding that the modules aim to build. When using the AI facility, users should:

- (1) write prompts that are as specific as possible, stating the governing equations explicitly in  $\text{\LaTeX}$  notation and saying whether time is continuous (`deriv`) or discrete (`next`);
- (2) read the generated documentation and confirm that its equations are the ones intended, before running anything;
- (3) repeat the prompt and compare outcomes in the case of less familiar models, or try a second language model, and resolve any differences;
- (4) verify that the simulated behavior agrees with what intuition or analysis predicts.

The last step closes the loop that runs through this paper. The equilibria, eigenvalues, periods and bifurcation points derived in the worked examples of Section 4 are precisely the checks a student needs to decide whether an AI-built model, or a hand-coded one, is behaving correctly.

### 3.6. Beyond the classroom

Although our focus is teaching, the same apps serve research. Any Numerus WebKit<sup>TM</sup> app can be driven from R as a ‘virtual package’, with R controlling parameter values and runs while the browser carries out the simulation, so that model fitting and optimization can be done with standard R tools (Salter & Getz, 2026). Students who begin with the LVPP presets therefore learn a tool that they can carry into independent projects and research.

## 4. Teaching modules

This section and the next tell the Lotka-Volterra story in two parts. In this section, five modules build up a single prey-predator model one assumption at a time, each change introducing a new idea from dynamical systems theory. Section 5 then keeps the same mathematical tools but changes the cast: the

number of interacting populations and the kind of interactions between them. Table 1 lists the models, the concepts each one introduces, and the worked example and NWK DynSS LVPP preset that go with it. Each module and most of the extensions follow the same pattern: a description of the model and its ecological motivation, an analysis of its equilibria and their stability, a worked example with numbers that students can reproduce by hand and in the app, and suggestions for delivery and connections to ecology.

*Notation.* Throughout,  $x(t) \geq 0$  and  $y(t) \geq 0$  denote prey and predator densities, measured as numbers of individuals per unit area. The unit of area (a hectare or a square kilometre, say) is arbitrary but fixed, and every population value quoted in this paper—equilibria, initial conditions, carrying capacities, half-saturation constants and thresholds alike—is a density in these units, so that, for example, ‘prey density falls to 0.7’ means 0.7 individuals per unit area. The exceptions are the May-Leonard and Hastings-Powell models of Section 5.2, whose densities are dimensionless (scaled by a carrying capacity), and the consumer-resource systems of Section 5.3, whose densities are amounts of biomass or another currency per unit area. Following convention, the prey equation is written first, and we use  $(x, y)$  rather than subscripted variables to emphasize the trophic asymmetry between the two species. Subscripts are reserved for systems in which the populations play symmetric or repeated roles: competitors  $(x_1, x_2)$  in Section 5.1 and  $(x_1, x_2, x_3)$  in the May-Leonard model, and the levels  $x_1, x_2, \dots$  of a consumer-resource chain, fed by an abiotic resource  $x_0$ , in Section 5.3. The exception is the Hastings-Powell food chain, for which we keep the original authors’  $(x, y, z)$  so that students can read their paper alongside this note.

*An enabling mythology and how it is relaxed.* The classical model of Module 1 rests on a set of simplifying assumptions, which we make explicit to students as an ‘enabling mythology’ that the rest of the paper progressively relaxes:

- (1) each population is lumped (no spatial structure) and homogeneous (individuals are not differentiated by age, stage or sex, or by physiological, behavioral or genetic traits), with no migration, and its dynamics are deterministic, with constant parameters;
- (2) in the absence of predators, prey grow exponentially;
- (3) individuals encounter one another at random (mass action), so that the rate at which each predator consumes prey is proportional to prey density and does not depend on predator density;
- (4) there is no predator satiation: every encounter removes prey and adds predator biomass at the same rate, regardless of densities;
- (5) only two populations interact, one as prey and the other as predator.

Modules 2-5 relax assumptions 2-4. Module 2 (Section 4.2) replaces exponential prey growth with logistic growth, which turns the neutral cycles of Module 1 into a globally stable equilibrium and introduces structural stability and Lyapunov functions. Module 3 (Section 4.3) adds an Allee effect, a reduction in the per-capita growth rate of prey at low density, often due to difficulty in finding mates or to the loss of the benefits of group living (Courchamp et al., 2008); it brings in multiple attractors, separatrices, basins of attraction and catastrophic global bifurcations. Module 4 (Section 4.4) introduces predator satiation through the Holling functional responses, and with it Hopf bifurcations, limit cycles, critical slowing down and the paradox of enrichment. Module 5 (Section 4.5) combines these choices in a single culminating model with twelve switchable variants, and then relaxes the last part of assumption 3 by letting predators interfere with one another: predator-dependent responses such as Beddington-DeAngelis can damp the paradox of enrichment, and the ratio-dependent (Arditi-Ginzburg) response removes it altogether and creates an origin that attracts trajectories without being stable.

Section 5 relaxes assumption 5. Changing the signs of the interaction terms gives the Gause-Lotka-Volterra competition model (Section 5.1), with its outcomes of coexistence, competitive exclusion and saddle-mediated bistability. Adding a third population (Section 5.2) opens the door to new behavior: a heteroclinic cycle among three cyclic competitors in the May-Leonard model, and chaos in the Hastings-Powell food chain, which no two-dimensional system can show. The metaphysiological consumer-resource systems of Section 5.3 revisit assumptions 2-4 from a mechanistic standpoint, deriving logistic growth and predator interference from the extraction and conversion of resources and stacking any number of trophic levels into food chains whose length, stability and alternative states students can explore. Finally, May's stability-complexity analysis (Section 5.5) lets the number of species grow without limit. Assumption 1 is retained throughout; Section 6 discusses what is lost by doing so and how students might go further.

Figure B.1 in Appendix B previews the qualitative behavior that students encounter in Modules 1-4.

#### 4.1. Module 1: the classical Lotka-Volterra model

##### 4.1.1. Problem description

The LVPP equations, as typically presented in a modern ecology text, are

$$\begin{aligned}\frac{dx}{dt} &= rx - bxy, \\ \frac{dy}{dt} &= cxy - dy,\end{aligned}\tag{2}$$

with four positive parameters:  $r > 0$  is the per-capita growth rate of the prey in the absence of predators;  $d > 0$  is the per-capita rate at which predators decline in the absence of prey;  $b$  is the mass-action rate at which predators remove prey; and  $c$  converts prey captured into new predators, accounting for the fact that only a proportion of ingested prey biomass becomes predator biomass. Students are asked to interpret each term, to identify which assumptions above each term encodes, and to predict what will happen to both populations.

Volterra did not start from the equations but from three 'laws' that he expected empirically observed fluctuations to satisfy (Volterra, 1926a):

- I. *The fluctuation of the two species is periodic, the period depending only on the coefficients of increase and of destruction of the two species, and on the initial numbers of the individuals of the two species.*
- II. *The average numbers of the two species tend to constant values, whatever the initial numbers may have been, so long as the coefficients of increase or of destruction of the two species and also the coefficients of protection and attack remain constant.*
- III. *If we try to destroy individuals of both species uniformly and proportionately to their number, the average number of individuals of the eaten species grows and the average number of the eating species diminishes. But increased protection of the eaten species increases the average numbers of both.*

A satisfying arc for this module is to let students *derive* each of the three laws from Eq. (2).

##### 4.1.2. Equilibria and null-isoclines

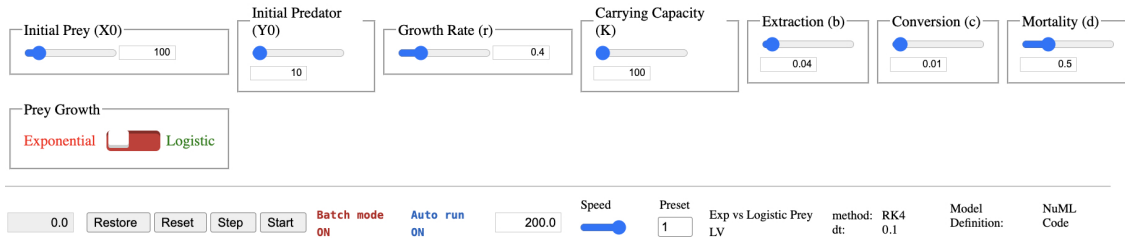
Setting  $dx/dt = x(r - by) = 0$  and  $dy/dt = y(cx - d) = 0$  gives the prey null-isoclines  $x = 0$  and  $y = r/b$ , the predator null-isoclines  $y = 0$  and  $x = d/c$ , and hence the trivial equilibrium  $(0, 0)$  and the coexistence equilibrium

$$x^* = \frac{d}{c}, \quad y^* = \frac{r}{b}.\tag{3}$$

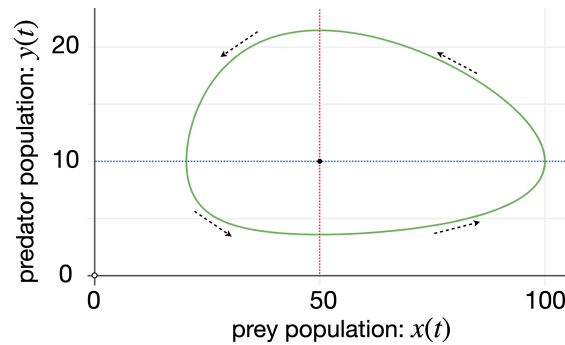
The cross-over structure of this result always surprises students: equilibrium prey density depends only on predator parameters, and vice versa (Worked example 1). Sketching the isoclines and the direction of flow in each of the four regions they define shows that trajectories rotate anticlockwise around  $(x^*, y^*)$ , but phase-plane arrows alone cannot decide whether they spiral in, spiral out, or close.

### Worked example 1: Isoclines, coexistence equilibrium and neutral stability

**Simulator setup:** Link to Preset 1. The ribbon of parameter slider values for this preset is shown below (cf. the full dashboard for Preset 1 in Fig. 1).



The value of  $K$  is not relevant unless the Prey Growth switch is on (green position). For this example it is off. With  $r = 0.4$ ,  $b = 0.04$ ,  $c = 0.01$ ,  $d = 0.5$  (rates per year), Eq. (3) gives the equilibrium densities  $x^* = 0.5/0.01 = 50$  and  $y^* = 0.4/0.04 = 10$  individuals per unit area.



The  $y$ -axis (i.e.,  $x = 0$ ) and  $x$ -axis (i.e.,  $y = 0$ ) are the trivial null-isoclines and are not distinguished here using colors, but the intersection at the origin  $(0, 0)$  (open circle) is an equilibrium with saddle point properties: close to  $(0, 0)$  in the positive quadrant, prey density increases and predator density decreases. The non-trivial prey null-isocline is  $y = 10$  (blue dotted line) and the predator null-isocline is  $x = 50$  (red dotted line). The equilibrium is their intersection  $x^* = 0.5/0.01 = 50$  and  $y^* = 0.4/0.04 = 10$  (black circle; see Eq. (3)). Counterintuitively, doubling the prey growth rate  $r$  doubles the predator equilibrium  $y^*$ , leaving  $x^*$  unchanged—a direct route into Volterra's third law. The fact that the trajectory is closed leads to the conclusion, as discussed next, that some measure (quantity) along the trajectory is conserved.

#### 4.1.3. Linearization and a conserved quantity

The Jacobian at  $(x^*, y^*)$  is

$$J^* = \begin{pmatrix} 0 & -bd/c \\ cr/b & 0 \end{pmatrix}, \quad \lambda = \pm i\sqrt{rd}, \quad (4)$$

so linearization predicts small oscillations of period  $2\pi/\sqrt{rd}$  (about 14 years for the parameters above), but—because the eigenvalues are purely imaginary—it is inconclusive about the nonlinear system. This fact points to an important limitation of linear stability analysis: when purely imaginary eigenvalues arise, deeper methods are needed. In the case of Eq. (2), the situation is resolved by demonstrating that the following function

$$V(x, y) = cx - d \ln x + by - r \ln y, \quad (5)$$

is constant along solutions. This is done by computing  $dV/dt$  using direct substitution and demonstrating that all terms cancel to obtain  $dV/dt = 0$ —that is, along any solution  $V(x, y) = V_0 = V(x_0, y_0)$ , a constant value determined by the initial condition. Since  $V$  itself is strictly convex with its minimum at the equilibrium solution  $(x^*, y^*)$ , and  $V \rightarrow \infty$  as  $x$  or  $y$  tends to 0 or  $\infty$ , its level sets  $V(x, y) = V_0$  are closed curves. Thus every positive solution of Eq. (2) runs around one of these level curves—that particular curve being determined by the initial conditions, thereby implying the solution is periodic. We see one such solution in Worked example 1, confirming Volterra’s first law. Integrating  $d(\ln y)/dt = cx - d$  over one period  $T$  gives  $\frac{1}{T} \int_0^T x \, dt = d/c = x^*$ , and similarly for  $y$ : the time averages equal the equilibrium values (Volterra’s second law). Replacing  $r$  by  $r - \varepsilon$  and  $d$  by  $d + \varepsilon$  to represent uniform harvesting then yields Volterra’s third law and D’Ancona’s observation in two lines.

#### 4.1.4. Numerical solution: what simulation does to a neutral center

The closed orbits of Eq. (2) are *neutrally* stable: their amplitude is set entirely by initial conditions. This makes the model an exceptionally sharp test of numerical methods. Forward Euler with step  $\Delta t$  moves each point along the tangent to the level curve of  $V$  through it; because  $V$  is strictly convex, every step strictly increases  $V$ , and the numerical solution spirals outwards (Figure B.1a). Students can prove this in a few lines, observe it in the Numerus WebKit™ preset by switching integrators, and then quantify how the drift scales with  $\Delta t$  for Euler and fourth-order Runge-Kutta. The lesson—that numerical methods can manufacture qualitative behavior absent from the model—is one that carries over to every later module, and opens a door to structure-preserving (symplectic) integrators for more advanced students (Hairer et al., 2006).

#### 4.1.5. Mode of delivery

In lectures, the equilibrium and isocline analysis can be developed on the board while the Numerus WebKit™ preset *Lotka-Volterra Prey Predator* is projected alongside. As an assessment, students can be asked to (i) derive Eq. (3) and the Jacobian, (ii) verify that  $V$  is conserved, (iii) prove that forward Euler increases  $V$ , and (iv) use simulation to estimate the period as a function of initial amplitude and compare it with  $2\pi/\sqrt{rd}$ .

#### 4.1.6. Connection between ecological context and mathematics

The neutral stability that makes the classical model mathematically elegant is also its principal ecological weakness: cycle amplitude depends on initial conditions, a prediction poorly supported by real predator-prey time series such as the Canadian lynx-hare data (Elton & Nicholson, 1942), which show cycles of relatively consistent amplitude and period (Turchin, 2003). Students who have just seen Euler’s method create spirals are well placed to appreciate the flip side: *any* small change to the model, numerical or biological, will generically destroy the center. This motivates Module 2.

### 4.2. Module 2: logistic prey growth and structural stability

#### 4.2.1. Problem description

Students replace exponential prey growth by logistic growth with carrying capacity  $K$ :

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{K}\right) - bxy, \\ \frac{dy}{dt} &= cxy - dy.\end{aligned}\tag{6}$$

#### 4.2.2. Analysis

The predator-free equilibrium  $(K, 0)$  is stable when  $K < d/c$  and loses stability to the coexistence equilibrium

$$x^* = \frac{d}{c}, \quad y^* = \frac{r}{b} \left(1 - \frac{d}{cK}\right)\tag{7}$$

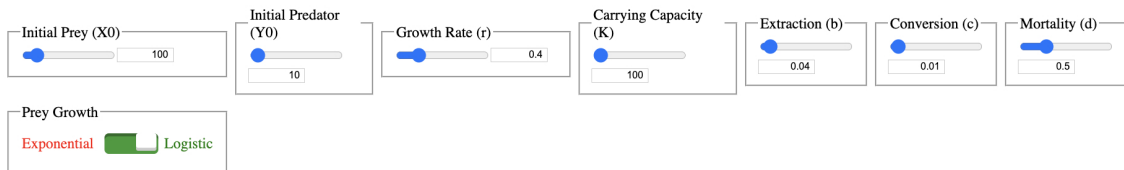
in a transcritical bifurcation at  $K = d/c$ . At  $(x^*, y^*)$  the Jacobian has trace  $-rx^*/K < 0$  and determinant  $bcx^*y^* > 0$ , so the equilibrium is always locally stable: a stable focus when  $(rx^*/K)^2 < 4bcx^*y^*$  (damped oscillations) and a stable node otherwise. With the Module 1 parameters and  $K = 100$ ,  $(x^*, y^*) = (50, 5)$  and the eigenvalues are  $-0.1 \pm 0.3i$  (Figure B.1b). Remarkably, the Module 1 function  $V$ , with  $(x^*, y^*)$  updated, still works: one finds

$$\frac{dV}{dt} = -\frac{rc}{K} (x - x^*)^2 \leq 0,\tag{8}$$

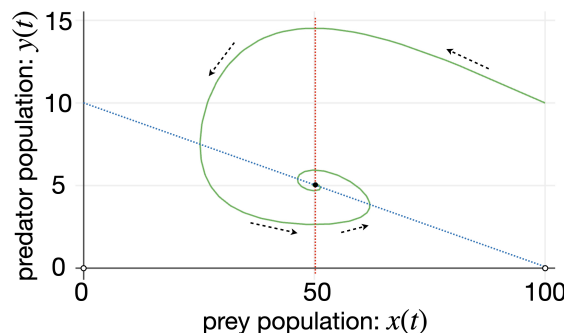
so by LaSalle's invariance principle every positive solution converges to the coexistence equilibrium. A single, arbitrarily weak self-limitation term has converted a center into a globally attracting focus—a concrete illustration of structural (in)stability. Worked example 2 applies this analysis to the parameters of Worked example 1.

#### Worked example 2: Damped spiral into a stable focus, and saddle point boundaries

**Simulator setup:** [Link to Preset 1](#). Keep the parameters of Worked example 1 but flip the Prey Growth switch to green. The ribbon of parameter slider values for this example is shown below.



Ensure prey carrying capacity is set to  $K = 100$ . Coexistence requires  $K > d/c = 50$ , which holds, and Eq. (7) gives the equilibrium densities  $x^* = 0.5/0.01 = 50$  and  $y^* = (0.4/0.04)(1 - 0.5/(0.01 \times 100)) = 10 \times 0.5 = 5$ .



The predator isocline is again the vertical line  $x = 50$  (red dotted line), but the prey isocline is now the sloping line  $y = (r/b)(1 - x/K) = 10(1 - x/100)$  (blue dotted line), running from  $(0, 10)$  to  $(100, 0)$ . The equilibrium  $(50, 5)$  is their intersection. There the Jacobian is

$$J^* = \begin{pmatrix} -rx^*/K & -bx^* \\ cy^* & 0 \end{pmatrix} = \begin{pmatrix} -0.2 & -2 \\ 0.05 & 0 \end{pmatrix},$$

with trace  $-0.2$  and determinant  $0.1$ , so  $\lambda = -0.1 \pm 0.3i$ . The trajectory that starts at  $(100, 10)$ —a point on the closed orbit of Worked example 1—no longer closes: it spirals into  $(50, 5)$ , with the oscillations decaying like  $e^{-0.1t}$  (the amplitude halves roughly every 7 years) and a period of  $2\pi/0.3 \approx 21$  years. Predator density peaks first at about 14.5 and then at only about 5.9. If  $K$  is reduced below  $d/c = 50$ , the prey isocline meets the  $x$ -axis to the left of the predator isocline, the coexistence equilibrium disappears, and the predators go extinct: the transcritical bifurcation at  $K = d/c$ .

### 4.2.3. Mode of delivery and connections

This module pairs naturally with the trace-determinant classification of planar linear systems. In simulation, students can vary  $K$  through the transcritical point and watch the predator invade, and can compare the decay rate of oscillations with the real part of the eigenvalues. Ecologically, the module raises the question of what regulates populations, and why real cycles persist despite self-limitation—leading to Modules 3 and 4.

## 4.3. Module 3: an Allee effect in the prey

### 4.3.1. Problem description

Small populations often struggle to find mates or defend against predators, so their per-capita growth rate declines at low density—an Allee effect (Courchamp et al., 2008). We implement it by replacing the constant  $r$  in Eqs. (2) or (6) with

$$f(x) = r \left( 1 - \gamma e^{-\alpha(x-L)} \right), \quad \alpha > 0, \gamma > 1, 0 < L < K. \quad (9)$$

The function  $f$  is a shifted, saturating exponential that students may recognize from von Bertalanffy growth or learning curves:  $r$  is the asymptote ( $f(x) \rightarrow r$  as  $x \rightarrow \infty$ );  $L$  shifts the curve horizontally without altering its shape;  $\gamma$  sets how far below zero the curve lies at  $x = L$ , where  $f(L) = r(1 - \gamma) < 0$ ; and  $\alpha$  controls how sharply  $f$  saturates. Our approach differs from that of Zeng and Yu (2024), who use the function  $f(x) = r(x - L)$ . This function has the advantage over ours of using only two parameters rather than four, but the tradeoff is that it acts globally rather than locally: ours saturates to  $r$  for large  $x$ , thereby preserving the interpretation of  $K$  as a carrying capacity and providing parameters  $\alpha$  and  $\gamma$  for better fits to data when available, while theirs increases linearly for  $x > L$ , thereby distorting the interpretation of  $r$  and  $K$  when  $x$  is large.

The predator-free Allee threshold associated with Eq. (9) is the root of  $f(x) = 0$

$$x_A = L + \frac{\ln \gamma}{\alpha}, \quad (10)$$

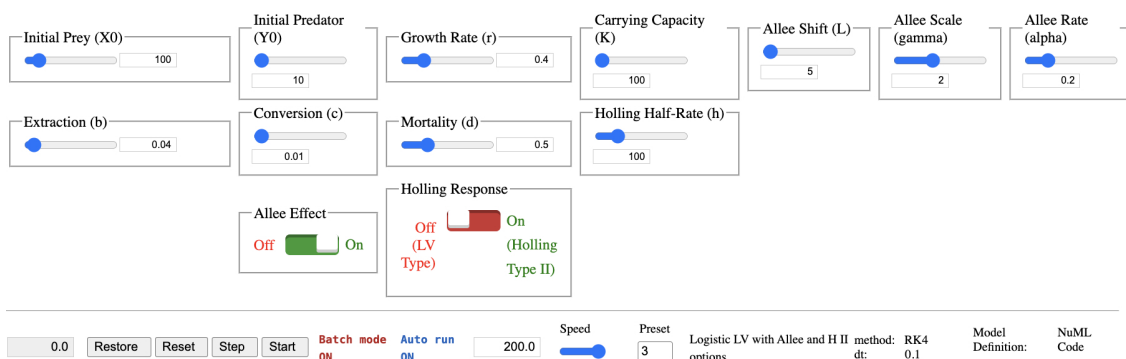
below which the prey declines even without predators.

### 4.3.2. Multiple attractors and basins of attraction

With logistic prey growth, the predator-free axis now has three equilibria,  $0 < x_A < K$ , and the origin is itself a stable node because  $f(0) < 0$ . For the parameters of Figure B.1c and Worked example 3 ( $x_A \approx 8.5$ ,  $x^* = 50$ ,  $y^* \approx 5$ ), the system is bistable: trajectories either approach coexistence or collapse to joint extinction. The most instructive observation is that the threshold in two dimensions is not the line  $x = x_A$  but a curve (the stable manifold of a saddle): a prey density well above  $x_A$  can still collapse if predator density is initially high. Basins of attraction are rarely computable analytically, so students map them by simulation, sweeping a grid of initial conditions in the Numerus WebKit™ preset and coloring each by its fate. Bistability is not the end of the story. Moving the predator isocline  $x = d/c$  to the left, for instance by lowering the predator mortality rate  $d$  with its slider (other parameters as in Worked example 3), takes students through a sequence of local and global bifurcations that is well worth exploring in class. For  $d > cK = 1$  predators cannot invade. Below  $d = 1$  the coexistence equilibrium is a stable node, becoming a stable focus for  $d < 0.91$ , and its basin of attraction is bounded by the stable manifold of the saddle  $(x_A, 0)$ , as in Worked example 3. At  $d \approx 0.31$  ( $x^* \approx 31$ ) the basin boundary changes character in a *heteroclinic bifurcation*: the stable manifold of  $(x_A, 0)$  joins the unstable manifold of  $(K, 0)$ , forming a loop with the segment of the prey axis between the two saddles, and as  $d$  decreases further this loop breaks into an *unstable* limit cycle around the equilibrium. For  $0.225 < d < 0.31$  the basin of coexistence is just the interior of this cycle, which shrinks as  $d$  falls (at  $d = 0.25$  prey density on the cycle ranges from about 13 to 43). At  $d \approx 0.225$ , where  $x^* \approx 22.5$  reaches the peak of the prey isocline, the cycle closes down onto the equilibrium in a *subcritical* Hopf bifurcation, and for smaller  $d$  every trajectory with predators present collapses to  $(0, 0)$ . The contrast with the supercritical Hopf bifurcation of Module 4 is instructive: there, loss of stability produces small, sustained oscillations, whereas here no stable cycle exists and loss of stability is catastrophic, an example of the ‘overexploitation’ that van Voorn et al. (2007) showed to be signalled by heteroclinic orbits in predator-prey models with a strong Allee effect. Students can find both thresholds with the sensitivity mode, sweeping  $d$  and starting each run close to the equilibrium (for the Hopf threshold) or close to  $(K, 0)$  with very few predators (for the heteroclinic threshold).

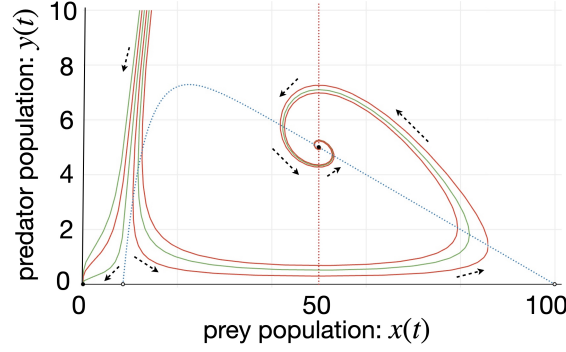
#### Worked example 3: Allee effect, separatrix and basins of attraction

**Simulator setup:** [Link to Preset 3](#). Keep the parameters of Worked example 2 ( $r = 0.4$ ,  $b = 0.04$ ,  $c = 0.01$ ,  $d = 0.5$ ,  $K = 100$ ). The ribbon of parameter slider values for this example is shown below; it now includes an Allee effect switch (Eq. (9)) in the “on” (default) position, with Allee function parameters  $\alpha = 0.2$ ,  $\gamma = 2$  and  $L = 5$ .



The Allee threshold is  $x_A = 5 + \ln 2/0.2 \approx 8.5$ , and  $f(0) = 0.4(1 - 2e) \approx -1.77 < 0$ . The predator isocline is still  $x = d/c = 50$ , and since  $f(50) \approx r$ , the coexistence equilibrium is

$(x^*, y^*) \approx (50, 5.0)$ —essentially the stable focus of Worked example 2, with  $\lambda \approx -0.10 \pm 0.30i$ . The prey isocline  $y = f(x)(1 - x/K)/b$  is now a hump that meets the  $x$ -axis at  $x_A \approx 8.5$  and at  $K = 100$  and peaks at  $y \approx 7.3$  near  $x \approx 22.5$ . There are four equilibria:  $(0, 0)$ , a stable node (eigenvalues  $f(0) \approx -1.77$  and  $-d = -0.5$ );  $(x_A, 0)$  and  $(K, 0)$ , both saddles; and  $(50, 5.0)$ , a stable focus.



