

Chapter 1. Introduction

click below for
• [guide to navigation](#)
• [index](#)

Contents

2. An intricate web and our objectives
7. The working model
10. Mathematical models and methods – just a nibble
14. Coming attractions
18. Notation
19. References



Reminder:
Use your right (left)
keyboard arrow key to page
forward (backward)
sequentially through the chapter.

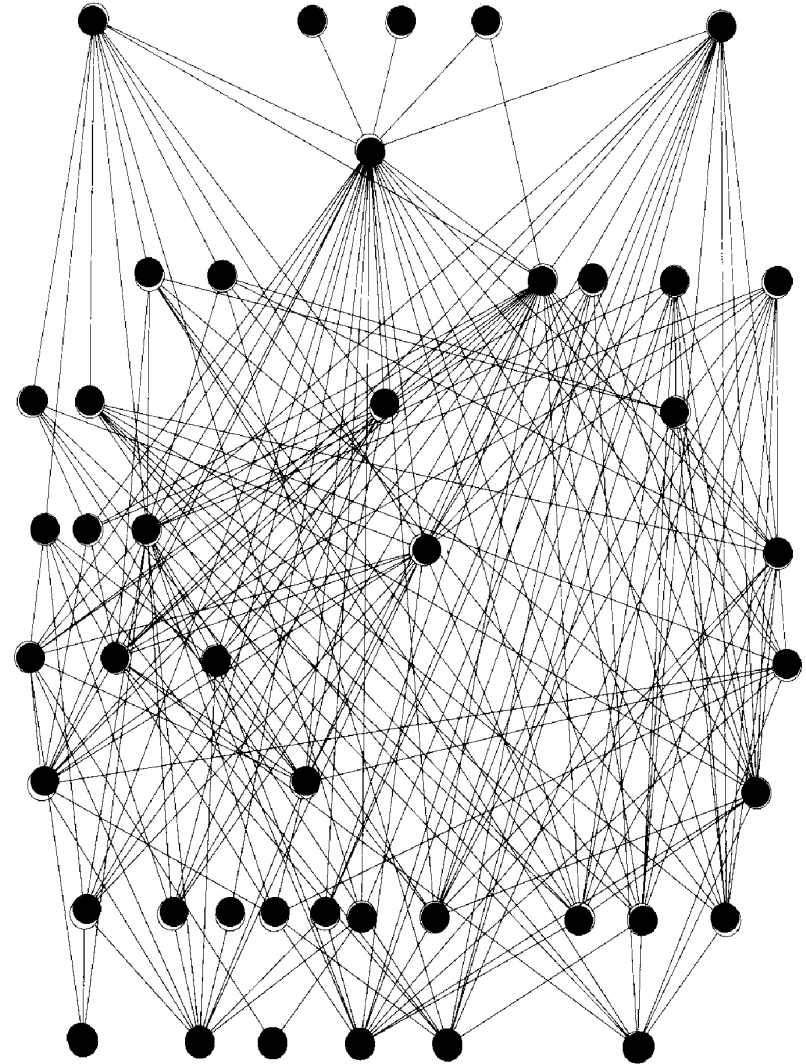
An intricate web and our objectives

Several years ago, shortly after I began studying ecosystem dynamics, I came across the picture shown on the right while browsing through the book by Roughgarden (1998; Figure 7.26). It depicts the terrestrial food web on St. Martin Island in the eastern Caribbean. Each circle in the picture represents a living or decaying species, or a group of like species, and the connecting lines show the food path – the species at the top end of any line consumes the species at the bottom end as one of its food sources. The picture describes a world of predation and competition – of consuming and being consumed. It's good to be at the top!

A caption on the figure in the book by Roughgarden identifies the occupants of the 44 circles, but to me, a chemical engineer, most of the biological names are unfamiliar. The identifications are beside the point for my purposes here.

I'm presenting the picture at the start because I've found it to be a useful aid in introducing my work in this field and in framing the questions that continue to motivate it. It's an example; similar pictures have been composed for other food webs, some much larger than this.

This placid schematic portrayal of a food web belies a dramatic history of species competition, predation and survival. The picture is a current snapshot of those characters in the drama that have been successful – so far, at least. Evolutionary processes, at work through numerous generations, have either honed the behavioral traits of any candidate species so as to make it “work” in the system, or they have rendered it extinct. Even those extinct species, though not now visible, may have left their mark. Indeed their presence at one time or another, though temporary, may have facilitated the entry of another, such that the



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current web structure could not have formed without their timely appearance, and its formation cannot be repeated in their absence.