The figure shows the predator isocline  $x = 50$  (red dotted line), the humped prey isocline (blue dotted line) rising from the saddle at  $(x_A, 0)$  (open circle), and the stable equilibria at  $(0, 0)$  and  $(50, 5)$  (black dots); the axes  $x = 0$  and  $y = 0$  are also null-isoclines. Six trajectories start with the same predator density,  $y_0 = 10$ , and prey densities  $x_0 = 12, 12.5, 13, 13.5, 14$  and  $14.5$  (colors alternate only to separate neighboring curves). All six start well above the predator-free Allee threshold  $x_A \approx 8.5$ , yet the three starting at  $x_0 \leq 13$  collapse to  $(0, 0)$ , while the three starting at  $x_0 \geq 13.5$  sweep out in a wide loop—on which predators fall to below one individual per unit area—before spiralling into coexistence at  $(50, 5)$ . Simulation places the boundary between the two basins of attraction at  $x_0 \approx 13.1$  when  $y_0 = 10$ , so a difference of half a prey individual per unit area decides the fate of both populations. The boundary or separatrix is therefore a curve in the phase plane (the stable manifold of the saddle at  $(x_A, 0)$ ), not the vertical line  $x = x_A$ : the higher the predator density, the higher the prey density needed to escape collapse (at  $x_0 = 20$ , for instance, the boundary lies near  $y_0 \approx 16.8$ ).

#### 4.3.3. Mode of delivery and connections

This module introduces the language of tipping points and resilience, and connects directly to conservation of small or harvested populations (Courchamp et al., 2008; Kleshnina et al., 2026).

### 4.4. Module 4: Holling functional responses and limit cycles

#### 4.4.1. Problem description

Real predators become satiated. Following Holling (1959a, 1959b) and Rosenzweig and MacArthur (1963), we write

$$\begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{K}\right) - b \phi(x) y, \\ \frac{dy}{dt} &= c \phi(x) y - dy, \end{aligned} \quad (11)$$

where  $\phi$  is one of the dimensionless Holling responses

$$\text{Type I: } \phi = \min\left(\frac{x}{h}, 1\right), \quad \text{Type II: } \phi = \frac{x}{x + h}, \quad \text{Type III: } \phi = \frac{x^2}{x^2 + h^2}, \quad (12)$$

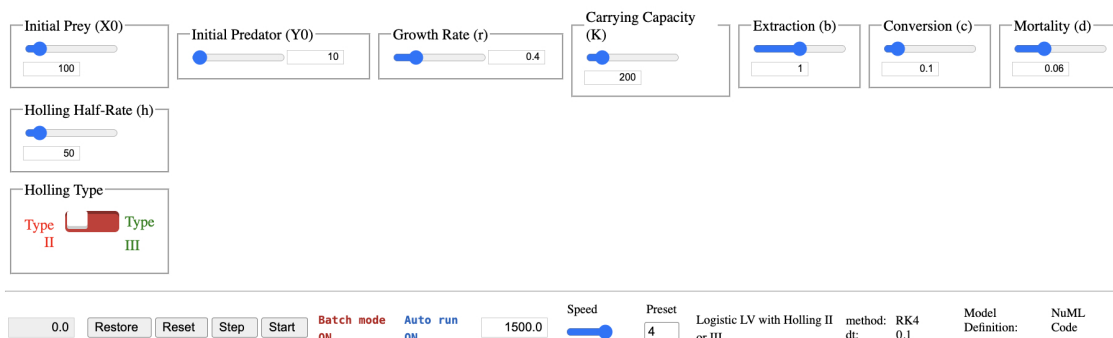
so that  $b$  is now the maximum per-predator consumption rate,  $c$  the maximum per-capita predator recruitment rate, and  $h$  the half-saturation prey density (for Type I, the density at which consumption saturates).

#### 4.4.2. Hopf bifurcation and the paradox of enrichment

For Type II, the coexistence equilibrium has  $x^* = hd/(c - d)$  (requiring  $c > d$ ), and the prey isocline  $y = (r/b)(1 - x/K)(x + h)$  is a parabola peaking at  $x = (K - h)/2$ . The Rosenzweig-MacArthur graphical criterion (Hammoum et al., 2023; Rosenzweig, 1971; Rosenzweig & MacArthur, 1963) states that the equilibrium is stable when the vertical predator isocline cuts the prey isocline to the right of its peak and unstable when it cuts to the left. The switch occurs at  $K_H = 2x^* + h$  through a Hopf bifurcation; since trajectories remain in a bounded region of the positive quadrant containing a single, unstable equilibrium, the Poincaré-Bendixson theorem (see Appendix A.4) guarantees a limit cycle. With the parameters of Worked example 4 ( $r = 0.4$ ,  $b = 1$ ,  $c = 0.1$ ,  $d = 0.06$ ,  $h = 50$ ), we have  $x^* = 75$  and  $K_H = 200$ :  $K = 150$  gives a stable focus and  $K = 250$  a large-amplitude limit cycle on which prey density ranges from about 6 to 213 (Figure B.1d). Enriching the prey's environment thus destabilizes the system: the paradox of enrichment (Rosenzweig, 1971). With further enrichment the troughs deepen: for  $K = 300$  prey density falls to about 0.7, below one individual per unit area, prompting a valuable discussion of when continuous-density models stop being credible. Type III responses, by contrast, provide a prey refuge at low density and tend to stabilize the interaction, which students can confirm with the preset's switches. Worked example 4 works through the Type II case with numbers, and Appendix C (Figure C.1) sets out the graphical stability criterion and its extension to predator interference in more detail.

#### Worked example 4: Hopf bifurcation and the existence of a stable limit cycle

**Simulator setup:** Link to Preset 4. Because  $b$  and  $c$  are now parameters in functions rather than constant rates, the parameters of Worked example 1 cannot be reused unchanged: predators persist only if  $c > d$ . We therefore keep  $r = 0.4$  but now take  $b = 1$ ,  $c = 0.1$ ,  $d = 0.06$  and  $h = 50$ , which are the default values on the Preset 4 dashboard shown below.



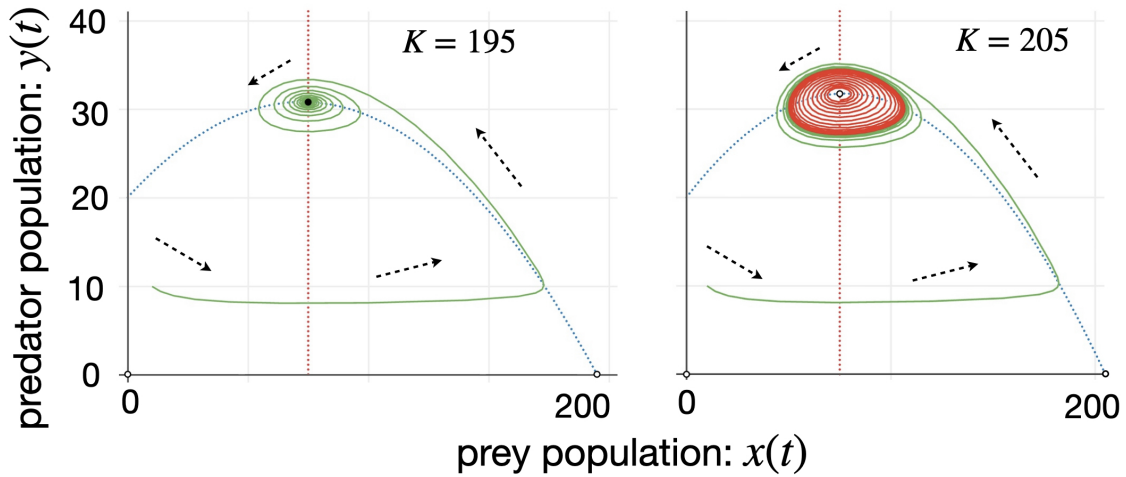
This ensures that  $c > d$  and  $x^* = hd/(c - d) = 50 \times 0.06/0.04 = 75$  is a reasonable value to work with. The ratio  $c/b = 0.1$  means that each prey eaten adds one-tenth of a predator, a 10% conversion efficiency in line with the familiar ‘ten per cent rule’ of energy transfer between trophic levels; and since  $d = 0.06$  is much smaller than  $r = 0.4$ , the predators are long-lived relative to their prey. The predator isocline is the vertical line  $x = 75$ , and the prey isocline  $y = (r/b)(1 - x/K)(x + h)$  is a hump that starts at  $y = rh/b = 20$  on the  $y$ -axis, peaks at  $x = (K - h)/2$  and falls to zero at  $x = K$ .

At  $(x^*, y^*)$  the Jacobian has

$$J_{11} = \frac{r x^* (K - h - 2x^*)}{K (x^* + h)}, \quad J_{12} = -\frac{b x^*}{x^* + h} = -0.6, \quad J_{21} = \frac{c h y^*}{(x^* + h)^2}, \quad J_{22} = 0,$$

so the trace  $J_{11}$  has the sign of  $K - h - 2x^* = K - 200$ : the Rosenzweig-MacArthur graphical criterion in algebraic form, with a Hopf bifurcation at  $K_H = 2x^* + h = 200$ . We compare two carrying capacities that differ by only about 5% and lie either side of  $K_H$ .

- $K = 195$ : the hump peaks at  $x = 72.5$ , to the left of  $x^* = 75$ . Then  $y^* = 30.77$ ,  $J_{21} = 0.00985$ , the trace is  $-0.0062$  and the determinant  $0.0059$ , giving  $\lambda = -0.0031 \pm 0.0768i$ . The equilibrium is a stable focus, but a weakly damped one: oscillations have a period of about 82 years, and their amplitude shrinks by only about 22% per cycle, halving roughly every 225 years.
- $K = 205$ : the hump peaks at  $x = 77.5$ , to the right of  $x^* = 75$ . Then  $y^* = 31.71$ ,  $J_{21} = 0.01015$ , the trace is  $+0.0059$  and the determinant  $0.0061$ , giving  $\lambda = +0.0029 \pm 0.0780i$ . The equilibrium is an unstable focus, and trajectories approach a limit cycle with a period of about 84 years on which prey density ranges from about 50 to 107 and predator density from about 27 to 34.5.



In the figure, the left panel shows  $K = 195$  and the right panel  $K = 205$ ; the dotted lines are the predator isocline  $x = 75$  (red) and the prey isocline (blue), the filled dot marks the stable equilibrium for  $K = 195$ , and open circles mark unstable equilibria, including the coexistence equilibrium for  $K = 205$  and the saddles at  $(0, 0)$  and  $(K, 0)$ . The green trajectories start from the same point,  $(10, 10)$ , in both panels. Because prey density is far below the density  $x^* = 75$  needed to sustain the predators, predator density at first declines (to about 8 within the first decade) while prey density grows almost logistically, to about 173 ( $K = 195$ ) or 182 ( $K = 205$ ) by year 25; the trajectory turns where it crosses the prey isocline, predators then increase on the abundant prey, and prey crash. This first, large excursion is almost identical in the two panels. Thereafter the paths diverge. For  $K = 195$  the trajectory spirals inwards to the stable focus  $(75, 30.8)$ : after 500 years prey density oscillates only between about 70 and 81, and by about 2000 years the system is at equilibrium. For  $K = 205$  the green trajectory spirals inwards too, but onto the limit cycle (prey density between about 50 and 107), which it reaches after about 1000 years. The red trajectory starts at  $(75, 31)$ , just below the unstable equilibrium  $(75, 31.7)$ , and spirals *outwards* onto the same cycle, taking

about 1500 years to reach it. Trajectories approaching the cycle from both inside and outside show that it is a stable, attracting limit cycle—the signature of a supercritical Hopf bifurcation. Table 2 compares the two cases, and the lessons they teach are discussed after this worked example.

**Table 2.** The Holling Type II model of Worked example 4 ( $r = 0.4$ ,  $b = 1$ ,  $c = 0.1$ ,  $d = 0.06$ ,  $h = 50$ , so  $x^* = 75$ ) for carrying capacities either side of the Hopf bifurcation at  $K_H = 200$ . Long-term outcomes were confirmed by RK4 simulations run for 20 000 years.

|                              | $K = 195$                             | $K = 205$                                                 |
|------------------------------|---------------------------------------|-----------------------------------------------------------|
| Peak of prey isocline        | $x = 72.5$ (left of $x^* = 75$ )      | $x = 77.5$ (right of $x^* = 75$ )                         |
| Predator equilibrium $y^*$   | 30.77                                 | 31.71                                                     |
| Eigenvalues $\lambda$        | $-0.0031 \pm 0.0768i$                 | $+0.0029 \pm 0.0780i$                                     |
| Long-term outcome            | stable focus                          | limit cycle: $50 \leq x \leq 107$ , $27 \leq y \leq 34.5$ |
| Period of oscillation        | $\approx 82$ years                    | $\approx 84$ years                                        |
| Time to settle from (10, 10) | $\approx 2000$ years (to equilibrium) | $\approx 1000$ years (to cycle)                           |
| Time to settle from (75, 31) | —                                     | $\approx 1500$ years (to cycle)                           |

These two similar systems teach three lessons that extend well beyond predator-prey theory.

- (1) *A small change in a parameter can change the long-term outcome qualitatively.* Raising  $K$  by about 5%, from 195 to 205, turns coexistence at a stable point into perpetual oscillation in which prey density more than doubles between trough and peak: the paradox of enrichment at its sharpest. Near a bifurcation, small uncertainties in parameter values translate into large uncertainties in qualitative predictions (Appendix A.7).
- (2) *Near a bifurcation, dynamics become slow ('critical slowing down').* Because the real parts of the eigenvalues ( $\pm 0.003$ ) are small compared with the frequency (0.078), the amplitude of oscillation changes by only about 20% per 80-year cycle. Started from (10, 10), the two systems trace almost the same large first excursion, and a century later they still look alike: between years 100 and 200, prey density oscillates between about 54 and 109 for  $K = 195$  and between about 44 and 115 for  $K = 205$ —a difference that would be hard to detect in noisy field data. Only after several cycles does one trajectory settle at the equilibrium while the other converges onto its limit cycle, and the red trajectory for  $K = 205$ , started close to the unstable equilibrium, still has prey density confined to between about 65 and 86 after 200 years. These time scales are inversely proportional to the distance from the bifurcation: for  $K = 199$  and  $K = 201$ , which lie five times closer to  $K_H$ , the real parts of the eigenvalues are five times smaller and the times to settle stretch to several thousand years (about 8000 years for  $K = 199$  to reach equilibrium). Students should therefore run simulations long enough to separate transient from long-term behavior.
- (3) *The case is a useful test of numerical methods.* With  $\lambda = \alpha \pm i\omega$ , forward Euler with step  $\Delta t$  multiplies the amplitude of small oscillations by  $|1 + \lambda\Delta t|$  per step, adding a spurious growth rate of roughly  $\omega^2\Delta t/2$ , so Euler gets the stability of the equilibrium right only if  $\Delta t < 2|\alpha|/\omega^2 \approx 1$ . With  $\Delta t = 0.5$  Euler gives the correct qualitative answer but the wrong numbers: the damping for  $K = 195$  appears about half as strong as it really is, and the  $K = 205$  limit cycle is inflated (prey density between about 45 and 115 instead of 50 and 107). With  $\Delta t = 1.5$ , Euler produces a sustained cycle for  $K = 195$  (prey density between about 59 and 93) where none exists. RK4 with the NWK DynSS LVPP default  $\Delta t = 0.5$  gives the correct answer in both cases—an echo, near a bifurcation, of the numerical lesson of Module 1.

#### 4.4.3. Mode of delivery and connections

Analytically, students locate  $x^*$ , apply the graphical criterion and compute  $K_H$ ; numerically, they construct a bifurcation diagram by sweeping  $K$  and recording the maxima and minima of  $x(t)$  after transients. This module is where analysis and simulation most clearly need each other: the Hopf theorem tells students that a cycle exists, while simulation tells them what it looks like.

### 4.5. Module 5: a culminating prey-predator system

#### 4.5.1. Problem description

The final module combines all of the preceding assumptions in a single model,

$$\begin{aligned}\frac{dx}{dt} &= g(x) f(x) - b \phi(x) y, \\ \frac{dy}{dt} &= c \phi(x) y - d y,\end{aligned}\tag{13}$$

where  $g(x) = x$  (exponential prey growth) or  $g(x) = x(1 - x/K)$  (logistic growth);  $f(x) = r$  (no Allee effect) or Eq. (9) (Allee effect); and  $\phi(x) = x$  (mass action, recovering Modules 1–3) or a Type II or III response from Eq. (12). In the Numerus WebKit™ preset these choices are implemented as dashboard switches, giving  $2 \times 2 \times 3 = 12$  model variants that can be overlaid on the same graph. A natural further option, discussed below, is to let  $\phi$  depend on predator as well as prey density.

Before students start switching assumptions on and off, it is worth asking what the parameters of Eq. (13) actually represent. The metaphysiological view of population growth (Getz, 1991, 1993, 2011) treats every population, prey and predator alike, as a consumer whose biomass changes according to a budget: biomass is gained by *extracting* resources and *converting* them into its own tissue, and lost through *metabolism* (maintenance respiration), *senescence* (all deaths other than being eaten) and *extraction* by its own consumers. Read this way, the predator equation is a balance sheet. The total rate at which prey biomass is removed is  $b \phi y$ ; if a fraction  $\eta$  of each kill is not eaten (it is *diverted* to carcasses) and the remainder is converted to predator biomass with efficiency  $\kappa$ , then

$$c = \kappa (1 - \eta) b \quad \text{and} \quad d = \alpha + \mu,\tag{14}$$

where  $\alpha$  is the predators' per-capita metabolic rate and  $\mu$  their per-capita senescence rate. The ratio  $c/b = \kappa(1 - \eta)$  is the overall efficiency with which prey biomass becomes predator biomass, which is why it should lie well below one: the value  $c/b = 0.1$  of Worked example 4 corresponds, for example, to predators that, like cheetahs, abandon about 15% of each kill (Getz, 2011) and convert the rest with an efficiency of about 12%. The prey equation can be read in the same way, since prey are themselves consumers of an environmental resource; the logistic term  $g(x)$  then emerges from intraspecific competition for that resource rather than being imposed. This reinterpretation changes nothing in the mathematics of Modules 1–4, but it gives each parameter a physiological meaning that students can reason about, estimate and check for plausibility.

#### 4.5.2. Model comparison and structural sensitivity

Students are given a table of the twelve variants (Table 3), asked to predict the qualitative behavior of each from the modules already completed, and then to test their predictions by simulation. Discrepancies between prediction and simulation become the focus of discussion. The broader lesson is that qualitative conclusions can depend more on the *form* of a model than on its parameter values, a point with direct consequences for how models are used in resource management.

**Table 3.** Long-term behavior of the coexistence state in the culminating model, Eq. (13). Wherever the Allee effect is included, the origin is also an attractor. Entries were checked by simulation with the parameters of Worked examples 2 and 3 (mass action) and 4 (Types II and III,  $h = 50$ ), with  $\alpha = 0.2$ ,  $\gamma = 2$  and  $L = 5$  in the Allee rows; the values of  $K$  given are for these parameters.

| Prey growth         | Mass action                                                                                                                          | Holling Type II                                                                                 | Holling Type III                                                                                                                                                                                  |
|---------------------|--------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Exponential         | Neutral center (closed orbits)                                                                                                       | Unstable (focus or node); prey escape predator control                                          | Locally stable if $x^* < h$ (prey can still escape from low predator densities); unstable, with prey escaping predator control, if $x^* > h$ (as for the parameters used here, $x^* \approx 61$ ) |
| Logistic            | Globally stable point (if $K > d/c$ )                                                                                                | Stable point or limit cycle (Hopf at $K_H$ )                                                    | Stable point or limit cycle; more stable than Type II                                                                                                                                             |
| Exponential + Allee | Weakly unstable focus; oscillations grow slowly until both species collapse to $(0, 0)$                                              | Unstable; prey either escape predator control or both species collapse                          | As without the Allee effect, plus collapse to $(0, 0)$ : here ( $x^* > h$ ) prey either escape predator control or both species collapse                                                          |
| Logistic + Allee    | Bistable: coexistence or collapse (Figure B.1c); collapse for all starts once $x^*$ lies left of the prey isocline's peak (Module 3) | Bistable for $K < K_H = 200$ ; stable limit cycle for $200 < K < 222$ ; collapse for larger $K$ | Same sequence at higher $K$ : Hopf at $K \approx 367$ , cycle up to $K \approx 488$ , then collapse                                                                                               |

#### 4.5.3. Beyond prey dependence: predator interference and ratio dependence

Every functional response used so far, from mass action to Holling Types I–III, depends only on prey density:  $\phi = \phi(x)$ . This is the oldest and most widely taught assumption in predation theory, and it fits data from small, well-mixed laboratory systems well (Tyutyunov & Titova, 2021). Its geometric signature is the vertical predator isocline  $x = x^*$ , which students have met in every module. A vertical isocline means that a fixed density of prey can sustain predators at *any* density, with three counter-intuitive consequences. Enriching the prey's environment raises the predator equilibrium but leaves the prey equilibrium unchanged; it can also destabilize the system (the paradox of enrichment of Module 4); and a biological control agent can hold a pest at a low density only by inducing large-amplitude oscillations (the paradox of biological control). Field data from large-scale ecosystems rarely show these patterns, and Arditi and Ginzburg (1989) traced the contradiction to the verticality of the predator isocline itself (see also Arditi & Berryman, 1991; Arditi & Ginzburg, 2012; Jensen & Ginzburg, 2005).

The remedy they proposed is to let predators interfere with one another, so that each predator's rate of consumption declines as predators become more abundant. Arditi and Ginzburg (1989) framed the possibilities as a spectrum of functional responses,

$$\phi(x) \longleftarrow \phi(x, y) \longrightarrow \phi(x/y), \quad (15)$$

running from *prey dependence* on the left, where predators do not share prey at all, to *ratio dependence* on the right, where prey are shared perfectly and what matters is the amount of prey available per

predator. In the dimensionless notation of Eq. (12), two widely used predator-dependent responses are

$$\text{Beddington-DeAngelis: } \phi(x, y) = \frac{x}{x + h_H + h_r y}, \quad (16)$$

and its special case

$$\text{Arditi-Ginzburg: } \phi(x, y) = \frac{x/y}{x/y + h_r} = \frac{x}{x + h_r y}. \quad (17)$$

In Eq. (16),  $h_H \geq 0$  is the Holling half-saturation density of Eq. (12) and  $h_r \geq 0$  is the ratio-dependent parameter. In the Beddington-DeAngelis response,  $h_r$  is a measure of the strength of interference among predators (Beddington, 1975; DeAngelis et al., 1975), whereas in the Ardit-Ginzburg response, Eq. (17), it is the prey-to-predator ratio at which predators feed at half their maximum rate. The Ardit-Ginzburg response is simply the Holling Type II response with prey density replaced by prey per predator; it adds no parameters, which is why its authors advocate it as a minimal, or ‘null’, model of predator interference (Arditi & Ginzburg, 1989, 2012). Table 4 summarizes these and other widely used responses in the notation of this paper, together with the shape of the predator isocline each one produces. It also has an instructive history. The first trophic function to account for interference among predators, proposed by Ivlev from feeding experiments on fish, was already ratio dependent (Ivlev, 1961). And in microbiology, the Type II form is Monod’s model of bacterial growth while the ratio-dependent form is Contois’s: Monod worked at low bacterial densities and Contois at high ones, so each found the edge of the spectrum appropriate to his conditions (Contois, 1959; Monod, 1949; Tyutyunov & Titova, 2021).

The effect on the phase plane is easy for students to derive. Setting  $dy/dt = 0$  with the Ardit-Ginzburg response gives the predator isocline

$$y = \frac{c - d}{d h_r} x, \quad (18)$$

a straight line through the origin rather than a vertical line: more predators now require more prey to sustain them. With logistic prey growth, the coexistence equilibrium can be found in closed form,

$$x^* = K \left( 1 - \frac{b(c - d)}{c r h_r} \right), \quad y^* = \frac{c - d}{d h_r} x^*, \quad (19)$$

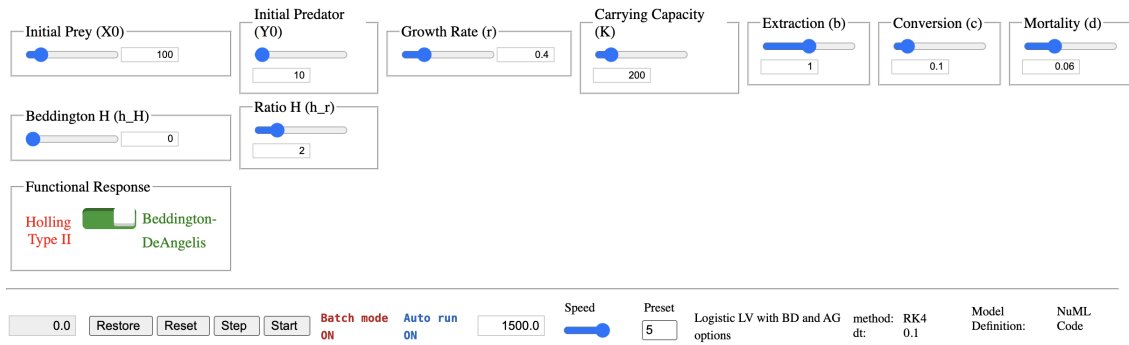
provided that  $c r h_r > b(c - d)$ . Both equilibrium densities are proportional to  $K$ , so enrichment raises prey and predators together, and a short calculation shows that every entry of the Jacobian at  $(x^*, y^*)$  is independent of  $K$ . Enrichment therefore cannot change the stability of the equilibrium: the paradox of enrichment disappears (Worked example 5).

#### Worked example 5: Non-destabilizing enrichment and a strange equilibrium point

**Simulator setup:** [Link to Preset 5](#). In this case we use the parameters of Worked example 4 ( $r = 0.4$ ,  $b = 1$ ,  $c = 0.1$ ,  $d = 0.06$ ), but with **Switch1** on (green), so that the Holling Type II response function is replaced by the Ardit-Ginzburg response of Eq. (17), a special case of the Beddington-DeAngelis response of Eq. (16) when  $h_H = 0$ . Additionally set  $h_r = 2$  and  $K = 200$ , the value at which the prey-dependent model of Worked example 4 sits exactly at its Hopf bifurcation. Thus the setup we now have for Preset 5 is

**Table 4.** Functional responses  $\phi$  arranged along the prey-dependent to ratio-dependent spectrum of Eq. (15), in the notation of the culminating model, Eq. (13):  $dx/dt = g(x)f(x) - b\phi y$  and  $dy/dt = c\phi y - d y$ , with  $\phi(x)$  generalized to  $\phi(x, y)$  where predators interfere. Except for mass action,  $\phi$  is dimensionless, so that  $b$  and  $c$  are the maximum per-predator consumption and recruitment rates;  $h$  is a prey density and  $h_r$  a prey-to-predator ratio at which consumption is half (Holling Types II and III, and, in the absence of predators, Beddington-DeAngelis, Crowley-Martin, Arditi-Ginzburg) or  $1 - e^{-1} \approx 63\%$  (Ivlev) of its maximum. The fourth column gives the predator null-isocline obtained from  $c\phi = d$ ; the parameter in the third column controls the strength of predator interference. In the metaphysiological interpretation of Eq. (14),  $c = \kappa(1 - \eta)b$  and  $d = \alpha + \mu$  for every response in the table. Adapted and extended from Table 1 of Tyutyunov and Titova (2021), with the addition of the consumer-competition response of Getz (2011).

| Response (typical setting)                                    | $\phi$                                    | Interference                                                                                                                     | Predator isocline ( $c\phi = d$ )                                                                          | Key references                                       |
|---------------------------------------------------------------|-------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------|------------------------------------------------------|
| <i>Prey dependent: <math>\phi = \phi(x)</math></i>            |                                           |                                                                                                                                  |                                                                                                            |                                                      |
| Lotka-Volterra mass action (random encounters, no satiation)  | $x$                                       | none                                                                                                                             | vertical: $x = d/c$                                                                                        | Lotka (1925) and Volterra (1926a)                    |
| Holling Type I (filter feeders)                               | $\min\left(\frac{x}{h}, 1\right)$         | none                                                                                                                             | vertical: $x = hd/c$                                                                                       | Holling (1959a)                                      |
| Holling Type II; Monod (handling time)                        | $\frac{x}{x + h}$                         | none                                                                                                                             | vertical: $x = \frac{hd}{c - d}$                                                                           | Holling (1959b) and Monod (1949)                     |
| Gause-Ivlev (fish rations)                                    | $1 - e^{-x/h}$                            | none                                                                                                                             | vertical: $x = -h \ln\left(1 - \frac{d}{c}\right)$                                                         | Gause (1934) and Ivlev (1961)                        |
| Holling Type III (prey switching, refuges)                    | $\frac{x^2}{x^2 + h^2}$                   | none                                                                                                                             | vertical: $x = h\sqrt{\frac{d}{c - d}}$                                                                    | Holling (1959a) and Real (1977)                      |
| <i>Predator dependent: <math>\phi = \phi(x, y)</math></i>     |                                           |                                                                                                                                  |                                                                                                            |                                                      |
| Beddington-DeAngelis (interference while searching)           | $\frac{x}{x + h + w y}$                   | $w \geq 0$ ; $w = 0$ is Type II                                                                                                  | sloping line: $y = \frac{(c - d)x - d h}{d w}$                                                             | Beddington (1975) and DeAngelis et al. (1975)        |
| Crowley-Martin (interference even when handling)              | $\frac{x}{(x + h)(1 + \beta y)}$          | $\beta \geq 0$ ; $\beta = 0$ is Type II                                                                                          | rising curve, leveling off at $y = \frac{c - d}{d \beta}$                                                  | Bazykin et al. (1981) and Crowley & Martin (1989)    |
| Getz (competition for food with abrupt onset)                 | $\frac{x}{x + h [1 + (y/\gamma)^\theta]}$ | $\gamma > 0$ , $\theta \geq 1$ ; $\theta = 1$ is Beddington-DeAngelis ( $w = h/\gamma$ ), $\gamma \rightarrow \infty$ is Type II | rising curve from $x = \frac{hd}{c - d}$ : $y = \gamma \left( \frac{(c - d)x}{d h} - 1 \right)^{1/\theta}$ | Getz (1984, 1996, 2011)                              |
| Hassell-Varley-Holling (aggregating predators, parasitoids)   | $\frac{x}{x + h y^m}$                     | $m \geq 0$ ; $m = 0$ is Type II, $m = 1$ is ratio dependent                                                                      | through the origin: $y = \left( \frac{(c - d)x}{d h} \right)^{1/m}$                                        | Arditi & Akçakaya (1990) and Hassell & Varley (1969) |
| <i>Ratio dependent: <math>\phi = \phi(x/y)</math></i>         |                                           |                                                                                                                                  |                                                                                                            |                                                      |
| Arditi-Ginzburg; Contois (prey shared among active predators) | $\frac{x}{x + h_r y}$                     | none (fixed at the ratio-dependent edge)                                                                                         | straight line through the origin: $y = \frac{(c - d)x}{d h_r}$                                             | Arditi & Ginzburg (1989) and Contois (1959)          |
| Ivlev ratio dependent (competing fed fish)                    | $1 - e^{-x/(h_r y)}$                      | none                                                                                                                             | straight line through the origin: $y = -\frac{x}{h_r \ln(1 - d/c)}$                                        | Ivlev (1961)                                         |



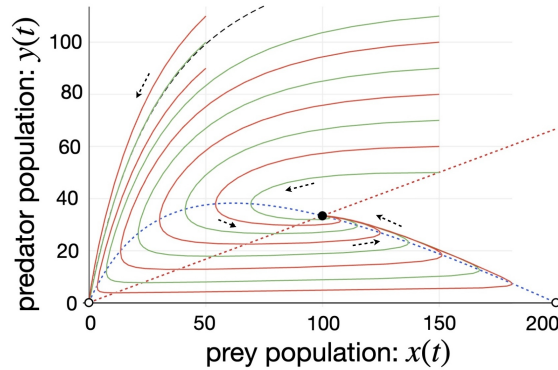
The coexistence condition holds, since  $c r h_r = 0.08 > b(c - d) = 0.04$ . The predator isocline, Eq. (18), is the line  $y = x/3$ . Setting  $dx/dt = 0$  and solving for  $y$  gives the prey isocline

$$y = \frac{r x (1 - x/K)}{b - r h_r (1 - x/K)} = \frac{0.4 x (1 - x/200)}{1 - 0.8 (1 - x/200)},$$

a hump that leaves the origin with slope  $r/(b - r h_r) = 2$ , peaks at about (61.8, 38.2) and falls to zero at  $x = K = 200$ . Eq. (19) gives  $x^* = K/2 = 100$  and  $y^* = K/6 = 33.3$ , and the Jacobian at this equilibrium is

$$J^* = \begin{pmatrix} -0.08 & -0.36 \\ 0.008 & -0.024 \end{pmatrix},$$

with trace  $-0.104$  and determinant  $0.0048$ , so  $\lambda \approx -0.052 \pm 0.046i$ : a stable focus whose oscillations halve in amplitude roughly every 13 years. Because the damping is strong relative to the frequency (one full turn would take about 137 years), trajectories make little more than half a turn before settling. The other two equilibria are the saddle  $(K, 0) = (200, 0)$  and the origin, which is a singular point of the Arditi-Ginzburg response (see below).



In the figure, the dotted lines are the predator isocline  $y = x/3$  (red) and the prey isocline (blue), the black dashed curve is a separatrix (discussed below), the filled dot marks the stable equilibrium (100, 33.3), and open circles mark the origin and the saddle (200, 0). Ten trajectories are shown, all starting at high predator densities: three from prey density  $x = 50$ , with predator densities  $y = 90, 100$  and  $110$ , and seven from  $x = 150$ , with  $y = 50, 60, \dots, 110$ . Every starting point lies above the prey isocline, so prey density at first declines, and every point except (150, 50), which lies on the predator isocline, also lies above the predator isocline, so predator density declines too: all trajectories head down and to the left.

The seven trajectories from  $x = 150$  all reach the equilibrium. The higher the initial predator density, the deeper the prey crash: prey density falls to minima of about 69, 54, 41, 30, 21, 13

and 7 (between years 25 and 55) as  $y(0)$  rises from 50 to 110. Each trajectory then turns, crosses the predator isocline, sweeps out to the right (to prey densities between about 103 and 167) and turns again where it crosses the prey isocline vertically. All approach the equilibrium from the lower right, traveling up the narrow wedge between the two isoclines, and are within one unit of (100, 33.3) after between about 106 and 194 years. The three trajectories from  $x = 50$  start with far fewer prey per predator, and their fates differ. From (50, 90), prey density falls to about 3.5 by year 61, when predator density is only about 6; the trajectory passes close to the origin, then escapes, sweeps out to a prey density of about 181 and reaches the equilibrium after about 219 years. From (50, 100) and (50, 110), the trajectories never turn: predators drive prey density below one individual per unit area by about year 60 and then starve, their own density falling below one individual per unit area by about year 90, and both populations collapse to the origin. The dashed separatrix is the boundary between these two outcomes: it passes through (50, 99.2) and leaves the frame near (75, 114); at  $x = 150$  it lies at  $y \approx 129.7$ , above all seven starts there.

*What kind of point is the origin?* Students who try to classify (0, 0) by the methods of Modules 1–4 run into a problem: the Jacobian does not exist there. The per-capita rate at which prey are eaten,  $b y / (x + h_r y)$ , tends to 0 as the origin is approached along the prey axis but to  $b/h_r$  along the predator axis, so the model's right-hand side, although continuous at the origin, is not differentiable, and the linearization theorem (Appendix A.4) cannot be applied. The way forward is to follow the ratio  $u = x/y$  of prey to predators, which is the natural variable of a ratio-dependent model. Near the origin the term  $x/K$  is negligible, and

$$\frac{du}{dt} = u F(u), \quad F(u) = r + d - \frac{b + c u}{u + h_r},$$

a one-dimensional equation that students can analyze with a phase line. Here  $F(0) = r + d - b/h_r = -0.04 < 0$  and  $F$  has a single root,

$$u^* = \frac{b - (r + d) h_r}{r + d - c} = \frac{0.08}{0.36} = \frac{2}{9},$$

so the ray  $y = x/u^* = 4.5x$  is (to leading order) invariant. Along this ray, both populations decline at the same per-capita rate, 0.05, and slide into the origin. Below it ( $u > u^*$ ),  $u$  increases: prey become relatively more abundant, and trajectories that approach the origin are eventually deflected away from it, as on the trajectory from (50, 90). Above it ( $u < u^*$ ),  $u$  decreases to zero: prey decline at the per-capita rate  $b/h_r - r = 0.1$ , faster than predators, which decline at rate  $d = 0.06$ , so both populations go extinct, prey first. The origin therefore has two sectors in the positive quadrant. Between the predator axis and the ray  $y = 4.5x$  lies an *attracting sector*, in which every trajectory enters the origin. Between the ray and the prey axis lies a *hyperbolic (saddle) sector*, in which trajectories approach the origin and then leave it, the prey axis itself being an outgoing trajectory along which prey grow at rate  $r$  towards the saddle (200, 0). The separatrix in the figure is the single trajectory that enters the origin along the ray  $y = 4.5x$ , and it divides the phase plane into the basin of the coexistence equilibrium and the basin of joint extinction; trajectories that leave the origin close to the prey axis pass near the saddle (200, 0) and end at the coexistence equilibrium, so no trajectory leaves the origin and returns to it.

The origin is thus an unusual object for students: it is *attracting* in the sense that a whole region of initial conditions, of positive area, converges to it, yet it is *not stable* in the sense of Lyapunov, since there are initial conditions arbitrarily close to it, just above the prey axis, whose trajectories move

far away. It is neither a node, a saddle, a focus nor a center, and it illustrates why the distinction between attraction and stability matters. The condition for the attracting sector to exist,  $F(0) < 0$ , can be written  $b/h_r > r + d$ : when prey are rare relative to predators, the per-capita rate at which they are eaten approaches  $b/h_r$ , however few prey there are, and if this exceeds  $r + d$ , prey decline faster than predators can starve. With  $h_r = 2$  the condition holds only narrowly ( $0.5 > 0.46$ ), which is why the attracting sector is thin, lying above the steep ray  $y = 4.5x$ . Raising  $h_r$  above  $b/(r + d) \approx 2.17$  removes it altogether, so that every trajectory starting with both species present reaches the coexistence equilibrium; lowering  $h_r$  widens it (to  $y > 1.36x$  for  $h_r = 1.6$ ). Under prey dependence this cannot happen: the per-capita rate at which rare prey are eaten,  $b y/(x + h)$ , tends to  $b y/h$ , which shrinks as predators starve, so the origin of the model of Worked example 4 is an ordinary saddle, attracting only along the predator axis. A complete classification of the origin of the ratio-dependent model, including parameter values for which some trajectories leave the origin and return to it, is given by Kuang and Beretta (1998), Jost et al. (1999) and Berezovskaya et al. (2001).

Prey dependence also tells a different story from the same starting points. In the model of Worked example 4 at  $K = 200$ , started from (150, 50), prey density still oscillates between about 64 and 88 after 900 years; started from (50, 110), prey density is driven down to about  $2 \times 10^{-7}$  per unit area—far below a single individual in any realistic area—yet the model lets them recover, because the predators starve first. Neither outcome is realistic, and comparing the two models from the same initial conditions is a good way to discuss what continuous-density models can and cannot say about extinction.

Changing  $K$  does not change the picture: since  $J^*$  does not depend on  $K$ , and every term of the model scales with  $K$ , the phase portrait for any other carrying capacity, separatrix included, is the one in the figure with both axes multiplied by  $K/200$ . For  $K = 150$  the equilibrium is (75, 25), and for  $K = 250$  it is (125, 41.7), both stable foci with the same eigenvalues. In the prey-dependent model of Worked example 4,  $K = 150$  also gives a stable focus at (75, 25), but  $K = 250$  lies well above the Hopf bifurcation and gives a large limit cycle (prey density from about 6 to 213).

In the NWK DynSS LVPP app this is a two-line change to the NuML code of Figure 3: `Predation @= b * Prey * Pred / (Prey + hr * Pred)`, with `Ingestion` changed in the same way. Running Worked examples 4 and 5 side by side in sensitivity mode, stepping  $K$  from 100 to 300, makes the contrast vivid.

Ratio dependence is not without difficulties, and the debate it provoked is itself good material for an advanced class (P. A. Abrams, 1994; P. A. Abrams & Ginzburg, 2000; Arditi & Ginzburg, 2012). Because the Arditi-Ginzburg response is undefined at  $x = y = 0$ , the origin is a singular point whose analysis requires special techniques (Berezovskaya et al., 2001), and when predators are efficient relative to prey growth the model predicts that both species can be driven to extinction together. Students can find this behavior in the app: with the parameters of Worked example 5, starts above the separatrix collapse to the origin; reducing  $h_r$  to 1.6 leaves the equilibrium stable (with  $\lambda \approx -0.012 \pm 0.059i$ ) but enlarges the set of collapsing initial conditions so much that even (50, 70) and (10, 20) collapse; and at  $h_r = 1.5$  the equilibrium itself is unstable. Empirically, fits of a family of responses that interpolate between the two edges of the spectrum often place real predators close to the ratio-dependent edge (Arditi & Akçakaya, 1990), and a survey of feeding experiments found mutual interference to be common and mostly intermediate in strength (DeLong & Vasseur, 2011); theory suggests that moderate interference is the most stabilizing, since both very weak and very strong interference increase the risk of predator extinction in a fluctuating environment (Arditi et al., 2004). Mechanistically, interference emerges

when predators move actively and aggregate where prey are abundant, so that passive consumption in well-mixed systems leads to prey dependence, whereas active predation in spatially heterogeneous landscapes leads towards predator and ratio dependence (Cosner et al., 1999; DeAngelis et al., 2021; Tyutyunov & Titova, 2021).

For the narrative theme of this paper, the lesson is a significant one. The Lotka-Volterra story, extended by Holling, is not the only defensible story of predation, and the choice between prey-dependent and ratio-dependent narratives changes qualitative predictions—whether enrichment destabilizes, whether biological control can be both effective and stable—more than any choice of parameter values. Ginzburg and Colyvan (2004) argue that a good minimal model should be judged, as in physics, by how well its simple assumptions capture the broad patterns of nature; asking students to compare the two narratives against that standard is a fitting capstone to the modules.

## 5. Competition and Multispecies Extensions

The predator-prey narrative of Section 4 is one of several interaction stories that Lotka and Volterra told with the same mathematics. Changing the signs of the interaction terms turns predation into competition; adding a third equation opens the door to dynamics that no two-species model can produce; and letting the number of species grow without limit leads to one of the central debates of modern ecology. Each of these steps uses the tools students have already acquired (isoclines, Jacobians, eigenvalues and careful simulation), so this section can be taught as a sequel to the modules or mined for projects.

### 5.1. Gause-Lotka-Volterra competition

Two species that share a limiting resource depress one another's growth. Lotka (1925) and Volterra (1926a) modeled this by adding a competition term to the logistic equation of Module 2,

$$\begin{aligned}\frac{dx_1}{dt} &= r_1 x_1 \left( 1 - \frac{x_1 + a_{12} x_2}{K_1} \right), \\ \frac{dx_2}{dt} &= r_2 x_2 \left( 1 - \frac{x_2 + a_{21} x_1}{K_2} \right),\end{aligned}\tag{20}$$

where  $K_i$  is the carrying capacity of species  $i$  on its own, and the competition coefficient  $a_{ij}$  converts a density of species  $j$  into the equivalent density of species  $i$ . Thus,  $a_{12} < 1$  means that an individual of species 2 uses less of species 1's resources than another individual of species 1 does. Gause (1934) was the first to confront these equations with experiments, growing yeasts and protozoa alone and together in the laboratory. When *Paramecium aurelia* and *P. caudatum* were cultured together on the same bacterial food, *P. aurelia* always persisted and *P. caudatum* always died out. Results like these became the *competitive exclusion principle*: two species competing for a single limiting resource cannot coexist indefinitely (Hardin, 1960). In Park's classic experiments with flour beetles (Park, 1948), the winner depended on temperature and humidity and, under some conditions, on the initial densities of each species, a result that the model also explains.

The analysis follows Module 2 step by step. Both null-isoclines are straight lines:  $x_1 + a_{12}x_2 = K_1$  for species 1 and  $x_2 + a_{21}x_1 = K_2$  for species 2. Their relative positions give four outcomes, which students can classify by sketching:

- the species coexist at a stable equilibrium if  $a_{12} < K_1/K_2$  and  $a_{21} < K_2/K_1$ , that is, if each species limits itself more than it limits its competitor (Worked example 6, Part 1);
- species 1 wins if  $a_{21} > K_2/K_1$  and  $a_{12} < K_1/K_2$ , and species 2 wins if the two inequalities are reversed (Worked example 6, Part 1);

- the outcome depends on initial conditions if  $a_{12} > K_1/K_2$  and  $a_{21} > K_2/K_1$ . Then the coexistence equilibrium is a saddle, and its stable manifold (the separatrix) divides the phase plane into two basins of attraction, one for each single-species equilibrium (Worked example 6, Part 2; the multiple attractors of Module 3 in a new guise).

An equivalent, and more general, way to state the coexistence condition is *mutual invasibility*: species 2 can invade a population of species 1 at its carrying capacity if its per-capita growth rate there,  $r_2(1 - a_{21}K_1/K_2)$ , is positive, and vice versa. This invasion criterion is the foundation of modern coexistence theory (Chesson, 2000).

The Jacobian provides a second lesson. At any coexistence equilibrium both off-diagonal entries are negative, so  $J_{12}J_{21} > 0$  and the discriminant  $(J_{11} - J_{22})^2 + 4J_{12}J_{21}$  is positive: the eigenvalues are always real. Unlike predators and prey, two competitors can never oscillate. Students who have just found centers, foci and limit cycles in Modules 1–4 are often surprised by this, and the contrast between the signs of the Jacobians— $J_{21} < 0$  for a competitor but  $J_{21} > 0$  for a predator, with  $J_{12} < 0$  in both—is an effective way to show how the qualitative behavior of a system can be read from the signs of its interactions.

### Worked example 6: Competition: coexistence, exclusion and a separatrix

**Simulator setup:** [Link to Preset 6](#). The default parameters for this setup are the parameters used in the coexistence case featured in the left panel of the first figure below, but with  $x_1(0) = 100$  and  $x_2(0) = 50$ . Starting values and model parameters need to be adjusted as listed for each case.



**Part 1: coexistence versus exclusion.** Take  $r_1 = 0.5$ ,  $r_2 = 0.8$  (per day),  $K_1 = 100$ ,  $K_2 = 80$  and  $a_{12} = 0.6$ , and compare  $a_{21} = 0.6$  with  $a_{21} = 1.0$ . The first coexistence condition,  $a_{12} = 0.6 < K_1/K_2 = 1.25$ , holds in both cases; the second,  $a_{21} < K_2/K_1 = 0.8$ , holds only in the first.

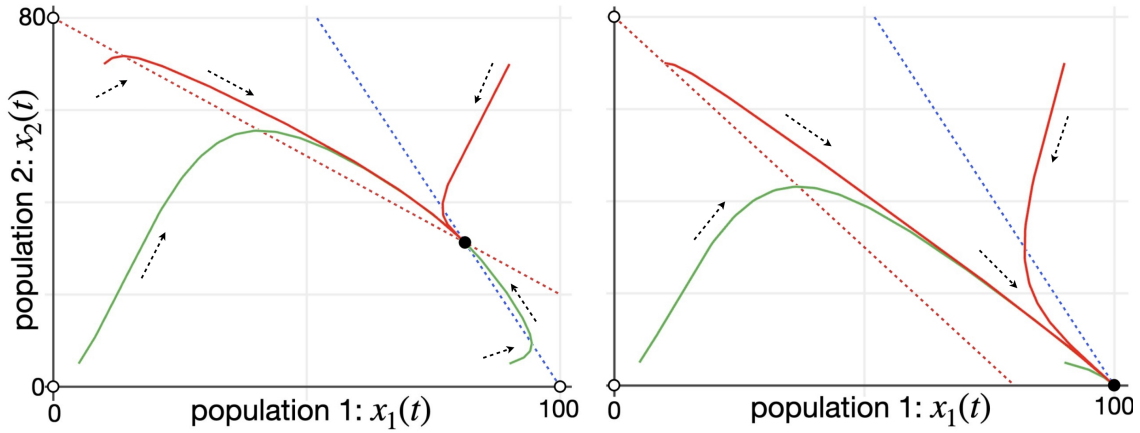
- $a_{21} = 0.6$ : the isoclines cross at

$$x_1^* = \frac{K_1 - a_{12}K_2}{1 - a_{12}a_{21}} = 81.25, \quad x_2^* = \frac{K_2 - a_{21}K_1}{1 - a_{12}a_{21}} = 31.25.$$

The Jacobian there has entries  $J_{11} = -r_1x_1^*/K_1 = -0.406$ ,  $J_{12} = -r_1a_{12}x_1^*/K_1 = -0.244$ ,  $J_{21} = -r_2a_{21}x_2^*/K_2 = -0.188$  and  $J_{22} = -r_2x_2^*/K_2 = -0.313$ , with trace  $-0.719$  and determinant  $0.081$ , so  $\lambda = -0.578$  and  $-0.141$ : a stable node. From  $(5, 5)$ , the density of species 2 overshoots to about 55 by day 7 and then declines steadily to its equilibrium; the trajectory is within one unit of  $(81.25, 31.25)$  by about day 34 and never spirals.

- $a_{21} = 1.0$ : the species 2 isocline,  $x_2 = 80 - x_1$ , now lies entirely inside the species 1 isocline,  $x_2 = (100 - x_1)/0.6$ , and the formula above gives  $(130, -50)$ , outside the positive quadrant. Species 1 wins:  $(100, 0)$  is a stable node with eigenvalues  $-0.5$  and  $r_2(1 - a_{21}K_1/K_2) = -0.2$ , and  $(0, 80)$  is a saddle, since species 1 can invade at rate  $r_1(1 - a_{12}K_2/K_1) = 0.26$ . From  $(5, 5)$ , species 2, the faster grower, at first races ahead, its density reaching about 43 on day 6

while that of species 1 is still about 36; it then declines, falling below one individual per unit area by about day 28 and below 0.1 by about day 40.



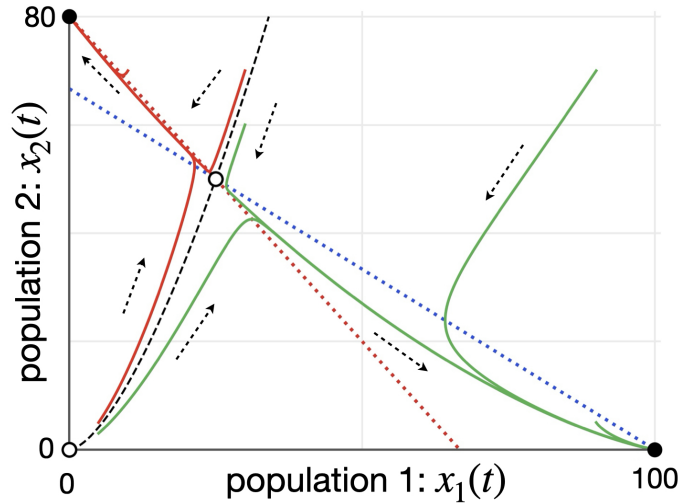
In the figure, the dotted lines are the species 1 isocline  $x_2 = (100 - x_1)/0.6$  (blue) and the species 2 isocline  $x_2 = 80 - a_{21}x_1$  (red); filled dots mark stable equilibria and open circles unstable ones ((0, 0), an unstable node, and the single-species saddles). Four trajectories start from the corners of the phase plane: (5, 5), (10, 70), (90, 5) and (90, 70). For  $a_{21} = 0.6$  (left), all four reach the coexistence equilibrium (81.25, 31.25), within one unit of it after between about 19 and 35 days: from (10, 70), the density of species 2 at first increases slightly, to about 72, before the trajectories from (5, 5) and (10, 70) merge and slide down towards the equilibrium; from (90, 5), the density of species 1 first overshoots to about 94; and from (90, 70), it first falls to about 77. Because the equilibrium is a node rather than a focus, the trajectories do not spiral: late in their approach they all run along the same line, the direction of the slow eigenvector (slope about  $-1.1$ , eigenvalue  $-0.141$ ), and they arrive from opposite sides of it. For  $a_{21} = 1.0$  (right), all four trajectories end at (100, 0). Those from (10, 70) and (90, 70), and the one from (5, 5) after its early rise, converge on the line  $x_2 = 100 - x_1$ , the slow eigenvector of (100, 0) (eigenvalue  $-0.2$ ), and slide along it to the equilibrium; only the trajectory from (90, 5), which starts close to the  $x_1$  axis, arrives from below. The faster grower losing is a useful corrective to the intuition that ‘the fittest’ is the species that grows fastest: in this model the outcome is decided by the carrying capacities and competition coefficients, not by  $r_1$  and  $r_2$ , which affect only how quickly it is reached. Students can confirm this by swapping  $r_1$  and  $r_2$ .

**Part 2: an unstable coexistence equilibrium and a separatrix.** Keep  $r_1$ ,  $r_2$ ,  $K_1$  and  $K_2$ , but make interspecific competition stronger than intraspecific competition for both species:  $a_{12} = 1.5 > K_1/K_2 = 1.25$  and  $a_{21} = 1.2 > K_2/K_1 = 0.8$ . The isoclines,  $x_2 = (100 - x_1)/1.5$  for species 1 and  $x_2 = 80 - 1.2x_1$  for species 2, now cross the other way round, at

$$x_1^* = \frac{100 - 1.5 \times 80}{1 - 1.5 \times 1.2} = 25, \quad x_2^* = \frac{80 - 1.2 \times 100}{1 - 1.5 \times 1.2} = 50.$$

The Jacobian there has entries  $J_{11} = -0.125$ ,  $J_{12} = -0.1875$ ,  $J_{21} = -0.6$  and  $J_{22} = -0.5$ , with trace  $-0.625$  and determinant  $-0.05 < 0$ , so  $\lambda \approx +0.072$  and  $-0.697$ : the coexistence equilibrium is a saddle. Both single-species equilibria are now stable nodes: (100, 0), with eigenvalues  $-0.5$  and  $r_2(1 - a_{21}K_1/K_2) = -0.4$ , and (0, 80), with eigenvalues  $-0.8$  and  $r_1(1 - a_{12}K_2/K_1) = -0.1$ . Each species can exclude the other, and which one does depends only on the starting point. The boundary between the two basins of attraction is the *separatrix*: the stable manifold of the saddle,

the pair of trajectories that run into  $(25, 50)$ , tangent there to the stable eigenvector (slope about 3.0). Integrating backwards in time from points just off the saddle along this eigenvector traces it out: one branch comes from the unstable node at the origin, passing through about  $(5, 4.1)$ ,  $(10, 12.2)$  and  $(20, 35.6)$ , and the other runs up through  $(30, 66.0)$  to leave the frame at about  $(34.1, 80)$ .



The figure shows seven trajectories, colored by their fate: green ones end at  $(100, 0)$  and red ones at  $(0, 80)$ . Three pairs are worth comparing. From  $(5, 3)$  species 1 wins, but from  $(5, 5)$ , where the density of species 2 is higher by only two individuals per unit area, species 2 wins, because the separatrix passes between the two starting points (at  $x_2 \approx 4.1$  when  $x_1 = 5$ ). Similarly,  $(30, 60)$  and  $(30, 70)$  lie either side of the separatrix (at  $x_2 \approx 66.0$ ) and end at opposite single-species equilibria. Trajectories that start near the separatrix are first drawn towards the saddle, passing within about 2 units of  $(25, 50)$ , and linger there before being repelled along its unstable eigenvector: the runs from  $(30, 60)$  and  $(30, 70)$  take about 57 and 85 days to come within one unit of their final equilibria, compared with between about 9 and 34 days for the runs from  $(90, 5)$ ,  $(10, 70)$  and  $(90, 70)$ , which start far from the separatrix. This is the multiple-attractor picture of Module 3, with the saddle at  $(x_A, 0)$  replaced by an interior saddle, and it is the model's explanation of the priority effects Park found in some of his beetle cultures: when each species inhibits the other more than itself, the species that is initially more abundant, relative to the separatrix, wins.

Equation (20) is phenomenological. It says that competitors harm one another without saying how. MacArthur (1970) showed that Lotka-Volterra competition emerges when consumers share self-renewing resources whose dynamics are fast, with the competition coefficients determined by the overlap in the consumers' resource use, and Tilman (1982) built a mechanistic theory of competition for resources from the same idea. These derivations lead to May and MacArthur's analysis of how similar coexisting species can be (May, 1973; May & MacArthur, 1972), and they foreshadow the resource-extraction view of Section 5.3.

## 5.2. Three species models

With a third species, students meet a new mathematical phenomenon. In two-dimensional autonomous systems, because 1-dimensional trajectories cannot cross each other (if they did uniqueness of the solution beyond the crossing point would be violated), the Poincaré-Bendixson theorem (see Appendix A.4) restricts long-term behavior to equilibria, limit cycles and cycles of trajectories connecting saddles; in

three dimensions, trajectories can weave around one another without ever repeating, and chaos becomes possible. Three-species models are therefore the natural place to introduce chaos, and also to ask which ecological structures actually produce it. We describe two such models, in increasing order of complexity (numbers of parameters and types of nonlinearities).

### 5.2.1. May-Leonard competitors

May and Leonard (1975) studied three competitors with equal carrying capacities, scaled to one (so that each  $x_i$  is a density measured in units of the common carrying capacity), and cyclically arranged competition coefficients,

$$\frac{dx_i}{dt} = x_i (1 - x_i - p x_{i+1} - q x_{i+2}), \quad i = 1, 2, 3 \text{ (indices modulo 3)}, \quad (21)$$

so that species 1 is affected by species 2 with strength  $p$  and by species 3 with strength  $q$ , and so on round the cycle. (We write  $p$  and  $q$  for May and Leonard's  $\alpha$  and  $\beta$ .) The symmetric coexistence equilibrium is  $x_i^* = 1/(1 + p + q)$ . When  $p < 1 < q$ , each species beats one of the others in pairwise competition and loses to the other: a game of rock-paper-scissors. If  $p + q < 2$  the coexistence equilibrium is stable, and the populations spiral in to it: three competitors can oscillate, which two cannot. If  $p + q > 2$  the equilibrium is unstable, and the populations take turns to dominate in a cycle that passes ever closer to each single-species state, approaching a cycle of trajectories connecting saddles (i.e., a *heteroclinic cycle*). Worked example 7 works through both cases and the borderline case  $p + q = 2$ , which turns out to have a conserved quantity like that of Module 1. Rock-paper-scissors competition has since been found in nature, in the mating strategies of side-blotched lizards (Sinervo & Lively, 1996) and in toxin-producing, toxin-resistant and sensitive strains of *E. coli*, which coexist only when interactions are local (Kerr et al., 2002). Three Lotka-Volterra competitors are nonetheless never chaotic: Hirsch (1988) proved that their long-term dynamics are effectively two-dimensional, and Zeeman (1993) classified all their possible phase portraits into 33 classes. Chaos requires at least four competitors (Vano et al., 2006), and in general (not necessarily Lotka-Volterra) competition models with five or more species, any dynamics whatsoever can occur (Smale, 1976).

#### Worked example 7: Rock-paper-scissors competition: spirals, neutral cycles and a heteroclinic cycle

**Simulator setup:** Link to Preset 7. In this exploration of Eq. (21), we have set  $p = 0.8$  and compare  $q = 1.1$ ,  $q = 1.2$  and  $q = 1.3$ , starting each run from  $(x_1, x_2, x_3) = (0.9, 0.05, 0.05)$ .



**Pairwise contests.** Without species 3, Eq. (21) is the two-species model of Section 5.1 with  $K_1 = K_2 = 1$ ,  $a_{12} = p < 1$  and  $a_{21} = q > 1$ , so species 1 excludes species 2 (Worked example 6, Part 1). By the same argument species 2 excludes species 3, and species 3 excludes species 1. Each single-species equilibrium is therefore a saddle: at  $(1, 0, 0)$ , for example, the eigenvalues are  $-1$  (species 1 returning to its carrying capacity),  $1 - q < 0$  (species 2 cannot invade) and  $1 - p = 0.2 > 0$  (species 3 can). No two-species equilibrium lies in the positive quadrant: for the pair  $(x_1, x_2)$ , for example, it would be at  $x_1 = (1 - p)/(1 - pq)$  and  $x_2 = (1 - q)/(1 - pq)$ , which

have opposite signs whenever  $p < 1 < q$ .

*The coexistence equilibrium.* At  $x_i^* = 1/(1 + p + q)$  the Jacobian is  $J^* = -x^*A$ , where  $A$  is the circulant matrix with rows  $(1, p, q)$ ,  $(q, 1, p)$  and  $(p, q, 1)$ . The eigenvalues of a circulant matrix are known in closed form, which makes this a good exercise in linear algebra (Appendix A.2):

$$\lambda_0 = -1, \quad \lambda_{\pm} = -x^* \left(1 - \frac{p+q}{2}\right) \pm i x^* \frac{\sqrt{3}}{2} (q-p).$$

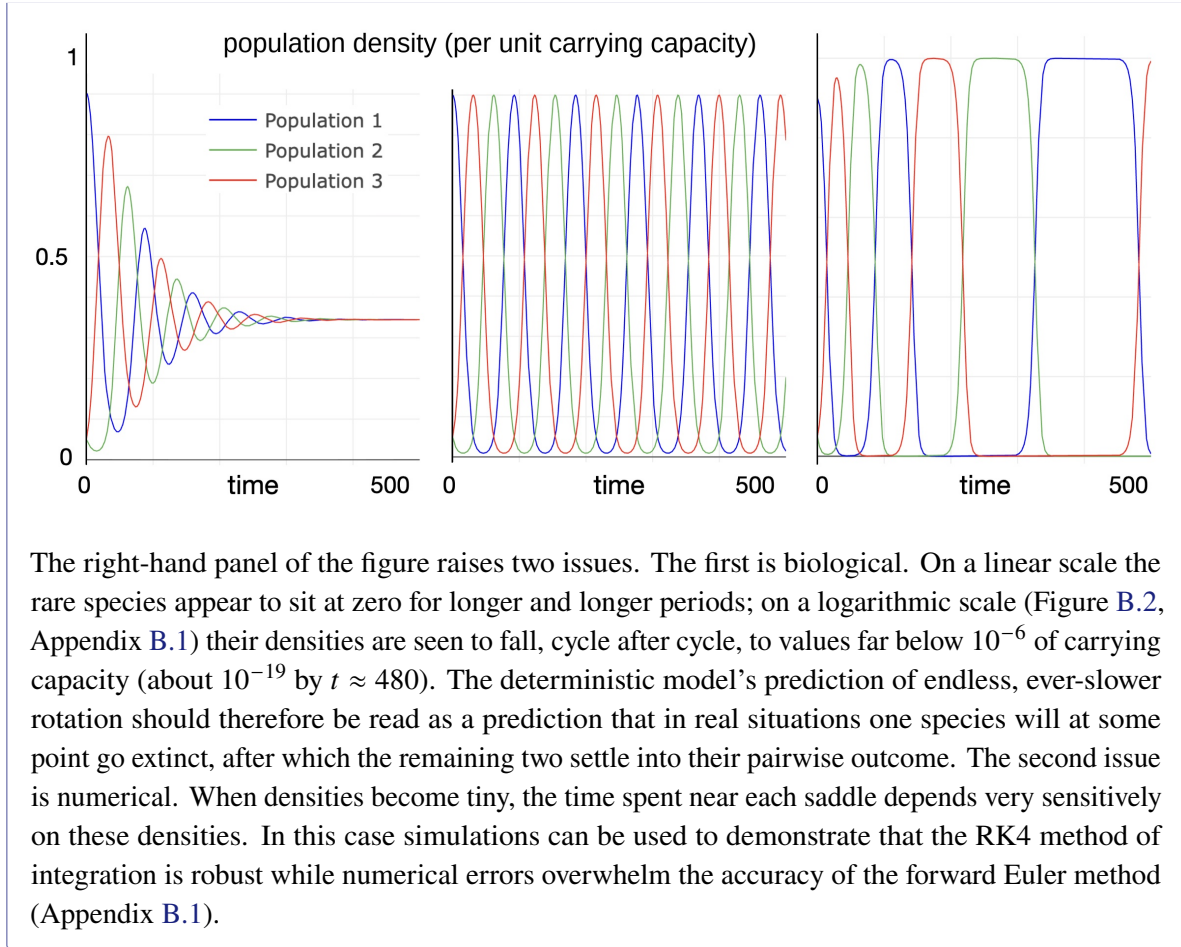
The real eigenvalue  $\lambda_0$  belongs to the direction  $(1, 1, 1)$ , along which the total density  $x_1 + x_2 + x_3$  relaxes quickly; the complex pair governs the rotation of dominance among the species, and its real part changes sign at  $p + q = 2$ .

*A Lyapunov function.* The quantity  $V = x_1 x_2 x_3 / (x_1 + x_2 + x_3)^3$  satisfies

$$\frac{d \ln V}{dt} = \left(1 - \frac{p+q}{2}\right) \frac{(x_1 - x_2)^2 + (x_2 - x_3)^2 + (x_3 - x_1)^2}{x_1 + x_2 + x_3},$$

which students can verify by differentiating (Appendix A.5).  $V$  takes its maximum value  $1/27$  on the line  $x_1 = x_2 = x_3$  through the coexistence equilibrium and is zero on the boundary, so the sign of  $2 - p - q$  decides everything.

- $q = 1.1$  ( $p + q < 2$ ) (left panel below):  $V$  increases, and the populations spiral in to  $x_i^* = 0.345$ , with  $\lambda_{\pm} = -0.017 \pm 0.090i$  (a damped oscillation with period about 70). Every species is within 0.01 of  $x^*$  by  $t \approx 270$ .
- $q = 1.2$  ( $p + q = 2$ ) (middle panel below):  $V$  is conserved, exactly as the quantity of Eq. (5) is conserved in Module 1, and the linearization gives a center. Each species oscillates for ever, between about 0.01 and 0.90, on a closed orbit fixed by the initial conditions. Because the starting point is close to  $(1, 0, 0)$ , this orbit passes close to the three single-species saddles, where motion is slow, so its period, about 92, is much longer than the period  $2\pi/\text{Im}(\lambda_{\pm}) \approx 54$  of small oscillations about  $x^*$ .
- $q = 1.3$  ( $p + q > 2$ ) (right panel below):  $V$  decreases to zero, and the trajectory spirals out from  $x_i^* = 0.323$  ( $\lambda_{\pm} = +0.016 \pm 0.140i$ ) towards the heteroclinic cycle. Dominance passes from species 1 to species 3 to species 2 and back to species 1, as the invasion eigenvalues predict, and after the first switch the total density stays between about 0.975 and 1, so the trajectory stays close to the plane  $x_1 + x_2 + x_3 = 1$  and, except during the brief switches, one species is near its carrying capacity and the other two are rare. Each period of dominance lasts longer than the one before, by a factor that approaches  $(q - 1)/(1 - p) = 1.5$ , and each time a species is rare it is rarer than the time before (Appendix B.1).



### 5.2.2. Hastings-Powell food chain

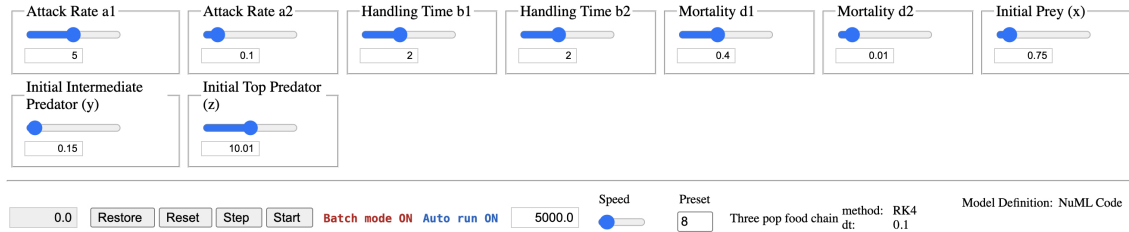
Hastings and Powell (1991) took a different route to three dimensions: they placed a top predator on the Rosenzweig-MacArthur model of Module 4, creating a food chain in which each link is a Holling Type II response. In their dimensionless form,

$$\begin{aligned}\frac{dx}{dt} &= x(1-x) - \frac{a_1x}{1+b_1x}y, \\ \frac{dy}{dt} &= \frac{a_1x}{1+b_1x}y - \frac{a_2y}{1+b_2y}z - d_1y, \\ \frac{dz}{dt} &= \frac{a_2y}{1+b_2y}z - d_2z,\end{aligned}\tag{22}$$

where  $x$ ,  $y$  and  $z$  are the scaled (dimensionless) densities of the prey, an intermediate predator and a top predator, and time is measured in units of the prey's inverse intrinsic growth rate. We keep Hastings and Powell's symbols so that students can read the original paper alongside this note; in the notation of Eq. (12), the first link has half-saturation constant  $h = 1/b_1$  and maximum rate  $a_1/b_1$ . The model contains no external forcing and no randomness, yet for biologically reasonable parameters it is chaotic, which was the paper's main point. Its chaotic attractor, shaped like a teacup, has become one of the most widely reproduced pictures in theoretical ecology. Worked example 8 reproduces it.

### Worked example 8: A food chain from equilibrium to chaos

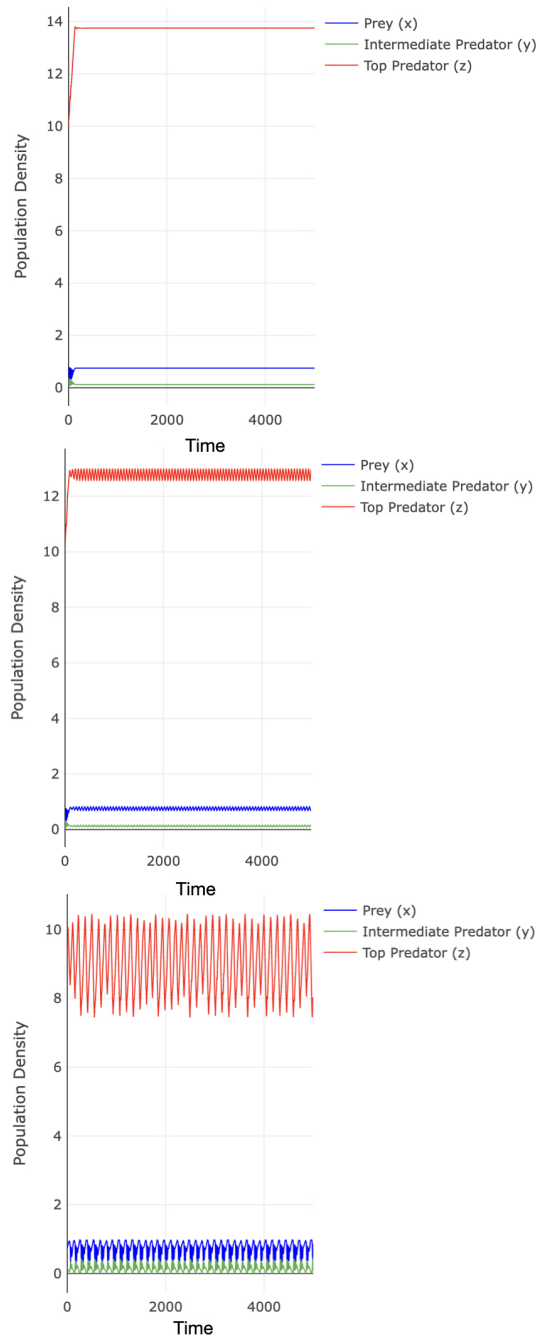
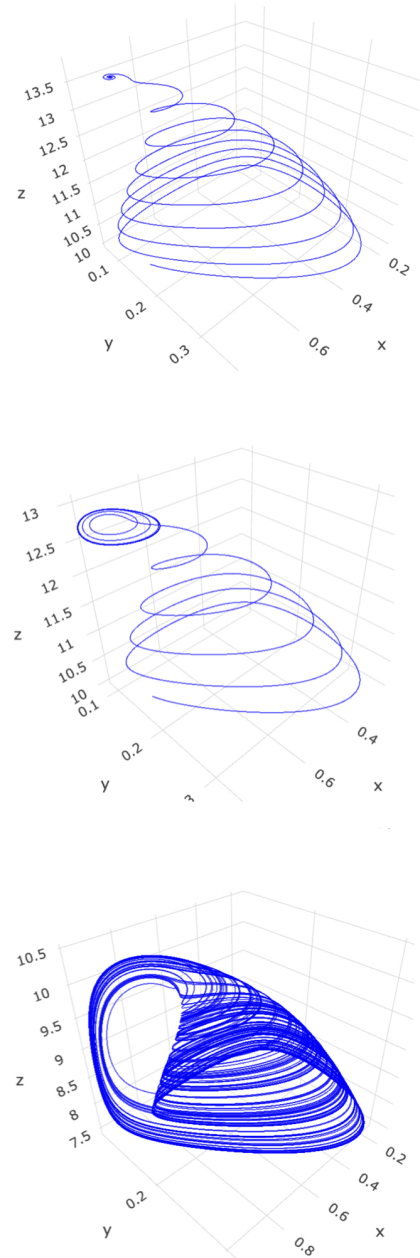
**Simulator setup:** [Link to Preset 8](#). In this exploration of Eq. (22), we have set  $a_1 = 5$ ,  $a_2 = 0.1$ ,  $b_2 = 2$ ,  $d_1 = 0.4$  and  $d_2 = 0.01$ , start at  $(x, y, z) = (0.75, 0.15, 10)$  (the preset uses  $z(0) = 10.01$ , which changes nothing below except the precise timing of the chaotic fluctuations),



and vary  $b_1$ , which controls how quickly the intermediate predator becomes satiated. For  $b_1 = 2.0$ , 2.2 and 3.0 we obtain the following behavior:

- $b_1 = 2.0$ : the trajectory converges to a stable equilibrium at  $(0.75, 0.125, 13.75)$ . Students can verify this by hand:  $dz/dt = 0$  gives  $y^* = d_2/(a_2 - b_2 d_2) = 0.125$ ; then  $dx/dt = 0$  gives  $(1 - x^*)(1 + b_1 x^*) = a_1 y^*$ , so  $x^* = 0.75$ ; and  $dy/dt = 0$  gives  $z^* = 13.75$ .
- $b_1 = 2.2$ : the equilibrium has lost stability, and the system settles onto a limit cycle on which  $x$  ranges between about 0.68 and 0.82 and top-predator density varies only slightly, between about 12.6 and 13.0. Its largest Lyapunov exponent is zero, as it must be for a cycle.
- $b_1 = 3.0$ : the dynamics are chaotic. Prey and intermediate-predator densities oscillate rapidly and irregularly ( $x$  between about 0.15 and 0.98,  $y$  between about 0.015 and 0.43), while top-predator density drifts slowly and irregularly between about 7.5 and 10.5. The largest Lyapunov exponent is about 0.007, so nearby trajectories separate by a factor of  $e$  roughly every 140 time units. Changing the initial value of  $z$  from 10 to 10.001 produces trajectories whose  $z$  values differ by more than 0.01 after about 270 time units and by more than 1 (an error of about 10%) after about 800.

Food Chain Dynamics (Prey, Intermediate, Top Predator)

Prey (x) vs Intermediate Predator (y)  
vs Top Predator(z) Phase Space

The figure shows, for  $b_1 = 2.0$  (top row),  $2.2$  (middle) and  $3.0$  (bottom), the three densities against time over 5000 time units (left) and the same trajectory in  $(x, y, z)$  phase space (right). As  $b_1$  increases, the trajectory spirals into the equilibrium, then onto a small limit cycle near  $z \approx 12.8$ , and finally onto the chaotic teacup attractor, on which top-predator density fluctuates irregularly between about 7.5 and 10.5. The numerical lesson of Module 1 returns in a new form. RK4 runs with steps of  $\Delta t = 0.1$  and  $\Delta t = 0.05$  from the same initial point give  $z$  values that differ by more than 1 after about 2300 time units. Neither run is ‘correct’ over that horizon, because round-off and truncation errors are amplified exactly as differences in initial conditions are. Yet the two runs

trace out attractors of the same shape and statistics. For chaotic systems, simulation can be trusted to reveal the geometry of the attractor and the long-run averages, but not the precise state of the system far into the future, which is a fundamental limit on ecological forecasting rather than a defect of the software.

The Hastings-Powell paper prompted a substantial literature. Gilpin (1979) had earlier found ‘spiral chaos’ in a model of two prey and one predator, and Klebanoff and Hastings (1994) mapped the bifurcations through which the food chain becomes chaotic, including a period-doubling cascade. McCann and Yodzis (1994) asked whether chaos survives when the parameters are constrained by the body sizes and metabolic rates of real organisms, and found that chaos can occur for biologically plausible parameter values. Kuznetsov and Rinaldi (1996) explained the teacup by separating time scales: a fast prey-predator oscillation (the limit cycle of Module 4) is modulated by a slowly varying top predator. P. A. Abrams and Roth (1994) showed that enrichment of three-species chains produces counterparts of the paradox of enrichment. Whether nature is chaotic was reviewed by Hastings et al. (1993) and by Ellner and Turchin (1995), who developed methods for detecting chaos in noisy time series. Chaos was then demonstrated in a laboratory microbial food web (Becks et al., 2005) and in a long-term laboratory experiment with a plankton community (Benincà et al., 2008), and Rogers et al. (2022) found evidence of chaos in more than 30% of the long ecological time series they analyzed. Chaos in ecological models had first come to prominence in May’s work on single-species difference equations (May, 1974, 1976); the Hastings-Powell model showed that interactions among three species in continuous time are enough.

### 5.3. Consumer-Resource Systems

Modules 1–5 and Sections 5.1–5.2 treat prey and predators, and competitors and their resources, as populations at trophic levels that lie above resources. In the generalized Lotka-Volterra system  $dx_i/dt = x_i(r_i + \sum_j a_{ij}x_j)$ , which underlies May’s analysis in Section 5.5, and in MacArthur’s consumer-resource model (Chesson, 1990; MacArthur, 1972), predators can also be viewed as consumers of prey and prey as resources of predators. In these settings the predators and prey obey structurally different equations, in that predators have explicit resource-extraction terms that prey do not possess. Yet prey are also consumers of resources that lie a trophic level below themselves (e.g., plant material: leaves, stems, roots, and fruits). Recasting all the predators as consumers  $N_i$  and all the prey as resources  $R_j$ , Lotka-Volterra-MacArthur (LVM) systems take the general form

$$\begin{aligned}\frac{dN_i}{dt} &= \varepsilon_i N_i \left( -\sigma_i + \sum_{j=1}^m a_{ij} v_{ij} R_j \right), & i = 1, \dots, n, \\ \frac{dR_j}{dt} &= r_j R_j \left( 1 - \frac{R_j}{K_j} \right) - R_j \sum_{i=1}^n a_{ij} N_i, & j = 1, \dots, m,\end{aligned}\tag{23}$$

This asymmetry in the equations for  $N_i$  and  $R_j$  in this general LVM system led Getz (1991, 1994) to articulate the following conundrums. First, consumers and resources in LVM systems are modeled from different points of view, although every population other than a top predator is both a resource and a consumer—and even the top predator can be consumed by parasites and pathogens. In LVM systems consumers/predators decay exponentially when their explicit resources/prey disappear, while resources/prey grow logistically towards a carrying capacity, so the items they feed upon or extract (vegetation) are implicit in their carrying capacity parameter  $K$  (as Eq. (28) below demonstrates). Second, the growth rate of a population is made a function of the *density* of its resources, or is set

proportional to what it eats, rather than being a function of the rate at which each unit of the population actually acquires resources. Third, intraspecific interference is added as an extra term (the logistic  $K$ , for example) rather than emerging from the way consumers extract their resources. The metaphysiological approach (Getz, 1991, 1993, 1994) rectifies all three by building every population equation, at every trophic level, from the same two processes: extraction from the trophic level below, where plants, so to speak, feed on photons and nutrients; and conversion of extracted biomass and energy particles (photons) and molecules (ATP, etc.) into the population's own biomass (weight gain, female production of young).

*Process approach.* Choose a currency (biomass, energy or a limiting nutrient) and let  $x_i(t)$  be the amount of it per unit area (its density) in trophic level  $i$  of a food chain or *trophic stack*, with  $x_0$  an abiotic resource at the bottom (energy from light or heat radiation). *Extraction* is the process by which each unit of level  $i$  removes currency from level  $i - 1$ , at a per-unit rate  $g_i(x_{i-1}, x_i)$ ; *conversion* is the process by which level  $i$  turns what it has extracted into its own currency, at a net per-unit rate  $f_i(g_i)$  that is negative when  $g_i$  is below what is needed for maintenance. Every level then obeys the same equation,

$$\frac{dx_i}{dt} = x_i f_i(g_i(x_{i-1}, x_i)) - x_{i+1} g_{i+1}(x_i, x_{i+1}), \quad i = 1, \dots, n, \quad (24)$$

with  $g_{n+1} = 0$  for the top level: growth from what a level eats, minus what is eaten by the level above. The bottom of the stack is classified by how  $x_0$  behaves: in *non-retentive* systems it is a specified input flux (sunlight, or nutrients flushed through a stream); in *retentive* systems it accumulates in a pool,  $dx_0/dt = k(t) - m_0(x_0) - x_1 g_1$ ; and in *recycling* systems decomposers return currency from all levels to the pool.

*Conversion.* In the Lotka-Volterra and MacArthur models, conversion is linear,  $f(g) = \varepsilon g - d$ . With  $g = b\phi$ , this is exactly the predator equation of Eq. (13), with  $\varepsilon = c/b$ , and the metaphysiological reading of Eq. (14) interprets  $\varepsilon$  and  $d$ . Linear conversion implies that a population deprived of all food declines at the constant per-capita rate  $d$ , which is reasonable only for organisms that can live for long periods on stored reserves. Getz (1991, 1993) proposed instead the *hyperbolic* conversion function

$$f(g) = \rho \left( 1 - \frac{m}{g} \right), \quad (25)$$

where  $\rho$  is the maximum per-unit conversion rate and  $m$  is the per-unit extraction rate at which the population just breaks even (its maintenance requirement). The function rises steeply through zero at  $g = m$ , saturates at  $\rho$  for large  $g$ , and tends to  $-\infty$  as  $g \rightarrow 0$ , so that a population without food crashes rather than decaying exponentially; the requirement that conversion never exceed extraction,  $f(g) < g$ , implies  $\rho < 4m$ . Students can check this last result by asking when the quadratic  $g^2 - \rho g + \rho m$  has no positive root.

*Extraction.* Most of the functional responses in Table 4 reappear as extraction functions, now written per unit of consumer: resource limited (mass action,  $g = a x_{i-1}$ ), consumer limited ( $g = b$ , the satiation rate), Holling Types I–III, and the resource-per-consumer (ratio-dependent) form  $g = b x_{i-1} / (h_r x_i + x_{i-1})$ , which Getz (1984) proposed for consumer-resource systems five years before Arditi and Ginzburg (1989) introduced it to predator-prey theory. Prey dependence and ratio dependence are both special cases of the *resource-and-consumer* form

$$g_i(x_{i-1}, x_i) = \frac{b_i x_{i-1}}{h_i + w_i x_i + x_{i-1}}, \quad (26)$$

which is the Beddington-DeAngelis response of Table 4 with  $b_i$  the maximum extraction rate,  $h_i$  a half-saturation density and  $w_i$  the strength of self-interference among consumers (DeAngelis et al., 1975; Getz, 1984). Getz (1994) argues that neither edge of the spectrum is adequate on its own: prey dependence ( $w_i = 0$ ) fails at high consumer densities, and ratio dependence ( $h_i = 0$ ) fails when consumers and resources are both scarce, since consumers are then limited by resources, not by one another. Replacing  $w_i x_i$  with  $w_i x_i^p$  and  $x_{i-1}$  with  $x_{i-1}^\theta$  gives a more general form, with  $p = 2$  reflecting encounters between pairs of consumers and  $\theta > 1$  a prey refuge, as in Holling Type III; the Getz response function of Table 4, whose exponent  $\theta$  plays the role of  $p$  here, is a close relative.

*The logistic equation emerges.* Consider a single consumer population  $N = x_1$  growing on a constant resource  $R = x_0$ , with hyperbolic conversion and resource-and-consumer extraction. Equations (24)–(26) give

$$\frac{dN}{dt} = \rho N \left( 1 - \frac{m(h + R + wN)}{bR} \right), \quad (27)$$

which, as students can verify with a line of algebra, is the logistic equation  $dN/dt = rN(1 - N/K)$  with

$$r = \rho \left( 1 - \frac{m}{b} \right) - \frac{\rho m h}{b R} \quad \text{and} \quad K = \frac{(b - m) R}{w m} - \frac{h}{w} \quad (28)$$

(Getz, 1991, 1993). These identities make three points that the logistic equation of Module 2 hides. First,  $K$  is finite only if  $w > 0$ : a carrying capacity requires interference among consumers, which is a strong argument for including consumer interference in functional responses, the theme of Module 5. Second,  $r$  and  $K$  are not independent constants of a species but composites of physiological parameters ( $\rho, m$ ), extraction parameters ( $b, h, w$ ) and the state of the environment ( $R$ ), so that  $K$  changes in a predictable way when resources change, and  $r$  and  $K$  cannot evolve independently, which undermines the classical contrast between  $r$ - and  $K$ -selection (Getz, 1993, 1994). Third,  $r$  and  $K$  are both positive if and only if  $R > \frac{mh}{b-m}$ , so a population can persist on a sparse resource only if it is good at extracting scarce resources (small  $h$ ) or efficient at converting them (small  $m/b$ ). With the general extraction form, Eq. (27) becomes the generalized logistic model of Pella and Tomlinson (1969),  $dN/dt = rN(1 - N^p/K)$ , widely used in fisheries.

*Consumer-resource interactions.* If the resource is itself a population,  $x_1$ , growing on a constant abiotic input  $x_0$  and consumed by  $x_2$ , Eq. (24) with  $n = 2$  gives

$$\begin{aligned} \frac{dx_1}{dt} &= \rho_1 x_1 \left( 1 - \frac{m_1(h_1 + w_1 x_1 + x_0)}{b_1 x_0} \right) - \frac{b_2 x_1 x_2}{h_2 + w_2 x_2 + x_1}, \\ \frac{dx_2}{dt} &= \rho_2 x_2 \left( 1 - \frac{m_2(h_2 + w_2 x_2 + x_1)}{b_2 x_1} \right). \end{aligned} \quad (29)$$

Both equations now have the same structure: the resource is a consumer of  $x_0$ , with its own carrying capacity  $K_1$  given by Eq. (28) with  $R = x_0$ , and the consumer has a carrying capacity that varies with the abundance of its resource. Setting  $dx_2/dt = 0$  gives the consumer null-isocline

$$x_2 = \frac{(b_2 - m_2) x_1 - m_2 h_2}{m_2 w_2}, \quad (30)$$

a sloping line that crosses the resource axis at  $x_1 = m_2 h_2 / (b_2 - m_2)$ , rather than the vertical predator isocline of Modules 1–4; it has the same form as the Beddington-DeAngelis isocline of Table 4, with  $b_2$  and  $m_2$  in place of  $c$  and  $d$ . Consumer interference also has a less obvious effect. Because the total rate at which consumers can remove each unit of resource is bounded by  $b_2/w_2$ , however many consumers

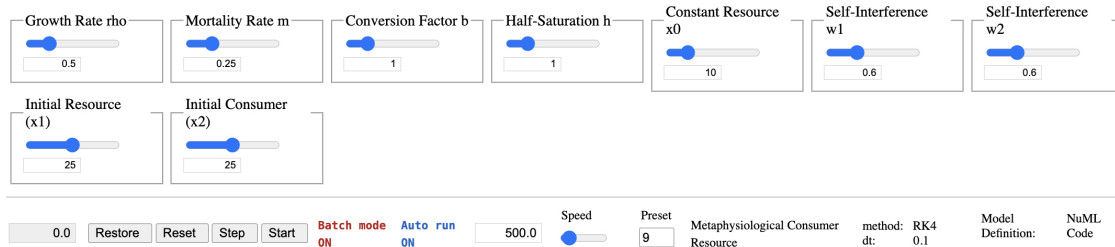
there are, the resource null-isocline has a pole at

$$\hat{x}_1 = K_1 - \frac{b_1 b_2 x_0}{\rho_1 m_1 w_1 w_2},$$

and when  $\hat{x}_1 > 0$  resources below this density always increase: the consumers' interference creates a *dynamic refuge* for their resource (Getz, 1991, 1994). Worked example 9 shows how strongly the self-interference parameters  $w_1$  and  $w_2$  shape the dynamics.

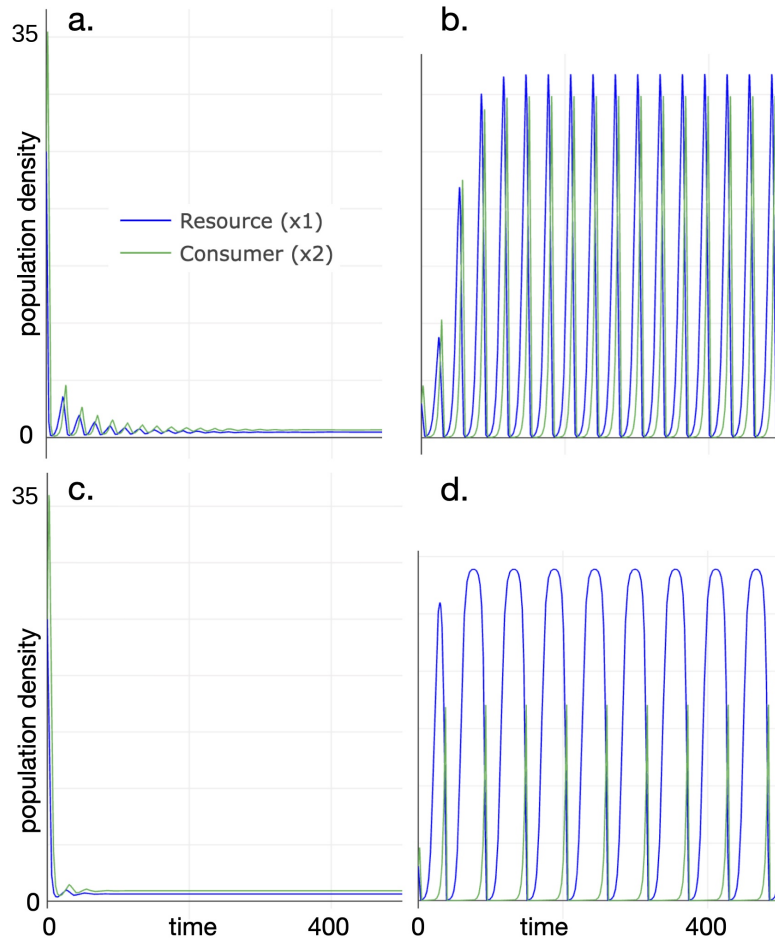
### Worked example 9: Self-interference and the stability of a consumer-resource system

**Simulator setup:** [Link to Preset 9](#). In this exploration of Eq. (29), take  $\rho_1 = \rho_2 = 0.5$ ,  $m_1 = m_2 = 0.25$ ,  $b_1 = b_2 = 1$ ,  $h_1 = h_2 = 1$  and  $x_0 = 10$  so that  $\rho < 4m$  for both populations.



We vary the self-interference parameters ( $w_1, w_2$ ) of the resource and consumer. The resource carrying capacity is  $K_1 = 29/w_1$ , but in every case the consumers hold the resource far below it, close to the root  $x_1 = 1/3$  of the consumer isocline, Eq. (30).

- $(w_1, w_2) = (0.6, 0.6)$ , from  $(25, 25)$ : after one large excursion, in which consumer density rises to about 35 while resource density collapses, the system spirals into a stable focus at  $(0.47, 0.67)$ , with  $\lambda \approx -0.011 \pm 0.31i$ .
- $(w_1, w_2) = (0.4, 0.4)$ , from  $(3, 3)$ : reducing both interference parameters by a third destabilizes the equilibrium, now at  $(0.41, 0.60)$ , with  $\lambda \approx +0.008 \pm 0.33i$ . Both populations cycle with a period of about 31 time units, resource density between about 0.08 and 32 and consumer density between about 0.03 and 30: minima an order of magnitude below the equilibrium values and maxima fifty to eighty times above them.
- $(w_1, w_2) = (0.1, 1.0)$ , from  $(25, 25)$ : gregarious resources (weak self-interference) and territorial consumers (strong self-interference) give a strongly damped focus at  $(0.64, 0.93)$ , with  $\lambda \approx -0.046 \pm 0.26i$ .
- $(w_1, w_2) = (1.0, 0.1)$ , from  $(3, 3)$ : the reverse combination is unstable ( $\lambda \approx +0.034 \pm 0.36i$  at  $(0.35, 0.50)$ ) and produces outbreak dynamics, with a period of about 56 time units: consumer density spikes to about 17 and then crashes to around  $10^{-6}$ , persisting at extremely low levels for long periods before the next outbreak.



Self-interference therefore plays the stabilizing role that predator interference plays in Module 5, and the four cases suggest a biological conjecture: consumer-resource interactions are most likely to persist when consumers are strongly territorial (large  $w_2$ ) and resources gregarious (small  $w_1$ ) (Getz, 1994). The outbreak cycles of case (d) are, as Getz (1994) notes, not seen in the Rosenzweig-MacArthur model of Module 4. All four cases can be explored in Preset 9 of the NWK DynSS LVPP app by changing the sliders for  $w_1$  and  $w_2$  and the initial densities.

#### 5.4. Trophic stacks and multispecies assemblages

In this subsection, only outlines of worked examples are sketched with no presets for the NWK DynSS LVPP App provided. It is left to the instructor and students to explore the possibility of coding up their own models in Presets 10-25 of the NWK DynSS LVPP App following the guide laid out in Section 3.

Applying Eq. (24) to longer chains reveals what the conversion and extraction assumptions imply for whole ecosystems. With linear conversion and mass-action extraction, the Lotka-Volterra stack  $dx_i/dt = \rho_i a_i x_{i-1} x_i - m_i x_i - a_{i+1} x_i x_{i+1}$ , where  $\rho_i$  is a conversion efficiency and  $m_i$  a per-unit loss rate, has equilibria satisfying

$$\hat{x}_{n-1} = \frac{m_n}{\rho_n a_n}, \quad \hat{x}_{i+1} = \frac{\rho_i a_i \hat{x}_{i-1} - m_i}{a_{i+1}}, \quad (31)$$

in which  $\hat{x}_i$  cancels: each equilibrium level is linked directly only to the levels two steps above and below it (Getz, 1994). The level just below the top is fixed by the top consumer's parameters alone, generalizing the result of Module 1 that the prey equilibrium  $x^* = d/c$  depends only on the predator.

Enrichment at the base then propagates up through alternate levels, so that the effect of more resources depends on whether the chain has an odd or even number of levels. This is the mathematical core of the ‘food chain dynamics’ hypothesis (Fretwell, 1987; Hairston et al., 1960; Oksanen et al., 1981), and Wootton and Power (1993) found that in a four-level river food chain the first and third levels were indeed largely decoupled from the second and fourth. The decoupling, however, is an artifact of linearity: with hyperbolic conversion and resource-and-consumer extraction, consecutive levels are linked, and the height of the stack has a natural upper bound (Getz, 1991, 1994). If every level has the same parameters, and densities and time are scaled by  $h$  and  $b$  (so that densities are measured in units of the half-saturation density), Eq. (24) becomes (with  $\rho$  and  $m$  now measured in units of  $b$ ) the three-parameter model

$$\frac{dx_i}{ds} = \rho x_i \left( 1 - m \frac{1 + w x_i + x_{i-1}}{x_{i-1}} \right) - \frac{x_i x_{i+1}}{1 + w x_{i+1} + x_i}, \quad i = 1, \dots, n, \quad (32)$$

with  $x_{n+1} = 0$ . Table 5 lists its stable equilibria as the chain lengthens: parity still matters, since the basal level is lightly used (at 70–100% of its unexploited level) when  $n$  is odd and heavily used (below 10%) when  $n$  is even, but the levels are coupled, and the stacks are not pyramid-shaped. With a larger maintenance requirement,  $m = 0.5$ , and  $x_0 = 100$ , a four-level chain is unstable and its top level goes extinct, leaving a stable, pyramid-shaped three-level stack at (90.7, 1.94, 0.94). Self-interference is essential to this stability: with  $w = 0$ , even the two-level chain is unstable, with  $\lambda \approx 0.062 \pm 0.241i$  at (1.0, 0.495), and its oscillations span more than thirty-five orders of magnitude (Getz, 1994).

**Table 5.** Stable equilibria of the dimensionless trophic stack, Eq. (32), with  $\rho = 0.5$ ,  $m = 0.15$ ,  $w = 1$  and basal input  $x_0 = 1$ , for chains of  $n = 1$  to 5 levels. Values for  $n = 2$ –5 agree with Table 1 of Getz (1994); for  $n = 1$  the equilibrium is  $\hat{x}_1 = (x_0/m - 1 - x_0)/w \approx 4.67$  (the table in the original gives 6.67). All equilibria were recomputed numerically and confirmed to be stable.

| $n$ | $\hat{x}_1$ | $\hat{x}_2$ | $\hat{x}_3$ | $\hat{x}_4$ | $\hat{x}_5$ |
|-----|-------------|-------------|-------------|-------------|-------------|
| 1   | 4.67        |             |             |             |             |
| 2   | 0.29        | 0.63        |             |             |             |
| 3   | 3.80        | 0.33        | 0.88        |             |             |
| 4   | 0.43        | 0.67        | 0.26        | 0.50        |             |
| 5   | 3.29        | 0.49        | 0.96        | 0.29        | 0.62        |

*How long can a food chain be?* Getz (1994) left open whether chains longer than five levels can be supported. Students can answer this themselves with two tools. First, the equilibria of Eq. (32) can be computed level by level: given  $x_0$  and a trial value of  $\hat{x}_1$ , the equilibrium condition for level  $i$  determines  $\hat{x}_{i+1}$  from  $\hat{x}_{i-1}$  and  $\hat{x}_i$ , and  $\hat{x}_1$  is adjusted until the top level is exactly at its maintenance requirement (a one-dimensional ‘shooting’ problem). Second, a new top level can invade a stable  $n$ -level chain only if its per-unit growth rate when rare,  $\rho(1 - m(1 + \hat{x}_n)/\hat{x}_n)$ , is positive, that is, if  $\hat{x}_n > m/(1 - m)$ . With the parameters of Table 5, every chain of up to ten levels is stable and can be invaded by a further level; the eleven-level chain is stable, but its top level, at  $\hat{x}_{11} \approx 0.13$ , is below the invasion threshold  $m/(1 - m) \approx 0.18$ , so a twelfth level cannot invade. By this equilibrium criterion a chain therefore stops at eleven levels, although, as Appendix B.2 shows, a chain actually assembled by successive introductions with  $w = 1$  stops at seven, because the eighth level drives the chain into outbreak cycles. Two further patterns emerge along the way. The parity pattern of Table 5 fades: as  $n$  increases from 1 to 11,  $\hat{x}_1$  takes the values 4.67, 0.29, 3.80, 0.43, 3.29, 0.54, 2.85, 0.65, 2.31, 0.78 and 0.87, so the alternation between lightly and heavily used basal levels damps out. And longer chains

are less resilient: the real part of the leading eigenvalue rises from  $-0.35$  for  $n = 1$  to about  $-0.01$  for  $n = 11$ , so perturbations decay ever more slowly, in line with the argument of Pimm and Lawton (1977) that long food chains are dynamically fragile.

*Alternative stable chain lengths.* With the larger maintenance requirement  $m = 0.5$ , the picture changes. A two-level chain always has  $\hat{x}_1 < 2$  and  $\hat{x}_2 = \hat{x}_1 - 1 < 1 = m/(1 - m)$ , so a rare third level can never invade, however productive the base. Yet for basal inputs above about 22 (but not for 21 or below), a stable three-level chain also exists: with  $x_0 = 100$ , the two-level equilibrium  $(1.94, 0.94)$  and the three-level equilibrium  $(90.7, 1.94, 0.94)$  are both stable, separated by a saddle at about  $(2.33, 1.06, 0.06)$ . The mechanism is a trophic cascade. Once established, the top level suppresses level 2, which releases the basal level (from 1.94 to 90.7); the abundant basal level supports twice the density at level 2 (0.94 rises to 1.94), and this is enough to feed the top level, whose maintenance requires  $\hat{x}_2 > 1$ . Introductions of a top predator into the two-level chain at  $x_0 = 100$  show the consequences. Introduced at a density  $z$  between about 0.1 and 1.5, it establishes; introduced below about 0.1, it starves before it can trigger the cascade; and introduced above about 1.5, it overexploits level 2 and crashes. At  $x_0 = 300$  and 1000 the minimum successful introduction falls to about 0.022 and 0.006. This is an Allee effect that arises from community structure rather than from the biology of the top predator itself, an *emergent* Allee effect (de Roos & Persson, 2002), and it reprises the bistability of Module 3 and of Worked example 6, Part 2, at the level of a whole food chain. Its lesson is that the length of a food chain depends on history, the order and size of colonizations, as well as on productivity. Appendix B.2 shows that the strength of self-interference sets chain length too, with the longest chains at intermediate interference, and that the same chain can settle either at equilibrium or into outbreak cycles depending on how it was assembled.

*Multispecies assemblages.* Real food webs are not simple stacks. Writing  $g_{ij}$  for the rate at which each unit of population  $i$  extracts currency from population  $j$ ,  $v_{ij}$  for the relative nutritional value of  $j$  to  $i$ ,  $R_i$  for the set of resources of  $i$  and  $C_i$  for the set of its consumers, Eq. (24) generalizes to

$$\frac{dx_i}{dt} = x_i f_i \left( \sum_{j \in R_i} v_{ij} g_{ij} \right) - \sum_{\ell \in C_i} x_\ell g_{\ell i}, \quad i = 1, \dots, n, \quad (33)$$

for substitutable resources (Getz, 1994; Tilman, 1982). Competition, predation and mutualism are no longer represented by the signs of interaction coefficients, as in the generalized Lotka-Volterra equations, but by how the extraction functions depend on other species: two consumers  $i$  and  $j$  compete for resource  $k$  if  $g_{ik}$  decreases with  $x_j$  and  $g_{jk}$  with  $x_i$ , and are mutualists if  $g_{ij}$  and  $g_{ji}$  increase with  $x_j$  and  $x_i$ . Getz (1991) develops two cases of mutualism in this way, species that provide each other with resources and species that trade resources for protection, as when ants tend aphids. MacArthur's model, Eq. (23), is the special case with linear conversion and mass-action extraction; Eq. (33) also allows consumer interference to be embedded in the extraction functions rather than added separately. Whether  $n$  consumers can coexist on fewer than  $n$  resources in such models remains an open question (Getz, 1994).

### 5.5. Stability and Complexity in Multispecies Lotka-Volterra Models

As in the previous subsection, no worked example is provided here: some concepts relating to multispecies Lotka-Volterra equations are reviewed, and it is up to students to explore them further using models that they code into the NWK DynSS LVPP app.

*The generalized Lotka-Volterra system.* Every model of Modules 1 and 2 and of Sections 5.1 and 5.2 (except Hastings-Powell) is a special case of the generalized Lotka-Volterra system for  $S$  interacting

species with densities  $x_1, \dots, x_S$ :

$$\frac{dx_i}{dt} = x_i \left( r_i + \sum_{j=1}^S a_{ij} x_j \right), \quad i = 1, \dots, S, \quad (34)$$

where  $r_i$  is the per-capita growth rate of species  $i$  when all densities are low (negative for a predator that cannot live without its prey),  $a_{ii} \leq 0$  measures self-regulation, and  $a_{ij}$  ( $j \neq i$ ) is the per-capita effect of species  $j$  on the growth rate of species  $i$ . The signs of the pair  $(a_{ij}, a_{ji})$  define the interaction:  $(-, +)$  when  $j$  preys on  $i$ ,  $(-, -)$  for competition and  $(+, +)$  for mutualism. The logistic-prey model of Module 2, for example, is Eq. (34) with  $S = 2$ ,  $r_1 = r$ ,  $r_2 = -d$ ,  $a_{11} = -r/K$ ,  $a_{12} = -b$ ,  $a_{21} = c$  and  $a_{22} = 0$ ; the competition model, Eq. (20), has  $a_{ii} = -r_i/K_i$  and off-diagonal entries  $-r_i a_{ij}/K_i$ , where  $a_{ij}$  is the competition coefficient of that equation; and the May-Leonard model, Eq. (21), has  $r_i = 1$ ,  $a_{ii} = -1$  and off-diagonal entries  $-p$  and  $-q$ . Writing  $\mathbf{r} = (r_1, \dots, r_S)'$  and  $A = (a_{ij})$ , a coexistence equilibrium  $\mathbf{x}^*$  satisfies the linear equations

$$\mathbf{r} + A \mathbf{x}^* = \mathbf{0}, \quad \text{so that} \quad \mathbf{x}^* = -A^{-1} \mathbf{r}, \quad (35)$$

which is ecologically meaningful only if every  $x_i^* > 0$  (*feasibility*). Differentiating Eq. (34) and using Eq. (35), the Jacobian at  $\mathbf{x}^*$  has the particularly simple form

$$J_{ij}^* = x_i^* a_{ij}, \quad \text{that is,} \quad J^* = \text{diag}(\mathbf{x}^*) A, \quad (36)$$

known in ecology as the *community matrix*. The equilibrium is locally stable if every eigenvalue of  $J^*$  has negative real part (Appendix A.4). Students can check Eq. (36) against Worked example 2: with  $\mathbf{r} = (0.4, -0.5)'$  and  $A = \begin{pmatrix} -0.004 & -0.04 \\ 0.01 & 0 \end{pmatrix}$ , Eq. (35) gives  $\mathbf{x}^* = (50, 5)'$ , and Eq. (36) gives the Jacobian of that example, with eigenvalues  $-0.1 \pm 0.3i$ . In addition, Goh (1977) showed that if there is a diagonal matrix  $W$  with positive entries such that  $WA + A'W$  is negative definite, then a feasible equilibrium is globally stable, a result that generalizes the Volterra Lyapunov function of Appendix A.5.

*May's random community matrices.* Ecologists long held, following Elton (1958) and MacArthur (1955), that diverse communities with many interacting species are more stable than simple ones. May (1972) challenged this view by bypassing Eqs. (34)–(35) altogether and asking what happens near equilibrium in a community of  $S$  species, a fraction  $C$  (the *connectance*) of whose possible pairwise interactions are present. He assumed that each species regulates itself, and measured time in units of the self-regulation time so that the diagonal entries of the community matrix all equal  $-1$ . The remaining entries are drawn at random:

$$J = -I + B, \quad B_{ii} = 0, \quad B_{ij} = \begin{cases} 0 & \text{with probability } 1 - C, \\ Z_{ij} \sim \mathcal{N}(0, \sigma^2) & \text{with probability } C, \end{cases} \quad (37)$$

where  $I$  is the identity matrix. The eigenvalues of  $J$  are those of  $B$  shifted by  $-1$ . For large  $S$ , the *circular law* of random-matrix theory states that the eigenvalues of  $B$  are spread uniformly over a disc in the complex plane centered at the origin, with radius  $\sigma\sqrt{SC}$ . The eigenvalues of  $J$  therefore fill a disc centered at  $-1$  with that radius, and all of them have negative real parts if and only if the disc does not reach the imaginary axis. The equilibrium is thus almost certainly stable if

$$\sigma\sqrt{SC} < 1 \quad (38)$$

and almost certainly unstable otherwise (see also Gardner & Ashby, 1970). More species, more connections and stronger interactions all make stability less likely.

*Interaction types and the elliptic law.* In Eq. (37),  $B_{ij}$  and  $B_{ji}$  are independent, so among pairs in which both entries are non-zero, half are predator-prey pairs and a quarter each are competitive and mutualistic (and many interactions are one-sided). Real interactions come in pairs with correlated signs. Let

$$\rho = \frac{E[B_{ij}B_{ji}]}{\sigma^2}$$

be the correlation between the two members of an interacting pair, where the entries have mean zero and variance  $\sigma^2$ . For large  $S$ , the eigenvalues of  $B$  then fill an ellipse centered at the origin with semi-axes  $\sigma\sqrt{SC}(1 + \rho)$  along the real axis and  $\sigma\sqrt{SC}(1 - \rho)$  along the imaginary axis (Allesina & Tang, 2012). The stability criterion generalizes Eq. (38) to

$$\sigma\sqrt{SC}(1 + \rho) < 1. \quad (39)$$

A random community has  $\rho = 0$ , which recovers Eq. (38). If each interacting pair is a predator and its prey, with one positive and one negative entry whose magnitudes are drawn from the half-normal distribution  $|N(0, \sigma^2)|$  and whose orientation is random, then  $\rho = -2/\pi \approx -0.64$ , and the criterion relaxes to  $\sigma\sqrt{SC} < 1/(1 - 2/\pi) \approx 2.75$ . If instead both members of each pair have the same sign, a mixture of competition  $(-, -)$  and mutualism  $(+, +)$ , then  $\rho = +2/\pi$ , and the criterion tightens to  $\sigma\sqrt{SC} < 1/(1 + 2/\pi) \approx 0.61$ . Predator-prey interactions flatten the eigenvalue ellipse towards the imaginary axis, which produces oscillations rather than instability, whereas competition and mutualism stretch it along the real axis.

The results are easy to explore with a few lines of code. With  $S = 50$  and  $C = 0.2$ , Eq. (38) gives the threshold  $\sigma = 1/\sqrt{10} \approx 0.32$ . In our trials (400 random matrices for each value of  $\sigma$ ), 99.5% of random community matrices were stable for  $\sigma = 0.25$ , 90% for  $\sigma = 0.30$  and only 46% for  $\sigma = 0.35$ . Imposing the predator-prey sign structure of Modules 1-5 changes the picture completely, as Eq. (39) predicts, since the threshold rises to  $\sigma \approx 0.87$ : all such matrices were stable at  $\sigma = 0.4$ , more than 99% at  $\sigma = 0.6$ , 51% at  $\sigma = 1.0$  and 20% at  $\sigma = 1.2$ . With same-sign pairs the threshold falls to  $\sigma \approx 0.19$ : only 49% of matrices were stable at  $\sigma = 0.2$ , and fewer than 1% at  $\sigma = 0.25$ . At this moderate size the transitions are gradual rather than sharp, because the edge of the eigenvalue disc or ellipse fluctuates from one matrix to the next; they sharpen as  $S$  grows. Students can code Eq. (34) for three or four species into one of the user presets of the NWK DynSS LVPP app, directly in NuML or through the AI window, and watch the transition from stability to instability as the off-diagonal interactions are strengthened.

*The follow-on literature.* In May (1973) these results sit alongside analyses of the predator-prey and competition models of this paper, time delays and environmental noise. The book recast the question from ‘does complexity beget stability?’ to ‘what special structures allow real, complex ecosystems to persist?’, and the answers form much of the follow-on literature. Pimm (1984) distinguished the several meanings of ‘stability’ (resilience, resistance, persistence and variability) and showed that they need not change together with complexity. McCann et al. (1998) showed that many weak interactions can damp the oscillations generated by a few strong ones, and Neutel et al. (2002) found that interaction strengths in real soil food webs are arranged so that long feedback loops contain weak links, which makes the webs far more stable than random ones. McCann (2000) reviewed this diversity-stability debate. Allesina and Tang (2012) derived Eq. (39) and its extensions to structured communities, and so proved what the experiment above suggests: predator-prey interactions are stabilizing, while competition and

mutualism are destabilizing. Mougi and Kondoh (2012) showed that a mixture of interaction types can make diversity stabilizing again. For students, the sequence from Lotka and Volterra's two equations, through the three-species models of this section, to Eqs. (34)–(39) traces how an elementary model can be scaled up into a question about the architecture of whole ecosystems, a question still being actively researched.

## 6. Discussion

Much attention has been given to embedding stronger quantitative skills in biology curricula (Thompson et al., 2013), and to embedding ecological and sustainability contexts in mathematics curricula (Kleshnina et al., 2026). The LVPP narrative serves both aims while asking very little of instructors. The Lotka-Volterra model is already in many applied math and ecology syllabuses. The modules and extensions presented here simply allow instructors to enrich their current course work by letting students explore the behavior of the models using a simulator for which there is virtually no learning curve. Looking back over the paper as a whole, three threads run through it: a single ecological narrative that unfolds into most of the core ideas of dynamical systems theory; a small number of mathematical motifs that recur, in new guises, at every stage of that narrative; and a consistent pairing of analysis with simulation. We draw these threads together below, then consider how the material can be used with students in the biological, social and applied sciences, and what it leaves out.

### 6.1. One narrative, many mathematical ideas

The organizing principle of the modules is that every new mathematical idea arrives as the answer to an ecological question raised by the previous model. Table 6 summarizes the sequence. Relaxing the assumption that prey grow without limit turns the neutral center of Module 1 into the stable focus of Module 2, and teaches structural stability. Adding an Allee effect introduces multiple attractors and the separatrices that divide them (Module 3). Satiating the predator produces a Hopf bifurcation, a limit cycle and the paradox of enrichment (Module 4). Letting predators interfere with one another removes the paradox but creates a non-differentiable equilibrium that attracts without being classifiable as stable using Jacobian matrix stability theory (Module 5). Adding species brings competitive exclusion and priority effects, heteroclinic cycles and chaos (Section 5). Rebuilding every population from the same concepts of extraction and conversion derives the logistic equation, predicts trophic cascades and alternative food-chain structures, and makes chain length depend on self-interference and history (Section 5.3 and Appendix B.2). At no stage do students have to learn a new biological system, only a modification of the system at hand. At each stage, in Worked examples 1–9, students are introduced to a new mathematical concept in dynamical systems theory.

### 6.2. Recurring motifs

Read across the modules rather than down them, the paper returns again and again to a handful of ideas, and drawing students' attention to these recurrences is perhaps the most valuable synthetic exercise an instructor can set.

*Thresholds and the geometry of separatrices.* The boundary between persistence and collapse appears first as the stable manifold of the Allee saddle in Module 3, then as the trajectory entering the singular origin of the ratio-dependent model (Worked example 5), then as the stable manifold of an interior saddle in competition (Worked example 6, Part 2), and finally as the boundary between a two-level and a three-level food chain, where a top predator introduced at too low a density fails while one introduced at a sufficient density succeeds (Section 5.3). In each case the threshold is a curve in the

**Table 6.** The LVPP narrative as a course in dynamical systems: each step relaxes one assumption of the previous model, introduces a new mathematical idea, and teaches a new ecological lesson.

| Assumption relaxed           | Mathematical ideas                                                                                             | Ecological lessons                                                                                     | Where                       |
|------------------------------|----------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------|-----------------------------|
| — (classical model)          | Equilibria, isoclines, linearization, conserved quantities, neutral centers; numerical drift of Euler's method | Predator-prey interactions can generate cycles                                                         | Module 1, WE 1              |
| Unlimited prey growth        | Structural stability; trace-determinant classification; Lyapunov functions and global stability                | Self-limitation of prey damps cycles                                                                   | Module 2, WE 2, App. A.5    |
| No difficulty at low density | Multiple attractors; saddles and separatrices; basins of attraction                                            | Extinction thresholds depend on both species                                                           | Module 3, WE 3              |
| Insatiable predators         | Hopf bifurcation; limit cycles; Poincaré-Bendixson; critical slowing down                                      | Paradox of enrichment; transients can mislead                                                          | Module 4, WE 4              |
| Predators feed independently | Non-differentiable equilibria; attraction versus stability; ratio variables                                    | Enrichment without destabilization; joint extinction                                                   | Module 5, WE 5              |
| Only two species             | Real eigenvalues and saddles in competition; heteroclinic cycles; chaos and Lyapunov exponents                 | Competitive exclusion; priority effects; rock-paper-scissors; limits to forecasting                    | Section 5, WE 6–8           |
| Phenomenological rates       | Derived (emergent) logistic growth; $n$ -dimensional stacks; bistability between equilibria and cycles         | $K$ as a composite parameter; trophic cascades; emergent Allee effects; history-dependent chain length | Section 5.3, WE 9, App. B.2 |

phase space, not a single number, and in each case it is found most easily by combining analysis (to locate the saddle and its eigenvectors) with simulation (to approximately trace the separatrix because its shape can rarely be found analytically).

*Self-limitation as the great stabilizer.* Logistic prey growth turns the neutral cycles of Module 1 into damped oscillations; predator interference removes the paradox of enrichment (Module 5); self-interference among consumers determines whether a consumer-resource interaction settles, cycles or erupts in outbreaks (Worked example 9); and in trophic stacks it sets both the stability and the maximum length of food chains, with intermediate interference supporting the longest chains (Appendix B.2). The metaphysiological derivation of the logistic equation, Eq. (28), explains why: a finite carrying capacity requires interference among consumers. Students thus see a single biological mechanism acting at three levels of organization, and the same mathematical signature, a negative diagonal entry in the Jacobian, at each.

*Stability, attraction and the limits of linearization.* The classical center (Module 1), the singular origin of the ratio-dependent model (Worked example 5) and the neutral cycles of the May-Leonard model at  $p + q = 2$  (Worked example 7) are all cases in which the Jacobian is silent or absent. Each requires a deeper tool: a conserved quantity, a change of variables to the prey-to-predator ratio, or a Lyapunov function (Appendix A.5), and each teaches that stability can be settled beyond the reach of the Jacobian, and that stability and attraction are different properties.

*Slow dynamics and long transients.* Near the Hopf bifurcation of Module 4, damping is so weak that

two qualitatively different systems look alike for a century; near the saddle of a competitive separatrix, trajectories linger; on the heteroclinic cycle of Worked example 7, each period of dominance becomes nearly half again as long as the last; and in the outbreak cycles of trophic stacks, top predators spend most of their time at biologically unrealistically low densities. Whenever students are tempted to read the long-term behavior of a system from a short simulation, or of an ecosystem from a short time series, these examples argue for caution.

*Trust in computation.* Forward Euler inflates the neutral cycles of Module 1, invents a limit cycle near the Hopf bifurcation of Module 4, and stretches the switching times of the heteroclinic cycle (Appendix B.1). In the chaotic food chain, even RK4 runs with different step sizes part company within a few thousand time units (Worked example 8). The lesson is not that simulation is unreliable, but that it must be checked against analysis wherever analysis is possible and interpreted statistically where it is not.

### 6.3. Narratives, models and scientific judgement

We began with the observation that science advances through competing narratives. The predation narratives developed here (prey-dependent, ratio-dependent and metaphysiological) are not mathematically equivalent in the way that the matrix and wave formulations of quantum mechanics turned out to be. They make different predictions about enrichment, biological control, the possibility of joint extinction and the structure of food chains. That is precisely what makes comparing them so instructive. Students who have worked through the modules can read any of these models as a variation on a theme they already understand, and can see that the classical equations are the simplest member of a family rather than a law of nature. Narratives in science are judged both by their internal coherence and by how well they capture the broad patterns of nature (Ginzburg & Colyvan, 2004). The modules give students the means to apply both tests. They also offer a principled answer to the question every modeler faces: what to include. Getz (2011) recommends building models around *first-order* processes, defined as those whose effects on the outputs of interest are at least an order of magnitude larger than the effects of others; more generally, the level of process detail should match the questions being asked and the data available to parameterize and test the model, which is the theme of the ‘appropriate complexity’ and ‘model adequacy’ frameworks of Larsen et al. (2016) and Getz, Marshall, et al. (2018). The first-order criterion is one that students can apply directly with the sensitivity tools of Appendix A.7 and the sensitivity mode of the NWK DynSS LVPP app. Finally, the trophic-stack results of Appendix B.2 show that a uniformly constructed model, explored with a simulator and a little curiosity, can still yield findings that are new to its authors.

### 6.4. Teaching dynamical systems in the biological, social and applied sciences

The material can be used in several ways. In a one-semester course on mathematical modeling or dynamical systems, Modules 1–5 provide the backbone, Section 5 the advanced topics, and Appendix A the remedial support that a mixed class requires (Section 2). In a biology or ecology course with limited time, Modules 1 and 2 with their worked examples can be taught in two or three sessions, with the app carrying the computation. In an upper-division or graduate seminar, the extensions (ratio dependence, heteroclinic cycles, chaos, metaphysiological food chains) are suitable for projects in which students change one assumption, predict the consequences, test their predictions by simulation and explain the discrepancies. Because each model in the app is defined by a few lines of NuML, and can be modified with the help of an AI assistant (Section 3), such projects do not require students to be programmers.

For students in the biological sciences beyond ecology, the same mathematics transfers almost unchanged. Mass-action encounters between predators and prey are the encounters between infected and

susceptible individuals in the epidemic models of Kermack and McKendrick (1927), and the thresholds and outbreak dynamics of Modules 3–5 have direct counterparts in the epidemic threshold and in recurrent epidemics (Getz, Salter, et al., 2018); consumer-resource models describe nutrient uptake by cells and tissues as well as by populations; and bistability and separatrices are central to models of cellular decision-making and gene regulation. For students in the social sciences, Lotka-Volterra structures underlie classic models of economic growth cycles, in which the wage share of income plays the role of the predator and the employment rate that of the prey (Goodwin, 1967), and of competition between languages, in which a minority language faces the competitive exclusion of Section 5.1 unless it has a sufficient initial share or status (D. M. Abrams & Strogatz, 2003). Also, closely related systems of coupled rate equations describe arms races (Richardson, 1960). Concepts such as tipping points, path dependence, hysteresis and the limits of forecasting, which social scientists often meet only verbally, acquire precise meanings through the separatrices, alternative stable states and chaotic dynamics of the worked examples. For students in applied science and engineering, mass-action kinetics are the starting point of chemical reaction engineering, and Lotka's own first model was of oscillating chemical reactions (Lotka, 1910). The logistic and consumer-resource models underlie the bioeconomics of fisheries and other renewable resources (Clark, 1990), and the paradox of enrichment and the paradox of biological control are directly relevant to pest management and to the operation of bioreactors. In every case, the transferable skills are the same: formulating rates from mechanisms, finding and classifying equilibria, recognizing when linearization fails, mapping basins of attraction, and judging when a simulation can be trusted.

### **6.5. From using models to building them: presets and the AI window**

The worked examples of this paper are deliberately finished products: each preset loads a model whose behavior has been analyzed in advance. Their larger purpose, however, is to serve as starting points from which students extend the models and, eventually, build their own. Two features of the NWK DynSS LVPP app make this progression practical for students who are not programmers (Salter & Getz, 2026).

The first is the preset system. The factory presets are fixed, so a student can always return to a known, working model; the remaining preset slots (Presets 10–25 in current versions) record everything about a run, from the NuML code and parameter values to the slider ranges, graphs and integration settings, and they persist in the browser between sessions. A whole bank of presets can be saved to a file and restored in another browser. Instructors can therefore distribute a single file containing one preset per module or exercise, and students can hand in their work in the same form, so that an instructor can rerun exactly the model a student built. Because the presets of Section 4 and Section 5 are expressed in a few lines of NuML that read almost like the equations in the text, the natural first step is to modify one of them by hand. For example, students could add a harvesting term to the competition model of Preset 6, a third species to the consumer-resource model of Preset 9, or a top predator to the Rosenzweig-MacArthur model of Preset 4, which then turns it into the Hastings-Powell food chain of Worked example 8.

The second is the AI window, in which a student describes a model in words and a large language model returns both NuML code and a documentation page that states the model's equations in mathematical notation. The two outputs are saved into the app together, can be run at once, and can be refined through further prompts. The conversation with each language model is retained while the student works on a model, and is reset when the student moves to a different preset, so that one exercise does not contaminate the next (Salter & Getz, 2026). Experience with the facility suggests a simple rule for prompts. For a model that is well known by name, such as the Lotka-Volterra or Hodgkin-Huxley equations, plain prose suffices. For anything new, a structured prompt works better. Specifically, bold

headings separate the requirements for the model, the sliders, the displays and the documentation. The governing equations may be given explicitly in L<sup>A</sup>T<sub>E</sub>X notation or, for well-known models, just named as they appear in the literature. Variable names may be enclosed in backticks so that the generated code uses them. A prompt for the three-level metaphysiological food chain of Section 5.3, for example, might read:

```
**Model** Build a continuous-time three-level trophic stack,  $i = 1, 2, 3$ ,
with a constant basal resource 'x0' and

$$\frac{dx_i}{dt} = \rho x_i \left( 1 - m \frac{1 + w x_i + x_{i-1}}{x_{i-1}} \right) - \frac{x_i x_{i+1}}{1 + w x_{i+1} + x_i}, \quad x_4 = 0.$$

**Sliders** 'rho' (0 to 1), 'm' (0 to 0.5), 'w' (0 to 5), 'x0' (0.1 to 100),
and initial values of 'x1', 'x2', 'x3'.
**Displays** A time graph of 'x1', 'x2', 'x3'; a phase graph of 'x2' against 'x1'.
**Documentation** H3 headings; a table of parameters; the equations in LaTeX.
```

The student who submits such a prompt has already done the most important modeling work, which is to decide what the model should be. The AI facility removes only the need to code accurately using the NuML syntax.

These features support a sequence of increasingly independent exercises: run a preset and reproduce a worked example; predict, then test, the effect of changing one parameter; modify the NuML code by hand to relax one assumption; ask the AI window to implement a model taken from the literature and check it against published results; and finally design and build a new model to answer a question of the student's own. At every stage the verification steps of Section 3 apply, and they are what turns this sequence into an education rather than a demonstration: the equilibria, eigenvalues, bifurcation points and conserved quantities derived in the worked examples are exactly the checks that reveal whether a model, however it was built, behaves as intended. Because the app also supports discrete-time and stochastic models, as well as a sensitivity mode that reruns a model many times and plots means and standard deviations, students can carry the deterministic models of this paper into territory the paper does not cover, for example by adding demographic stochasticity to the heteroclinic cycle of Worked example 7 or the outbreak cycles of Appendix B.2 and estimating how long the rarest population survives. This iterative cycle of building, testing and revising a model of appropriate complexity (Getz, Salter, et al., 2018; Larsen et al., 2016) is the same whether the student is an ecologist, an epidemiologist (Getz et al., 2022) or a social scientist, and learning it is, we suggest, the most lasting benefit of the approach. It also responds to a broader concern: as AI takes over more of the routine computation in science and society, intuition about how dynamical systems behave risks being lost unless students gain hands-on experience in building, running and questioning models themselves (Salter & Getz, 2026).

## 6.6. Limitations

The models in this paper are deterministic, spatially homogeneous and unstructured. Real populations are subject to demographic and environmental stochasticity, which makes the deep troughs of outbreak and heteroclinic cycles fatal rather than merely temporary. Populations are distributed in space, which can stabilize or destabilize interactions. They also have age and stage structure, and storage mechanisms (resource hoarding, body fat) that allow individuals to survive without food for shorter or longer periods. Phenomenologically, storage introduces time delays that can create new oscillatory mechanisms. These elaborations can be included in the models, but soon the complexity of such inclusion will overwhelm both the student and the simulation app. Finally, although the modules have been developed through teaching, we have not yet evaluated them formally in the classroom.

## 7. Conclusions

The Lotka-Volterra prey-predator model is usually taught as a single example. We have argued, and tried to show, that the LVPP model is better treated as the opening chapter of a story that can carry an entire course on dynamical systems. Relaxing its assumptions one at a time leads naturally from equilibria and linearization, through structural stability, multiple attractors, bifurcations and limit cycles, to non-hyperbolic equilibria, heteroclinic cycles, chaos and high-dimensional food webs. Additionally, the ecological questions that motivate each step keep the mathematics anchored in meaning. Pairing each analytical result with simulation in a browser-based app, and testing numerical methods against analysis, teaches students both to use computation and to appropriately question and evaluate the solutions produced. Because similar, if not the same, mathematical structures describe epidemics, economies, languages, chemical reactors and harvested resources, the skills acquired transfer well beyond ecology. Above all, by comparing alternative narratives of predation that make different predictions, students learn that models are arguments to be tested, refined and sometimes replaced, which is how quantitative knowledge in the biological, social and applied sciences is built.

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## Author contributions

CRedit: **Wayne M. Getz:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing; **Richard Salter:** Software, Methodology, Writing – review & editing.

## Data availability statement

Data sharing is not applicable; no new data were generated. All models in this paper can be run, without installation or programming, in the NWK DynSS LVPP app, a browser-based simulator built on the Numerus WebKit™ platform, and the script used to produce Figure B.1 is provided as supplementary material. Each preset of the app stores a complete model specification—its NuML code, parameter values and slider ranges, initial conditions, switch settings and integration method—and loads with (or close to) the settings used in the corresponding worked example. Users can view and edit the NuML code, change parameters with sliders, overlay runs for comparison, explore parameter sensitivity, and save modified presets to their browser or to a file. The presets used in this paper are available at the following URLs:

**Preset 0, General LVPP:** <https://nuwebkit.models.numerus.app/dynsslvpp/?preset=0>. The full prey-predator model of Eq. (13), with switches for exponential or logistic prey growth, an Allee effect, and a mass-action, Holling Type II or Type III functional response; the factory settings from which the other prey-predator presets are derived (Module 5).

**Preset 1, Exponential versus logistic prey:** <https://nuwebkit.models.numerus.app/dynsslvpp/?preset=1>. The classical Lotka-Volterra model, Eq. (2), and, with the Prey Growth switch on, the logistic-prey model, Eq. (6): neutral cycles, the conserved quantity  $V$ , the numerical drift of Euler's method, and damped spirals into a stable focus (Modules 1 and 2; Worked examples 1 and 2).

**Preset 2, Prey-predator model with a Holling Type II response:** <https://nuwebkit.models.numerus.app/dynsslvpp/?preset=2>. The predator's mass-action term replaced by a saturating Holling Type II response, for exploring how predator satiation alone changes the dynamics of the classical model (Module 4 and Table 3).

**Preset 3, Logistic prey with an Allee effect:** <https://nuwebkit.models.numerus.app/dynsslvpp/?preset=3>. Logistic prey growth with the Allee function of Eq. (9), and an optional Holling Type II response: multiple attractors, a saddle at the Allee threshold and the separatrix dividing persistence from collapse (Module 3; Worked example 3).

**Preset 4, Logistic prey with a Holling Type II or III response:** <https://nuwebkit.models.numerus.app/dynsslvpp/?preset=4>. The Rosenzweig-MacArthur model and its Type III variant: the Hopf bifurcation at  $K_H$ , limit cycles, critical slowing down and the paradox of enrichment (Module 4; Worked example 4).

**Preset 5, Logistic prey with Beddington-DeAngelis and Arditi-Ginzburg responses:** <https://nuwebkit.models.numerus.app/dynsslvpp/?preset=5>. Predator-dependent and ratio-dependent functional responses: enrichment without destabilization, the separatrix and the singular origin of the ratio-dependent model (Module 5; Worked example 5).

**Preset 6, Gause-Lotka-Volterra competition:** <https://nuwebkit.models.numerus.app/dynsslvpp/?preset=6>. Two-species competition, Eq. (20): coexistence, competitive exclusion, and bistability with a saddle and separatrix (Section 5.1; Worked example 6).

**Preset 7, Three-species competition (May-Leonard):** <https://nuwebkit.models.numerus.app/dynsslvpp/?preset=7>. The rock-paper-scissors model, Eq. (21): damped spirals, neutral cycles and the approach to a heteroclinic cycle (Section 5.2; Worked example 7).

**Preset 8, Hastings-Powell food chain:** <https://nuwebkit.models.numerus.app/dynsslvpp/?preset=8>. The three-species food chain of Eq. (22): equilibrium, limit cycle and chaos as the satiation parameter  $b_1$  is increased (Section 5.2; Worked example 8).

**Preset 9, Metaphysiological consumer-resource:** <https://nuwebkit.models.numerus.app/dynsslvpp/?preset=9>. The consumer-resource model of Eq. (29), with hyperbolic conversion and resource-and-consumer extraction: the effects of self-interference on stability, cycles and consumer outbreaks (Section 5.3; Worked example 9).

## Disclosure statement

The authors are each part owners of Numerus Inc., which developed the Numerus WebKit™ platform on which the NWK DynSS LVPP app is built. Numerus Inc. has not marketed, and is not currently marketing, its modeling software, and all apps and presets referred to in this paper can be used free of charge. The authors use Numerus software in their own research and to develop instructional materials.

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## Appendices to: Getz and Salter, Teaching Dynamical Systems With Lotka-Volterra

### A. Mathematical background for students from diverse disciplines

This appendix collects, in one place, the minimum mathematics that students need to fully engage with the modules in Section 4. Students may still use the NWK DynSS LVPP app to generate solutions, but this appendix is written for students who are missing one or more pieces rather than for those learning the material for the first time, and each subsection can be read on its own. Every subsection follows the same pattern: the *key ideas*, what students should *be able to do*, an *example* drawn from the LVPP models of this note, and *self-check* exercises with answers. Students who can complete the self-checks quickly can safely skip that subsection. Pointers to fuller treatments are given at the end of each subsection; good general companions are Otto and Day (2007), Bodine et al. (2014), Edelstein-Keshet (2005) and Strogatz (2024).

Table 7 summarizes the six areas, with Lyapunov functions, part of the fourth, given a section of their own, together with the level of competence expected and where each is used.

**Table 7.** Background areas, minimum expected competence, and where each is used in the teaching modules.

| Area                                                | Minimum competence                                                                                                               | Used in modules           |
|-----------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------|---------------------------|
| A.1 Complex numbers                                 | Arithmetic; modulus; Euler's formula; reading growth rate and frequency from $\alpha \pm i\omega$                                | 1, 2, 4                   |
| A.2 Matrices                                        | $2 \times 2$ determinant, trace and eigenvalues; eigenvectors; trace-determinant relations                                       | 1–5                       |
| A.3 ODE solution theory                             | Separable and linear equations; existence and uniqueness; solutions of $\dot{\mathbf{x}} = A\mathbf{x}$ ; nondimensionalization  | 1–5                       |
| A.4 Linearization and stability                     | Jacobians; classification of planar equilibria; Lyapunov functions; limit cycles; basic bifurcations                             | 1–5                       |
| A.5 Lyapunov functions (part of the stability area) | Computing $dV/dt$ by the chain rule; conserved quantities; Volterra's function; LaSalle's principle; stability versus attraction | 1, 2, 5; Sections 5.1–5.2 |
| A.6 Simulation and numerical analysis               | Euler and Runge-Kutta methods; order of accuracy; step-size control; numerical instability                                       | 1, 3–5                    |
| A.7 Sensitivity analysis                            | Derivatives and elasticities of outputs with respect to parameters; parameter sweeps; idea of global methods                     | 2, 4, 5                   |

#### A.1. Complex numbers

*Key ideas.* A complex number  $z = \alpha + i\omega$  has a real part  $\alpha$  and an imaginary part  $\omega$ , where  $i^2 = -1$ . It can be pictured as the point  $(\alpha, \omega)$  in the complex plane, with modulus  $|z| = \sqrt{\alpha^2 + \omega^2}$  and argument  $\theta = \arg z$ , so that  $z = |z|(\cos \theta + i \sin \theta)$ . Its complex conjugate is  $\bar{z} = \alpha - i\omega$ , and  $z\bar{z} = |z|^2$ . Complex numbers are added, subtracted and multiplied like polynomials in  $i$ , replacing  $i^2$  by  $-1$  wherever it appears.

Complex numbers enter population dynamics through the quadratic formula. The roots of  $\lambda^2 + p\lambda + q = 0$  are  $\lambda = \frac{1}{2}(-p \pm \sqrt{p^2 - 4q})$ ; when  $p^2 < 4q$  the square root is of a negative number, and the roots are the complex-conjugate pair  $\lambda = -\frac{p}{2} \pm i \frac{1}{2}\sqrt{4q - p^2}$ . The single most important formula is Euler's,

$$e^{i\theta} = \cos \theta + i \sin \theta, \quad \text{so} \quad e^{(\alpha+i\omega)t} = e^{\alpha t} (\cos \omega t + i \sin \omega t). \quad (\text{A.1})$$

Equation (A.1) says that the real part  $\alpha$  of an exponent controls growth ( $\alpha > 0$ ) or decay ( $\alpha < 0$ ), while the imaginary part  $\omega$  produces oscillation with angular frequency  $\omega$  and period  $2\pi/\omega$ . Because the

differential equations in this note have real coefficients, complex solutions always appear in conjugate pairs whose sum is real; the physically meaningful solutions are combinations of  $e^{\alpha t} \cos \omega t$  and  $e^{\alpha t} \sin \omega t$ .

*Students should be able to.*

- add, multiply and divide complex numbers, and compute moduli and conjugates;
- find the complex roots of a real quadratic;
- read off a decay (or growth) rate and an oscillation period from an eigenvalue  $\alpha \pm i\omega$ .

*Example.* For the classical LVPP model, linearization at the coexistence equilibrium gives  $\lambda^2 + r\lambda + d = 0$ , so  $\lambda = \pm i\sqrt{rd}$ : with  $\alpha = 0$  there is neither growth nor decay, and the period of small oscillations is  $2\pi/\sqrt{rd} \approx 14$  years for  $r = 0.4$ ,  $d = 0.5$ . With logistic prey ( $K = 100$ ; Module 2) the characteristic equation becomes  $\lambda^2 + 0.2\lambda + 0.1 = 0$ , giving  $\lambda = -0.1 \pm 0.3i$ : oscillations now decay like  $e^{-0.1t}$  (halving roughly every 7 years) with period  $2\pi/0.3 \approx 21$  years.

*Self-check.* (1) Compute  $(2 + 3i)(1 - i)$ . (2) Find  $|\lambda|$  for  $\lambda = -0.1 + 0.3i$  and compare it with the constant term of the quadratic it solves. (3) A solution behaves like  $e^{0.05t} \cos(0.4t)$ . Is the equilibrium stable? What is the period? *Answers:* (1)  $5 + i$ . (2)  $|\lambda| \approx 0.316 = \sqrt{0.1}$ ; for a conjugate pair  $|\lambda|^2$  equals the product of the roots, i.e. the constant term. (3) Unstable (growing oscillations); period  $2\pi/0.4 \approx 15.7$ .

*Further reading.* Needham (1997, ch. 1); Otto and Day (2007).

## A.2. Matrix theory

*Key ideas.* A system of  $n$  interacting populations is described by a state vector  $\mathbf{x} = (x_1, \dots, x_n)'$  (a column, hence the transpose  $'$ ). Near an equilibrium, its dynamics are governed by an  $n \times n$  matrix, and almost everything we need to know about that matrix is captured by its eigenvalues. A scalar  $\lambda$  and non-zero vector  $\mathbf{v}$  are an eigenvalue-eigenvector pair of  $A$  if  $A\mathbf{v} = \lambda\mathbf{v}$ : along the direction  $\mathbf{v}$ , multiplication by  $A$  is just scaling by  $\lambda$ . Eigenvalues are the roots of the characteristic polynomial  $\det(A - \lambda I) = 0$ .

For the  $2 \times 2$  case, which covers every prey-predator model in this note,

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \quad \tau = \text{tr } A = a_{11} + a_{22}, \quad \Delta = \det A = a_{11}a_{22} - a_{12}a_{21}, \quad \lambda^2 - \tau\lambda + \Delta = 0, \quad (\text{A.2})$$

so  $\lambda_{1,2} = \frac{1}{2}(\tau \pm \sqrt{\tau^2 - 4\Delta})$ , with  $\lambda_1 + \lambda_2 = \tau$  and  $\lambda_1\lambda_2 = \Delta$ . These two identities are worth memorising, because they let students infer the signs of the eigenvalues without computing them: if  $\Delta < 0$  the eigenvalues are real with opposite signs; if  $\Delta > 0$  and  $\tau < 0$  both have negative real parts; if  $\Delta > 0$  and  $\tau > 0$  both have positive real parts; and they are complex whenever  $\tau^2 < 4\Delta$ .

For  $n = 3$  (e.g. food chains), the characteristic polynomial is a cubic,  $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$ , and the Routh-Hurwitz conditions  $a_1 > 0$ ,  $a_3 > 0$  and  $a_1a_2 > a_3$  guarantee that all three roots have negative real parts, without the need to find them (see Edelstein-Keshet, 2005).

*Students should be able to.*

- multiply matrices and vectors, and compute  $2 \times 2$  and  $3 \times 3$  determinants;
- find the eigenvalues and eigenvectors of a  $2 \times 2$  matrix;
- use the trace and determinant to determine the signs, or the real or complex nature, of  $2 \times 2$  eigenvalues.

*Example.* For the logistic-prey model (Module 2) at  $(x^*, y^*) = (50, 5)$  with  $r = 0.4$ ,  $b = 0.04$ ,  $c = 0.01$ ,  $d = 0.5$ ,  $K = 100$ ,

$$J^* = \begin{pmatrix} -rx^*/K & -bx^* \\ cy^* & 0 \end{pmatrix} = \begin{pmatrix} -0.2 & -2 \\ 0.05 & 0 \end{pmatrix}, \quad \tau = -0.2, \quad \Delta = 0.1,$$

so  $\Delta > 0$ ,  $\tau < 0$  (stable) and  $\tau^2 = 0.04 < 4\Delta = 0.4$  (complex), which is exactly the damped spiral of Figure B.1b.

*Self-check.* (1) Find the eigenvalues and eigenvectors of  $\begin{pmatrix} -1 & 2 \\ 0 & -3 \end{pmatrix}$ . (2) Without solving, classify the eigenvalues of  $\begin{pmatrix} 1 & 2 \\ 3 & -1 \end{pmatrix}$ . (3) Show that the classical LVPP Jacobian at  $(x^*, y^*)$  has  $\tau = 0$  and  $\Delta = rd$ .

*Answers:* (1)  $\lambda = -1$  with  $\mathbf{v} = (1, 0)'$ ;  $\lambda = -3$  with  $\mathbf{v} = (1, -1)'$ . (2)  $\Delta = -7 < 0$ : real, opposite signs (a saddle). (3)  $J^*$  has zero diagonal, off-diagonals  $-bd/c$  and  $cr/b$ , so  $\Delta = rd$ .

*Further reading.* Strang (2016, chs. 5–6); Otto and Day (2007).

### A.3. Elementary differential equation solution theory

*Key ideas.* An ordinary differential equation (ODE)  $\mathbf{dx}/dt = \mathbf{f}(\mathbf{x})$  specifies how fast each state variable changes as a function of the current state; together with an initial condition  $\mathbf{x}(0) = \mathbf{x}_0$  it forms an initial value problem. All models in this note are *autonomous* (time does not appear explicitly on the right-hand side) and *nonlinear*.

*Existence and uniqueness.* If  $\mathbf{f}$  has continuous first partial derivatives, as all our models do (for  $x > 0$ ), then the initial value problem has exactly one solution for some interval of time. Two consequences are used repeatedly: trajectories in the phase plane can never cross, and any set that is made up of whole trajectories is invariant. For example, the axes  $x = 0$  and  $y = 0$  consist of whole trajectories of Eq. (2), so a solution that starts with positive densities stays positive—a basic requirement of any credible population model.

*Scalar equations.* The exponential equation  $dx/dt = rx$  has solution  $x(t) = x_0 e^{rt}$ . More generally, separable equations  $dx/dt = g(x)$  can be solved by writing  $\int dx/g(x) = \int dt$ ; the logistic equation  $dx/dt = rx(1 - x/K)$ , solved using partial fractions, gives

$$x(t) = \frac{K}{1 + (K/x_0 - 1)e^{-rt}}. \quad (\text{A.3})$$

Even when no closed-form solution exists, a scalar autonomous equation can be understood completely from its *phase line*: equilibria are the roots of  $g(x) = 0$ , and an equilibrium  $x^*$  is stable if  $g'(x^*) < 0$  and unstable if  $g'(x^*) > 0$ .

*Linear systems.* The system  $\mathbf{dx}/dt = \mathbf{A}\mathbf{x}$  with distinct eigenvalues  $\lambda_i$  and eigenvectors  $\mathbf{v}_i$  has general solution

$$\mathbf{x}(t) = \sum_i c_i \mathbf{v}_i e^{\lambda_i t}, \quad (\text{A.4})$$

with constants  $c_i$  fixed by the initial condition. All solutions decay to  $\mathbf{0}$  if and only if every eigenvalue has negative real part. This result is the bridge between Sections A.1–A.2 and the stability theory of Section A.4.

*Nondimensionalization.* Rescaling variables to remove units often reduces the number of parameters.

Setting  $u = cx/d$ ,  $v = by/r$  and  $\tau = rt$  transforms Eq. (2) into

$$\frac{du}{d\tau} = u(1 - v), \quad \frac{dv}{d\tau} = \rho v(u - 1), \quad \rho = \frac{d}{r}, \quad (\text{A.5})$$

which shows that the qualitative behavior of the four-parameter model depends on just one ratio. Students from biology should also routinely check that every term in a model has the same units—a quick and powerful error check.

*Students should be able to.*

- solve exponential, separable (including logistic) and first-order linear equations;
- analyze a scalar autonomous equation using a phase line;
- write down the general solution of a  $2 \times 2$  linear system with distinct eigenvalues;
- nondimensionalize a simple model and check units.

*Example.* In the absence of prey, Eq. (2) reduces to  $dy/dt = -dy$ , so  $y(t) = y_0 e^{-dt}$ : with  $d = 0.5$  per year, predator density halves every  $\ln 2/d \approx 1.4$  years.

*Self-check.* (1) Verify by differentiation that Eq. (A.3) satisfies the logistic equation. (2) Find and classify the equilibria of  $dx/dt = x(x - 2)(5 - x)$ . (3) Verify Eq. (A.5). *Answers:* (2)  $x = 0$  ( $g'(0) = -10 < 0$ , stable),  $x = 2$  ( $g'(2) = 6 > 0$ , unstable),  $x = 5$  ( $g'(5) = -15 < 0$ , stable): the simplest model of a strong Allee effect, with threshold  $x = 2$ .

*Further reading.* Hirsch et al. (2013, chs. 1–3); Strogatz (2024, chs. 2–5); Bodine et al. (2014).

#### A.4. Linearization and dynamical systems stability theory

*Key ideas.* An equilibrium  $\mathbf{x}^*$  satisfies  $\mathbf{f}(\mathbf{x}^*) = \mathbf{0}$ . It is *stable* if solutions that start close to it stay close, *asymptotically stable* if in addition they converge to it, and *unstable* otherwise. These are local properties; *global* stability means convergence from every initial condition in a region of interest (for example, all positive densities).

*Linearization.* Writing  $\mathbf{x} = \mathbf{x}^* + \boldsymbol{\xi}$  and expanding  $\mathbf{f}$  to first order gives  $d\boldsymbol{\xi}/dt \approx J^* \boldsymbol{\xi}$ , where  $J^*$ , a matrix of partial derivatives  $J_{ij} = \partial f_i / \partial x_j$  evaluated at  $\mathbf{x}^*$ , i.e.,

$$J^* = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \cdots & \frac{\partial f_1}{\partial x_n} \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} & \cdots & \frac{\partial f_2}{\partial x_n} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial f_n}{\partial x_1} & \frac{\partial f_n}{\partial x_2} & \cdots & \frac{\partial f_n}{\partial x_n} \end{pmatrix}_{\mathbf{x}=\mathbf{x}^*} \quad (\text{A.6})$$

plays the starring role in dynamical systems theory and is called the Jacobian, named for the prominent German mathematician Carl Gustav Jacob Jacobi (1804–1851) who made fundamental contributions to multiple fields of mathematics, including elliptic functions, dynamics, and differential equations. By Eq. (A.4), the perturbation vector  $\boldsymbol{\xi}(t) = \sum_i c_i \mathbf{v}_i e^{\lambda_i t}$  decays if every eigenvalue of  $J^*$  has negative real part. The Hartman-Grobman theorem guarantees that the linearization correctly predicts the local behavior whenever no eigenvalue has zero real part (a *hyperbolic* equilibrium) (Hirsch et al., 2013). When an eigenvalue does have zero real part—as in the classical LVPP center—linearization is inconclusive, and a deeper analysis is needed.

*Planar classification.* In two dimensions, the trace  $\tau$  and determinant  $\Delta$  of  $J^*$  classify the equilibrium:  $\Delta < 0$ , saddle;  $\Delta > 0$  and  $\tau < 0$ , stable node ( $\tau^2 \geq 4\Delta$ ) or stable focus ( $\tau^2 < 4\Delta$ );  $\Delta > 0$  and  $\tau > 0$ ,

unstable node or focus;  $\Delta > 0$  and  $\tau = 0$ , a linear center. Stable and unstable manifolds of saddles act as separatrices that divide the phase plane into basins of attraction (Module 3).

*Beyond linearization.* If a *Lyapunov function*  $V(\mathbf{x})$  can be found—a scalar function that has a minimum at the equilibrium  $\mathbf{x}^*$  and satisfies  $dV/dt \leq 0$  along solutions near it—then the equilibrium is stable (Module 1), and LaSalle’s invariance principle often upgrades this to global asymptotic stability (Module 2) (Khalil, 2002, ch. 4). Appendix A.5 develops these ideas. In the plane, the Poincaré-Bendixson theorem (Hirsch et al., 2013; Strogatz, 2024) states that a bounded trajectory that does not approach an equilibrium must approach a closed orbit, which is how the existence of limit cycles is established (Module 4). Conversely, the Bendixson-Dulac criterion (Hirsch et al., 2013; Strogatz, 2024) rules out closed orbits in a simply connected region in which  $\partial(Bf_1)/\partial x + \partial(Bf_2)/\partial y$  has one sign for some smooth function  $B(x, y)$ .

*Bifurcations.* As a parameter  $\mu$  changes, an equilibrium may change stability. In a *transcritical* bifurcation two equilibria pass through each other and exchange stability (predator invasion at  $K = d/c$  in Module 2). In a *saddle-node* bifurcation two equilibria collide and disappear. In a *Hopf* bifurcation a complex-conjugate pair of eigenvalues crosses the imaginary axis (Hirsch et al., 2013; Strogatz, 2024). In two dimensions this means that the trace  $\tau$  passes through zero while the determinant  $\Delta$  stays positive. A limit cycle is then born: a stable one that grows from the equilibrium in a *supercritical* Hopf bifurcation (the paradox of enrichment in Module 4), or an unstable one that shrinks onto the equilibrium in a *subcritical* Hopf bifurcation (Module 3).

*Discrete time.* Students who have met difference equations  $\mathbf{x}_{t+1} = \mathbf{F}(\mathbf{x}_t)$  should note that the stability condition for these systems is that all eigenvalues of the Jacobian have *modulus* less than one, rather than negative real part.

*Students should be able to.*

- find equilibria, draw null-isoclines and sketch the direction field of a planar system;
- compute a Jacobian, evaluate it at an equilibrium, and classify the equilibrium using  $\tau$  and  $\Delta$ ;
- explain when linearization is inconclusive;
- state, in words, what Lyapunov functions, the Poincaré-Bendixson theorem and Hopf bifurcations tell us.

*Example.* For the logistic-prey model, Eq. (6), take  $B = 1/(xy)$ . Then

$$\frac{\partial}{\partial x} \left[ \frac{r(1 - x/K) - by}{y} \right] + \frac{\partial}{\partial y} \left[ \frac{cx - d}{x} \right] = -\frac{r}{Ky} < 0$$

throughout the positive quadrant, so the model has no periodic orbits: any self-limitation of the prey, however weak, eliminates the Lotka-Volterra cycles.

*Self-check.* (1) For Eq. (6) with the Module 1 parameters but  $K = 20$ , find and classify the equilibria. (2) Why does the trace-determinant classification fail to settle the stability of the classical LVPP coexistence equilibrium? *Answers:* (1)  $(0, 0)$  is a saddle (eigenvalues 0.4 and  $-0.5$ ). At  $(K, 0) = (20, 0)$ ,  $J = \begin{pmatrix} -0.4 & -0.8 \\ 0 & -0.3 \end{pmatrix}$ , a stable node; no coexistence equilibrium exists because  $K < d/c = 50$ . (2)  $\tau = 0$ , so the equilibrium is non-hyperbolic; the conserved quantity  $V$  of Module 1 is needed to show that it is a nonlinear center.

*Further reading.* Strogatz (2024, chs. 5–8); Otto and Day (2007); Kot (2001).

### A.5. Lyapunov functions

*Key ideas.* Linearization (Appendix A.4) answers a local question, and only for hyperbolic equilibria. Lyapunov's second, or *direct*, method (Lyapunov, 1992) answers global questions, and works for non-hyperbolic equilibria too, without solving the differential equations. The idea is the one behind a ball rolling in a bowl: find a scalar function  $V(\mathbf{x})$  that has its minimum at the equilibrium  $\mathbf{x}^*$  and never increases along solutions. Its rate of change along a solution of  $d\mathbf{x}/dt = \mathbf{f}(\mathbf{x})$  follows from the chain rule,

$$\dot{V}(\mathbf{x}) = \frac{dV}{dt} = \sum_{i=1}^n \frac{\partial V}{\partial x_i} f_i(\mathbf{x}) = \nabla V \cdot \mathbf{f}(\mathbf{x}), \quad (\text{A.7})$$

which can be evaluated at every point of the state space without knowing a single solution. Suppose that  $V$  is continuously differentiable on a region  $D$  containing  $\mathbf{x}^*$ , that  $V(\mathbf{x}^*) = 0$  and that  $V(\mathbf{x}) > 0$  elsewhere in  $D$ . Then:

- if  $\dot{V} \leq 0$  in  $D$ , the equilibrium is *stable* (solutions that start close stay close);
- if  $\dot{V} < 0$  in  $D$  except at  $\mathbf{x}^*$ , it is *asymptotically stable*, and every solution that starts inside a level set  $\{V \leq c\}$  lying wholly in  $D$  converges to  $\mathbf{x}^*$ ;
- if  $\dot{V} \equiv 0$ ,  $V$  is a *conserved quantity* (a first integral): solutions stay on its level sets, and in the plane, closed level curves around  $\mathbf{x}^*$  are closed orbits, so the equilibrium is a nonlinear center.

Often  $\dot{V} \leq 0$  but  $\dot{V} = 0$  on a whole curve, not just at  $\mathbf{x}^*$ . *LaSalle's invariance principle* then says that bounded solutions approach the largest set of complete trajectories lying inside  $\{\dot{V} = 0\}$ ; if that set is just  $\{\mathbf{x}^*\}$ , the equilibrium is asymptotically stable after all (Khalil, 2002, ch. 4). A function with  $V(\mathbf{x}^*) = 0$  that takes positive values arbitrarily close to  $\mathbf{x}^*$ , and has  $\dot{V} > 0$  there, proves instability in the same way.

Three cautions are worth stating explicitly. First, there is no general recipe for constructing a Lyapunov function, and failing to find one proves nothing. Second, stability and attraction are different properties: the origin of Worked example 5 attracts a whole region of initial conditions yet is not stable, because solutions that start arbitrarily close to it, just above the prey axis, move far away. Third, *Lyapunov exponents*, used in Worked example 8 to measure the separation of nearby trajectories in chaotic systems, are a different concept named after the same mathematician.

*Lyapunov functions for Lotka-Volterra systems.* Volterra himself found the function that works for most of the models in this paper. For each species with positive equilibrium density  $x_i^*$ , the function  $x_i - x_i^* - x_i^* \ln(x_i/x_i^*)$  is zero at  $x_i = x_i^*$ , positive for every other  $x_i > 0$ , and tends to infinity as  $x_i \rightarrow 0$  or  $x_i \rightarrow \infty$ . Weighted sums of such terms,

$$V(\mathbf{x}) = \sum_{i=1}^n w_i \left( x_i - x_i^* - x_i^* \ln \frac{x_i}{x_i^*} \right), \quad w_i > 0, \quad (\text{A.8})$$

are the conserved quantity of the classical model of Module 1 (Eq. (5) with  $w_1 = c$  and  $w_2 = b$ , up to an additive constant), prove global stability of the logistic-prey model of Module 2 (Example below), and, for  $n$ -species Lotka-Volterra systems, prove global stability whenever weights  $w_i$  can be found that make the matrix  $WA + A^T W$  negative definite, where  $A$  is the matrix of interaction coefficients and  $W = \text{diag}(w_i)$  (Goh, 1977; Hofbauer & Sigmund, 1998). Volterra-type functions also prove global stability of the Rosenzweig-MacArthur model of Module 4 over part of the range in which its equilibrium is locally stable (Hsu, 1978). Not every Lyapunov function of an ecological model is of this form: the function  $x_1 x_2 x_3 / (x_1 + x_2 + x_3)^3$  of Worked example 7, which increases, is conserved or decreases according to the sign of  $2 - p - q$ , plays the same role for three competitors.

Students should be able to.

- compute  $\dot{V}$  from Eq. (A.7) for a given  $V$  and system, and decide its sign;
- verify that a function is a conserved quantity, and explain why closed level curves imply closed orbits;
- use the Volterra function, Eq. (A.8), together with LaSalle's invariance principle to prove global stability of a coexistence equilibrium;
- distinguish stability from attraction, and local from global stability.

*Example.* For the logistic-prey model, Eq. (6), with coexistence equilibrium  $x^* = d/c$  and  $y^* = (r/b)(1 - x^*/K)$ , take

$$V(x, y) = c \left( x - x^* - x^* \ln \frac{x}{x^*} \right) + b \left( y - y^* - y^* \ln \frac{y}{y^*} \right).$$

Then  $\dot{V} = c(1 - x^*/x)\dot{x} + b(1 - y^*/y)\dot{y} = c(x - x^*)[r(1 - x/K) - by] + b(y - y^*)(cx - d)$ . Using  $r(1 - x^*/K) = by^*$  and  $d = cx^*$ , the square bracket equals  $-(r/K)(x - x^*) - b(y - y^*)$  and the last factor equals  $c(x - x^*)$ , so the cross terms cancel and

$$\dot{V} = -\frac{cr}{K}(x - x^*)^2 \leq 0.$$

$\dot{V} = 0$  only on the line  $x = x^*$ , and on that line  $\dot{x} = bx^*(y^* - y)$ , which is non-zero unless  $y = y^*$ , so the only complete trajectory inside  $\{\dot{V} = 0\}$  is the equilibrium itself. By LaSalle's principle, every solution that starts with both species present converges to  $(x^*, y^*)$ : the equilibrium is *globally* asymptotically stable in the positive quadrant, which no amount of linearization could show. As  $K \rightarrow \infty$ ,  $\dot{V} \rightarrow 0$  and the classical conserved quantity of Module 1 is recovered. For the parameters of Worked example 2 ( $r = 0.4$ ,  $b = 0.04$ ,  $c = 0.01$ ,  $d = 0.5$ ,  $K = 100$ , so  $(x^*, y^*) = (50, 5)$ ),  $\dot{V} = -4 \times 10^{-5}(x - 50)^2$ ; along the trajectory from  $(100, 10)$ ,  $V$  falls from 0.215 to 0.006 by  $t = 20$  and is indistinguishable from zero by  $t = 50$ , decreasing at every step.

*Self-check.* (1) Show that  $V = x - K \ln(x/K)$  is a Lyapunov function for the logistic equation  $\dot{x} = rx(1 - x/K)$  on  $x > 0$ . (2) Why can no function of the form of Eq. (A.8) prove global stability of the Rosenzweig-MacArthur model when  $K > K_H$ ? (3) In the Example, why is LaSalle's principle needed rather than the second bullet point above? *Answers:* (1)  $\dot{V} = (1 - K/x)rx(1 - x/K) = -(r/K)(x - K)^2 \leq 0$ , with equality only at  $x = K$ . (2) For  $K > K_H$  the equilibrium is unstable and trajectories approach a limit cycle, so no function can decrease along all trajectories towards the equilibrium. (3) Because  $\dot{V} = 0$  on the whole line  $x = x^*$ , not only at the equilibrium.

*Further reading.* Khalil (2002, ch. 4); Hirsch et al. (2013, ch. 9); Strogatz (2024, sec. 7.2); Hofbauer and Sigmund (1998).

## A.6. Simulation algorithms and numerical analysis

*Key ideas.* Most nonlinear models cannot be solved in closed form, so we approximate solutions at discrete times  $t_n = n\Delta t$ . The simplest scheme, *forward Euler*, follows the tangent for one step:

$$\mathbf{x}_{n+1} = \mathbf{x}_n + \Delta t \mathbf{f}(\mathbf{x}_n). \quad (\text{A.9})$$

Its error per step is  $O(\Delta t^2)$ , and since the number of steps needed to reach a fixed time is proportional to  $1/\Delta t$ , its *global* error is  $O(\Delta t)$ : Euler is a first-order method. Higher-order methods sample  $\mathbf{f}$  several

times per step. The classical fourth-order Runge-Kutta method (RK4) is

$$\begin{aligned} \mathbf{k}_1 &= \mathbf{f}(\mathbf{x}_n), & \mathbf{k}_2 &= \mathbf{f}\left(\mathbf{x}_n + \frac{\Delta t}{2} \mathbf{k}_1\right), & \mathbf{x}_{n+1} &= \mathbf{x}_n + \frac{\Delta t}{6} (\mathbf{k}_1 + 2\mathbf{k}_2 + 2\mathbf{k}_3 + \mathbf{k}_4), \\ \mathbf{k}_3 &= \mathbf{f}\left(\mathbf{x}_n + \frac{\Delta t}{2} \mathbf{k}_2\right), & \mathbf{k}_4 &= \mathbf{f}(\mathbf{x}_n + \Delta t \mathbf{k}_3), \end{aligned} \quad (\text{A.10})$$

with global error  $O(\Delta t^4)$ : halving the step size reduces the error roughly sixteen-fold, compared with two-fold for Euler (Table 8).

**Table 8.** Absolute error at  $t = 5$  for the logistic equation  $dx/dt = 0.8x(1 - x/100)$ ,  $x(0) = 10$ , whose exact value is  $x(5) = 85.8486$ .

| Step size $\Delta t$ | 1                    | 0.5                  | 0.25                 | 0.125                |
|----------------------|----------------------|----------------------|----------------------|----------------------|
| Forward Euler        | 2.86                 | 0.991                | 0.422                | 0.196                |
| RK4                  | $3.7 \times 10^{-2}$ | $2.4 \times 10^{-3}$ | $1.5 \times 10^{-4}$ | $9.7 \times 10^{-6}$ |

Modern software (ode45 in MATLAB, solve\_ivp in Python's SciPy, deSolve in R) uses *adaptive* embedded Runge-Kutta pairs that estimate the local error at each step and adjust  $\Delta t$  to meet a user-specified tolerance. Students should know that these tolerances exist, what their defaults are, and that tightening them is the first check when a result looks suspicious. The NWK DynSS LVPP app takes a simpler approach: it offers forward Euler and RK4 with a fixed, user-set step size  $\Delta t$ , chosen in the run ribbon and stored with each preset (most presets use  $\Delta t = 0.1$ ), and no adaptive or stiff solvers (Salter & Getz, 2026). Accuracy is therefore checked by the protocol in the example below: halve  $\Delta t$  and confirm that nothing of interest changes.

Accuracy is not the only concern. Applied to the decay equation  $dx/dt = -kx$ , Euler gives  $x_{n+1} = (1 - k\Delta t)x_n$ , which decays only if  $|1 - k\Delta t| < 1$ , i.e.  $\Delta t < 2/k$ ; steps with  $\Delta t > 1/k$  already give negative values, and steps with  $\Delta t > 2/k$  give growing oscillations and negative populations. Systems that combine very fast and very slow processes (*stiff* systems) force explicit methods to take tiny steps and are better handled by implicit methods such as backward Euler. Finally, numerical methods can fail to respect the structure of a model: Euler turns the closed orbits of the classical LVPP model into outward spirals (Module 1), whereas symplectic or other structure-preserving methods do not (Hairer et al., 2006).

*Students should be able to.*

- implement Euler's method and RK4 for a system of two or three ODEs, or reproduce them in a spreadsheet;
- explain the order of a method and verify it empirically by repeatedly halving  $\Delta t$ ;
- recognize symptoms of numerical artifacts (negative densities, oscillations that change with  $\Delta t$ , slow drift in a conserved quantity) and know how to test for them;
- use an adaptive solver and set its tolerances.

*Example.* A simple convergence protocol, applicable to every simulation in the modules: (i) run with the default step size or tolerance; (ii) rerun with  $\Delta t$  halved (or the tolerance divided by ten); (iii) accept the result only if the quantities of interest—equilibrium values, cycle amplitude or period, or which attractor is reached—do not change appreciably. For the Allee model of Module 3 this check matters most near the separatrix, where small numerical errors can send a trajectory to the wrong attractor.

*Self-check.* (1) Apply two Euler steps with  $\Delta t = 0.5$  to  $dx/dt = -x$ ,  $x(0) = 1$ , and compare with the exact value at  $t = 1$ . (2) Repeat with a single step of  $\Delta t = 2.5$ . (3) Using Table 8, estimate the order of each method from the ratios of successive errors. *Answers:* (1)  $x_1 = 0.5$ ,  $x_2 = 0.25$ , versus

$e^{-1} \approx 0.368$ . (2)  $x_1 = -1.5$ : a negative ‘density’ (because  $\Delta t > 1/k = 1$ ) of growing magnitude (because  $\Delta t > 2/k = 2$ ). (3) Euler ratios  $\approx 2.9, 2.3, 2.2 \rightarrow 2^1$ ; RK4 ratios  $\approx 15.5, 15.7, 15.8 \rightarrow 2^4$ .

*Further reading.* Burden et al. (2016, ch. 5); Press et al. (2007, ch. 17); Hairer et al. (2006).

### A.7. Sensitivity analysis

*Key ideas.* Ecological parameters are rarely known precisely, so we need to know how strongly model outputs—equilibrium densities, cycle periods, extinction thresholds—depend on them. The *local sensitivity* of an output  $Y$  to a parameter  $p$  is the derivative  $\partial Y / \partial p$ . Because parameters have different units, it is usually more informative to report the dimensionless *elasticity*

$$E_p^Y = \frac{p}{Y} \frac{\partial Y}{\partial p} = \frac{\partial \ln Y}{\partial \ln p}, \quad (\text{A.11})$$

which gives the proportional change in  $Y$  per proportional change in  $p$ : an elasticity of 0.5 means that a 10% increase in  $p$  produces roughly a 5% increase in  $Y$  (elasticities are standard in matrix population models; Caswell, 2001).

When  $Y$  is a whole trajectory rather than an equilibrium, the sensitivities  $\mathbf{S} = \partial \mathbf{x} / \partial p$  satisfy the *forward sensitivity equations*  $d\mathbf{S}/dt = J(\mathbf{x})\mathbf{S} + \partial \mathbf{f} / \partial p$ ,  $\mathbf{S}(0) = \mathbf{0}$ , which can be solved alongside the model. In practice, sensitivities are often approximated by finite differences,  $[Y(p+h) - Y(p)]/h$ , using repeated simulations.

Local measures describe what happens near a nominal parameter set. *Global* sensitivity analysis varies all parameters simultaneously over plausible ranges—for example by Latin hypercube sampling—and summarizes their influence using partial rank correlation coefficients or variance-based (Sobol’) indices (Marino et al., 2008; Saltelli et al., 2008). Two further ideas matter for this note. First, sensitivity can be *qualitative*: near a bifurcation, a small change in a parameter alters the type of behavior (Module 4), and a one-parameter sweep displayed as a bifurcation diagram is the natural tool. Second, conclusions can be sensitive to the *form* of a model as well as its parameter values (structural sensitivity; Module 5).

*Students should be able to.*

- compute sensitivities and elasticities of closed-form equilibria;
- estimate sensitivities numerically by finite differences, and carry out one-parameter sweeps in simulation;
- explain the difference between local and global sensitivity analysis, and why both can mislead near a bifurcation.

*Example.* For the classical LVPP model,  $x^* = d/c$  has elasticities  $E_d^{x^*} = 1$ ,  $E_c^{x^*} = -1$  and  $E_r^{x^*} = E_b^{x^*} = 0$ : prey equilibrium density is completely insensitive to the prey’s own parameters, a striking restatement of the cross-over structure of Eq. (3). For logistic prey,  $y^* = (r/b)(1 - d/(cK))$ , and

$$E_K^{y^*} = E_c^{y^*} = \frac{d}{cK - d}, \quad E_d^{y^*} = -\frac{d}{cK - d}, \quad E_r^{y^*} = 1, \quad E_b^{y^*} = -1.$$

With the Module 2 parameters,  $E_K^{y^*} = 1$ : a 10% increase in carrying capacity raises equilibrium predator density by about 10% (9.1% exactly), even though prey density does not change at all. As  $K$  approaches  $d/c$  from above, this elasticity grows without bound—a signature of the nearby transcritical bifurcation.

*Self-check.* (1) For  $dx/dt = rx$ , derive and solve the sensitivity equation for  $S = \partial x / \partial r$ . (2) Verify  $E_K^{y*} = d/(cK - d)$ . (3) In Preset 4 of the NWK DynSS LVPP app, sweep  $K$  from 150 to 250 (other parameters as in Worked example 4) and record the maximum and minimum prey density after transients. At what value of  $K$  does the qualitative behavior change? *Answers:* (1)  $dS/dt = rS + x$ ,  $S(0) = 0$ , so  $S = tx_0 e^{rt}$ ; sensitivity grows with time. (3) Near  $K_H = 200$ , the Hopf bifurcation.

*Further reading.* Caswell (2001, ch. 9); Saltelli et al. (2008); Marino et al. (2008).

*A note on parameter estimation and identifiability.* Sensitivity analysis asks how outputs respond to parameters; parameter estimation asks the inverse question of which parameter values are consistent with observed outputs. The two are linked: a parameter to which every observable output is insensitive cannot be estimated from those outputs, and parameters whose effects are proportional to one another can be estimated only in combination. The classical LVPP model makes the point vividly. If only the time series of prey and predators are observed, the equilibrium ( $d/c, r/b$ ) and the period of small oscillations,  $2\pi/\sqrt{rd}$ , are well determined, but data on population densities in arbitrary units identify  $c$  and  $b$  only up to the scaling of  $x$  and  $y$ ; the nondimensional form, Eq. (A.5), shows that the shape of every orbit depends on the single ratio  $d/r$ . Such *structural* non-identifiability is a property of the model and the choice of observations, and it cannot be cured by collecting more data of the same kind; *practical* non-identifiability arises when the data are too few or too noisy to pin down parameters that are identifiable in principle. Students fitting models to data should therefore (i) count how many parameter combinations their observations can determine before fitting, (ii) look for long, flat valleys in the likelihood or sum-of-squares surface, which signal parameters that trade off against one another, and (iii) fix or measure independently any parameter that the data cannot determine—for example, by using the metaphysiological interpretation of Eq. (14) to bound the conversion efficiency  $c/b$ . Because any Numerus WebKit™ app can be driven from R as a virtual package (Salter & Getz, 2026), the presets of this note can be fitted to data with standard R optimization and likelihood tools.

## B. Additional material referred to in the main text

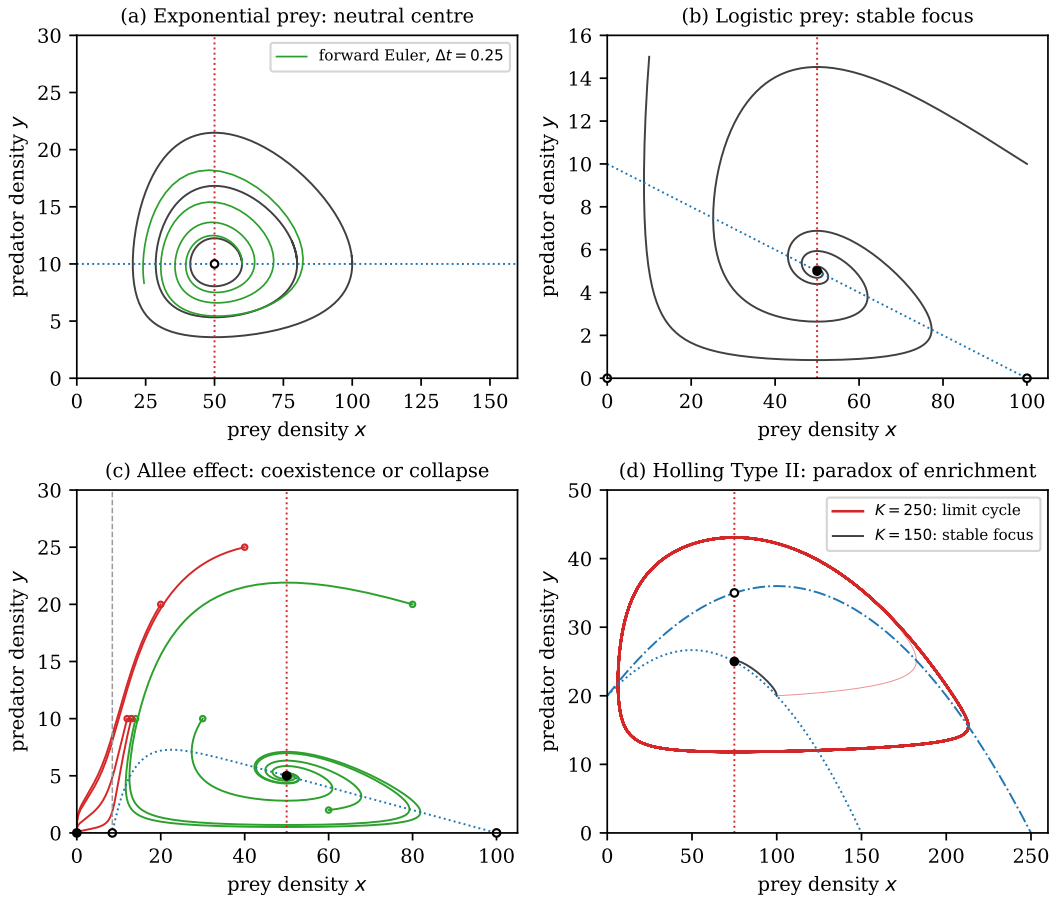


**Figure B.1.** Phase planes for Modules 1–4, with the parameters of Worked examples 1–4. Dotted lines are null-isoclines (red: predator; blue: prey); filled dots are stable and open circles unstable equilibria (the center in panel a, which is stable but not attracting, is shown open). (a) Classical model,  $r = 0.4$ ,  $b = 0.04$ ,  $c = 0.01$ ,  $d = 0.5$ : exact solutions (black) are closed orbits around  $(x^*, y^*) = (50, 10)$ , whereas forward Euler with  $\Delta t = 0.25$ , started from  $(60, 10)$ , spirals outwards (green)—a reason to solve differential equations with RK4 rather than Euler. (b) Logistic prey,  $K = 100$ : trajectories from  $(100, 10)$  and  $(10, 15)$  spiral into the stable focus  $(50, 5)$ . (c) Logistic prey with an Allee effect ( $\alpha = 0.2$ ,  $\gamma = 2$ ,  $L = 5$ ): depending on the starting point (small open circles), trajectories reach coexistence at  $(50, 5)$  (green) or collapse to  $(0, 0)$  (red); the gray dashed line marks the predator-free Allee threshold  $x_A \approx 8.5$ . (d) Holling Type II response ( $r = 0.4$ ,  $b = 1$ ,  $c = 0.1$ ,  $d = 0.06$ ,  $h = 50$ ) started from  $(100, 20)$ : for  $K = 150$  (prey isocline dotted) the trajectory spirals into a stable focus, whereas for  $K = 250$  (prey isocline dash-dotted) it approaches a limit cycle (thick red), with the transient shown faintly. The NWK DynSS LVPP app labels the step size  $dt$ ; here and elsewhere we write  $\Delta t$  to avoid confusion with the parameter  $d$ . The figure was produced with the Python script code/make\_phaseplanes.py.

### B.1. The heteroclinic cycle of Worked example 7

Figure B.2 shows the  $q = 1.3$  run of Worked example 7 ( $p = 0.8$ , starting from  $(0.9, 0.05, 0.05)$ ) over a longer time span, with  $\log_{10} x_i$  on the vertical axis. On this scale the approach to the heteroclinic cycle is a sequence of straight-line descents and ascents: near the single-species saddle at which species  $j$  dominates, the species that has just lost declines exponentially at rate  $q - 1 = 0.3$  and the next invader grows exponentially at rate  $1 - p = 0.2$ , so log-densities change linearly with time. Because each invader starts from a lower density than the previous one, it takes longer to grow, and the periods of dominance lengthen geometrically.

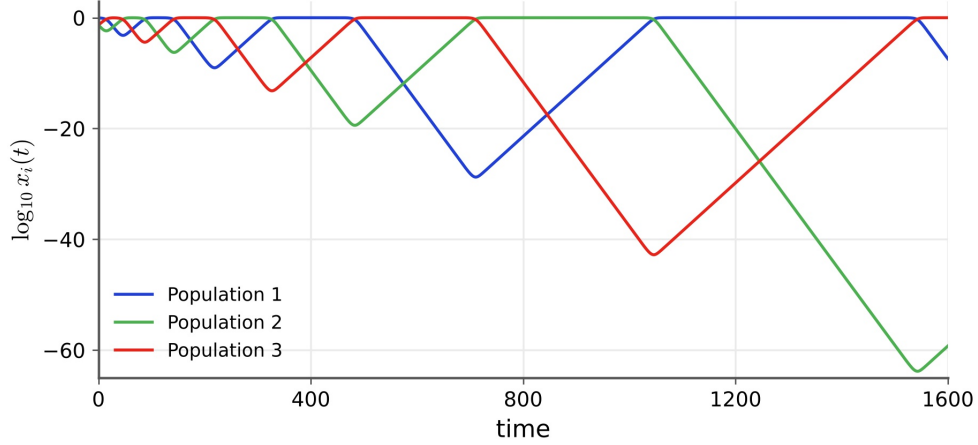


**Figure B.2.** The May-Leonard model, Eq. (21), with  $p = 0.8$  and  $q = 1.3$ , from  $(0.9, 0.05, 0.05)$ , plotted as  $\log_{10} x_i(t)$  for  $0 \leq t \leq 1600$  (population 1 blue, 2 green, 3 red). Computed with an adaptive high-order integrator applied to the log-densities.

*Switching times.* Taking the time at which the identity of the most abundant species changes as a switch, dominance passes from species 1 to 3 to 2 to 1 . . . at

$$t \approx 14, 45, 86, 141, 218, 326, 482, 710, 1045, 1542, 2281.$$

The ratios of successive periods of dominance are 1.30, 1.35, 1.39, 1.42, 1.44, 1.46, 1.47, 1.48 and 1.49, approaching  $(q - 1)/(1 - p) = 1.5$ . This limit is the ratio of the rate at which the losing species declines near each saddle,  $q - 1$ , to the rate at which the next invader grows there,  $1 - p$ : if a species falls to  $10^{-k}$  while losing, it must climb back from  $10^{-k}$  when it next invades, which takes  $(q - 1)/(1 - p)$  times as long as the descent that preceded it. After the first switch the total density stays between about 0.975 and 1.

*How rare is rare?* The density of the rarest species falls below  $10^{-3}$  of carrying capacity by  $t \approx 41$ , below  $10^{-6}$  by  $t \approx 136$ , below  $10^{-10}$  by  $t \approx 296$  and below  $10^{-50}$  by  $t \approx 1430$ ; the successive minima in Figure B.2 are about  $10^{-13}$ ,  $10^{-19}$ ,  $10^{-29}$ ,  $10^{-43}$  and  $10^{-64}$ , each roughly the 1.5th power of the one before.

*Numerical accuracy.* Table 9 compares the switching times computed by fixed-step methods applied directly to Eq. (21) with the accurate values above. RK4 reproduces them to within one time unit up to  $t \approx 2300$ , for steps from 0.01 (the NWK DynSS LVPP default for this preset) to 0.5, even though densities fall below  $10^{-90}$ . Forward Euler fails for a systematic reason: near a saddle it multiplies each density by  $1 + \Delta t g_i$  per step, so the decline rate 0.3 becomes  $-\ln(1 - 0.3\Delta t)/\Delta t$  and the invasion rate 0.2 becomes  $\ln(1 + 0.2\Delta t)/\Delta t$ . The ratio of successive periods of dominance therefore tends to about 1.54 for  $\Delta t = 0.1$  and 1.71 for  $\Delta t = 0.5$  instead of 1.5, and the error in the switching times grows

geometrically from switch to switch. With  $\Delta t = 0.5$ , Euler's eighth switch comes at  $t \approx 1338$  rather than 710.

**Table 9.** Times of the first nine switches in dominance for the run of Figure B.2, computed accurately and with fixed-step RK4 and forward Euler of step  $\Delta t$ .

| Switch                  | 1  | 2  | 3  | 4   | 5   | 6   | 7   | 8    | 9    |
|-------------------------|----|----|----|-----|-----|-----|-----|------|------|
| Accurate                | 14 | 45 | 86 | 141 | 218 | 326 | 482 | 710  | 1045 |
| RK4, $\Delta t = 0.5$   | 14 | 45 | 86 | 141 | 218 | 326 | 482 | 710  | 1045 |
| Euler, $\Delta t = 0.1$ | 14 | 46 | 88 | 147 | 230 | 351 | 530 | 799  | 1206 |
| Euler, $\Delta t = 0.5$ | 14 | 49 | 98 | 172 | 291 | 483 | 803 | 1338 | 2243 |

## B.2. Food-chain length, self-interference and alternative dynamics in trophic stacks

This section extends the trophic-stack results of Section 5.3 by asking how the length of a food chain depends on the strength of self-interference  $w$  in Eq. (32), with  $\rho = 0.5$ ,  $m = 0.15$  and  $x_0 = 1$  as in Table 5. Two answers can be computed. The *equilibrium* answer is the longest chain for which an equilibrium with all levels positive exists and the next level cannot invade it (Section 5.3). The *dynamic* answer is obtained by assembling the chain as an ecologist might observe it: starting from the basal consumer alone, a new top level is introduced at density  $10^{-3}$ , the system is simulated for 6000 time units, any level whose density falls below  $10^{-6}$  during the last 1800 time units is regarded as extinct, and the process is repeated until a newly introduced level fails to persist.

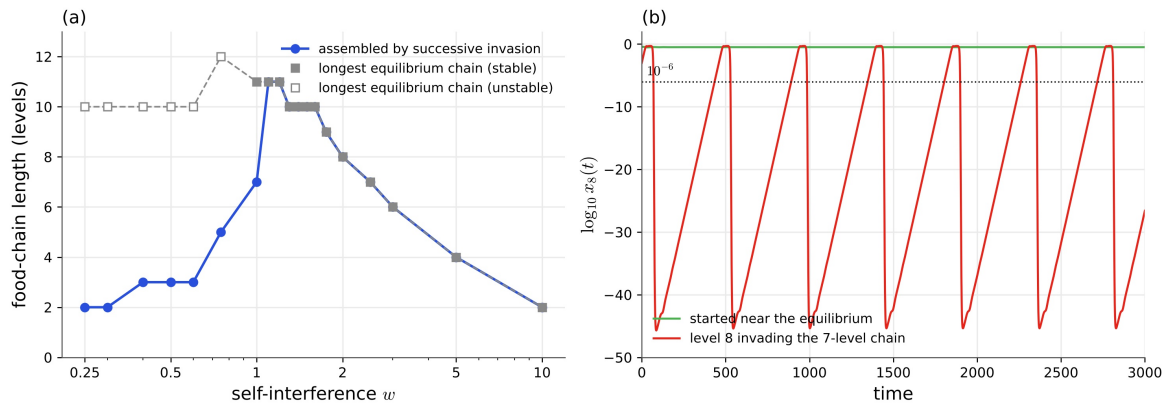


**Figure B.3.** Trophic stacks, Eq. (32), with  $\rho = 0.5$ ,  $m = 0.15$  and  $x_0 = 1$ . (a) Food-chain length as a function of self-interference  $w$  (logarithmic scale): chains assembled by successive invasion (blue), and the longest equilibrium chain (gray; filled squares stable, open squares unstable). (b) The top level,  $\log_{10} x_8(t)$ , of the eight-level chain with  $w = 1$ : started near its stable equilibrium (green) it stays there, but when level 8 invades the seven-level chain (red) the system settles into outbreak cycles; the dotted line marks  $10^{-6}$ .

*Intermediate interference maximizes chain length.* The assembled chain length rises and then falls with  $w$  (Figure B.3a):

| $w$    | 0.25–0.3 | 0.4–0.6 | 0.75 | 1.0 | 1.1–1.2 | 1.3–1.6 | 1.75 | 2 | 2.5 | 3 | 5 | 10 |
|--------|----------|---------|------|-----|---------|---------|------|---|-----|---|---|----|
| Levels | 2        | 3       | 5    | 7   | 11      | 10      | 9    | 8 | 7   | 6 | 4 | 2  |

Two different constraints are at work. For  $w \geq 1.1$  the assembled and equilibrium chain lengths agree exactly, and the limit is *energetic*: strong interference reduces the rate at which each level extracts currency from the level below, so that less and less reaches the top until a further level cannot meet its

maintenance requirement. For  $w \leq 1$  the limit is *dynamic*. Equilibria with 10 to 12 levels still exist, but for  $w \leq 0.75$  they are unstable, and populations cycle with troughs so deep that newly introduced top levels either fail to establish or are driven below  $10^{-6}$ . Chain length is therefore greatest, at 11 levels, for intermediate interference ( $w \approx 1.1$ – $1.2$ ), a result that complements the conclusion, drawn in Section 4.5 from predator-prey models, that moderate interference is the most stabilizing (Arditi et al., 2004).

*The same chain can be steady or oscillating.* With  $w = 1$ , the eight-level chain has a stable equilibrium, (0.652, 0.712, 0.506, 0.547, 0.376, 0.425, 0.233, 0.323), whose leading eigenvalue has real part  $-0.015$ . Started close to it, the chain stays there (Figure B.3b, green). But when level 8 is introduced into the seven-level chain, at any initial density between  $10^{-4}$  and  $10^{-1}$ , the system is drawn instead to a coexisting limit cycle (red). On this cycle levels 1–7 vary moderately (none falls below about  $10^{-2.2}$ ), but the density of the top level undergoes outbreaks with a period of about 456 time units, spending 85% of the time below  $10^{-3}$  and falling to about  $10^{-4.5}$  between outbreaks. The two attractors have different futures. A ninth level can invade the equilibrium chain, since its growth rate when rare,  $\rho(1 - m(1 + \hat{x}_8)/\hat{x}_8) \approx 0.19$ , is positive; but it cannot invade the cycling chain, because hyperbolic conversion, Eq. (25), makes its per-unit growth rate tend to  $-\infty$  whenever level 8 crashes. How long a chain can become thus depends not only on its parameters but on the route by which it was assembled. Coexisting equilibria and cycles are found in other cases too: with  $w = 0.3$ , the two-level chain has a stable equilibrium at (0.201, 0.463) (leading eigenvalue  $-0.0023$ ) and also a cycle, reached by invasion, on which the density of level 2 ranges from about 0.015 to 7.3; and with  $w = 0.5$ , the four-level equilibrium is unstable (leading eigenvalue  $+0.0009$ ) and the density of the top level cycles down to about  $10^{-68}$ , which in practice means extinction.

*No paradox of enrichment.* In the Rosenzweig-MacArthur model of Module 4, enrichment destabilizes. In the two-level stack it hardly matters: as  $x_0$  increases from 0.5 to 1000, the real part of the leading eigenvalue at the equilibrium stays at  $-0.021$  for  $w = 0.5$ , changes only from  $-0.060$  to  $-0.074$  for  $w = 1$ , and from  $-0.004$  to about 0 for  $w = 0.3$ . Stability is decided almost entirely by self-interference, with the switch from stable to unstable equilibria near  $w \approx 0.3$  at every level of enrichment. In this respect the metaphysiological stack behaves like the ratio-dependent model of Worked example 5 rather than the prey-dependent model of Worked example 4.

These results were obtained for a single set of physiological parameters, and how the curve in Figure B.3a shifts with  $m$ ,  $x_0$ , the introduction density and the extinction threshold remains to be explored; they are offered here as an illustration of how far a simple, uniformly constructed model can be pushed by students with a simulator and a little curiosity.

### C. Rosenzweig-MacArthur predator-prey model

The predator-prey model of Rosenzweig and MacArthur (1963) is a cornerstone of theoretical ecology. It introduces a mechanistic description of trophic interactions by coupling logistic prey growth with a saturating functional response for the predator. The autonomous system of differential equations is expressed as:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - \frac{cxy}{a + x}, \quad (\text{C.12})$$

$$\frac{dy}{dt} = y \left( \frac{ecx}{a + x} - d \right), \quad (\text{C.13})$$

where  $x(t)$  and  $y(t)$  denote the population densities of prey and predators at time  $t$ , respectively. The parameters are defined as follows:  $r$  is the intrinsic prey growth rate,  $K$  is the carrying capacity,  $c$  is the maximum consumption rate per predator,  $a$  is the half-saturation constant (capturing a Holling Type II

response),  $e$  is the conversion efficiency, and  $d$  is the density-independent predator mortality rate.

### C.1. The graphical stability criterion

To evaluate the local stability of the non-trivial coexistence equilibrium  $E^* = (x^*, y^*)$ , we analyze the system's nullclines. The predator nullcline ( $dy/dt = 0$ ) inside the positive quadrant yields the vertical line:

$$x^* = \frac{ad}{ec - d}. \quad (\text{C.14})$$

An interior equilibrium exists if and only if  $ec > d$  and  $x^* < K$ . The prey nullcline ( $dx/dt = 0$ ) expresses predator density  $y$  as a function of  $x$ :

$$y = f(x) = \frac{r}{c}(a + x) \left(1 - \frac{x}{K}\right). \quad (\text{C.15})$$

Differentiating  $f(x)$  with respect to  $x$  gives the slope of the prey nullcline:

$$f'(x) = \frac{r}{c} \left[1 - \frac{a}{K} - \frac{2x}{K}\right]. \quad (\text{C.16})$$

The apex of this parabolic curve occurs at  $x_{\text{apex}} = \frac{K-a}{2}$ .

#### C.1.1. Linearization and the Jacobian matrix

Let the right-hand sides of Eqs. (C.12) and (C.13) be  $P(x, y)$  and  $Q(x, y)$ , respectively. Evaluated at  $E^* = (x^*, y^*)$ , the components of the Jacobian matrix  $J$  simplify substantially because  $P(x^*, y^*) = 0$  and  $Q(x^*, y^*) = 0$ :

$$J = \begin{pmatrix} \frac{\partial P}{\partial x} & \frac{\partial P}{\partial y} \\ \frac{\partial Q}{\partial x} & \frac{\partial Q}{\partial y} \end{pmatrix}_{(x^*, y^*)} = \begin{pmatrix} \frac{c x^* f'(x^*)}{a + x^*} & -\frac{c x^*}{a + x^*} \\ \frac{ec a y^*}{(a + x^*)^2} & 0 \end{pmatrix}. \quad (\text{C.17})$$

The stability of  $E^*$  is governed by the sign of the trace ( $\text{Tr}(J)$ ) and the determinant ( $\text{Det}(J)$ ):

$$\text{Det}(J) = \frac{ec^2 a x^* y^*}{(a + x^*)^3} > 0, \quad (\text{C.18})$$

$$\text{Tr}(J) = \frac{c x^* f'(x^*)}{a + x^*}. \quad (\text{C.19})$$

Because  $\text{Det}(J)$  is strictly positive for any feasible interior equilibrium, stability depends entirely on the trace:

- If  $f'(x^*) < 0$ , then  $\text{Tr}(J) < 0$ , making  $E^*$  **locally asymptotically stable**. Geometrically, this means the predator nullcline intersects the prey nullcline to the right of its apex (the downward-sloping region).
- If  $f'(x^*) > 0$ , then  $\text{Tr}(J) > 0$ , rendering  $E^*$  **unstable**. The intersection occurs to the left of the apex. The system undergoes a supercritical Hopf bifurcation at  $f'(x^*) = 0$ , giving rise to a stable limit cycle.

### C.2. Extension: predator interference and the Beddington-DeAngelis response

A significant limitation of the Holling Type II response is that it models predators as completely independent units, ignoring crowding or aggressive encounters. To address this, Beddington (1975) and DeAngelis et al. (1975) independently introduced a functional response tracking predator interference.

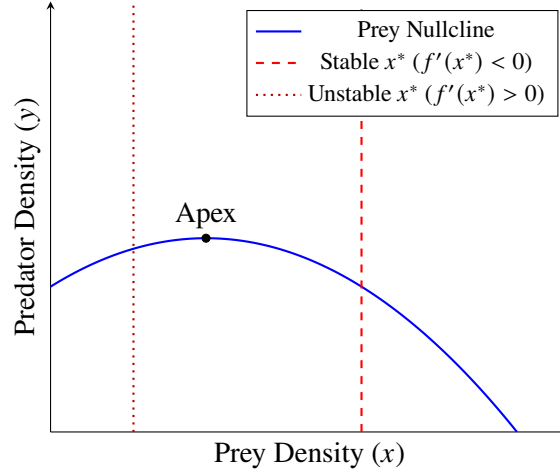


**Figure C.1.** The Rosenzweig-MacArthur graphical criterion illustration. When the predator nullcline intersects on the downward slope (dashed line), the system stabilizes. If it intersects on the upward slope (dotted line), the equilibrium destabilizes, provoking the paradox of enrichment if  $K$  is increased.

The modified system is formulated as:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - \frac{cxy}{a + x + By}, \quad (\text{C.20})$$

$$\frac{dy}{dt} = y \left( \frac{ecx}{a + x + By} - d \right), \quad (\text{C.21})$$

where  $B > 0$  scales the intensity of mutual predator interference.

### C.3. Altered geometry and stabilization

Setting  $dy/dt = 0$  yields the predator nullcline for the Beddington-DeAngelis model:

$$y = \frac{1}{B} \left( \frac{ec - d}{d} x - a \right). \quad (\text{C.22})$$

Crucially, the predator nullcline is no longer a rigid vertical line. Instead, it is a straight line with a **positive slope** equal to  $\frac{ec-d}{Bd}$ .

This shift has profound consequences for the system's stability architecture:

- (1) **Slanted Intersection Dynamics:** The prey nullcline becomes  $y = r(a+x)(1-x/K)/[c-rB(1-x/K)]$ . Because the predator nullcline now slopes upwards from  $x = ad/(ec-d)$ , the coexistence equilibrium lies to the right of the Rosenzweig-MacArthur value  $x^*$ , and moves further right as  $K$  increases.
- (2) **Trace Buffering:** When calculating the Jacobian matrix under the Beddington-DeAngelis framework, the element  $\frac{\partial Q}{\partial y}$  is no longer zero:

$$\frac{\partial Q}{\partial y} = -\frac{ecBx^*y^*}{(a+x^*+By^*)^2} < 0. \quad (\text{C.23})$$

The trace becomes  $\text{Tr}(J) = \frac{\partial P}{\partial x} + \frac{\partial Q}{\partial y}$ . Because  $\frac{\partial Q}{\partial y}$  is strictly negative, it makes a stabilizing contribution to the trace. Even if the equilibrium falls on the upward-sloping part of the prey nullcline ( $\partial P/\partial x > 0$ ), it can remain locally asymptotically stable, provided that  $\text{Det}(J) > 0$  (the

predator nullcline is steeper than the prey nullcline where they cross) and

$$\frac{\partial P}{\partial x} < \left| \frac{\partial Q}{\partial y} \right|. \quad (\text{C.24})$$

#### C.4. Resolution of the paradox of enrichment

The classic paradox of enrichment states that increasing a system's carrying capacity  $K$  (e.g., via fertilization) destabilizes a stable equilibrium into massive, extinction-prone oscillations because it expands the upward-sloping window of the prey nullcline.

Under the Beddington-DeAngelis response the predator nullcline slopes upwards, so enrichment raises the equilibrium prey density along with  $K$  and can keep the equilibrium on the descending limb of the prey nullcline. Whether this resolves the paradox depends on the strength of interference: with the parameters of Worked example 4 ( $r = 0.4$ ,  $c = 1$ ,  $e = 0.1$ ,  $d = 0.06$ ,  $a = 50$ ), the Hopf bifurcation moves from  $K = 200$  ( $B = 0$ ) to  $K \approx 215$ , 303 and 610 for  $B = 0.1$ , 0.5 and 1, whereas for  $B = 2$  the equilibrium remains stable for all  $K$ . Strong interference therefore protects the system against enrichment-driven oscillations; weak interference only postpones them.

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