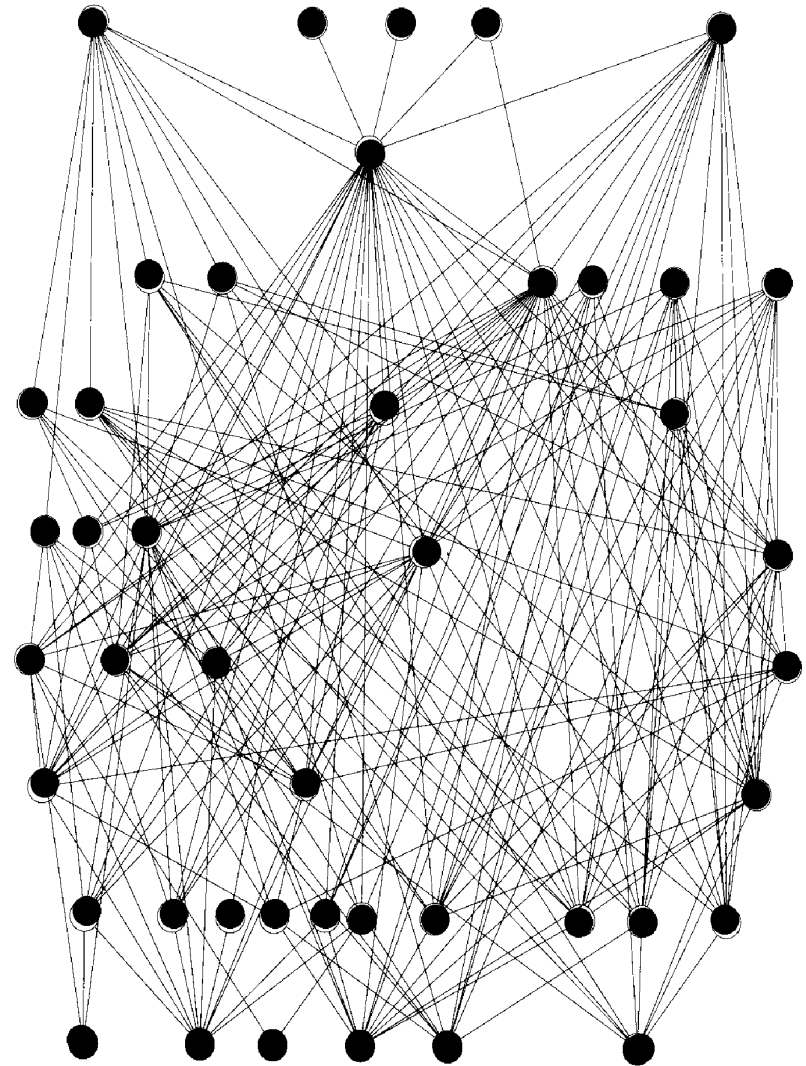
Corresponding to each circle is a set of data – at the minimum, a measure of the current population (abundance or mass) of the species. Other data might include distributions of ages, stages, sex, locations, etc.

Though we might think of the picture, and/or the data behind it, as being stable, even permanent, over our time of observation, it is quite likely still changing – evolving naturally with some species on their way to extinction – or changing in response to natural or anthropogenic disturbances, such as habitat changes, the application of pesticides, herbicides, and fertilizers, invasions of non-indigenous species, random and/or seasonal variations, and so on.

At a cursory inspection you can see that interconnections link all of the circles. Therefore, a change in the data for any one of them affects all of the others.

Possibly many ecosystems*, such as that containing the St. Martin Island food web, were once somewhat isolated, but nowadays global travels of humans spread foreign species rampantly, either deliberately or inadvertently. Suppose, for example, that a new species is suddenly thrust into the resident community of the St. Martin food web. What happens? Or better asked: What could happen? The answer is any one of three possibilities: (1) the invader cannot cope – it flees or dies away to a zero population; (2) the invader finds a workable spot in the

* Following the usual definition, I use “ecosystem” to refer to a community of living species along with processes and surroundings that sustain it – including the supply and/or replenishment of nutrients. A “food web” is a community of living species.



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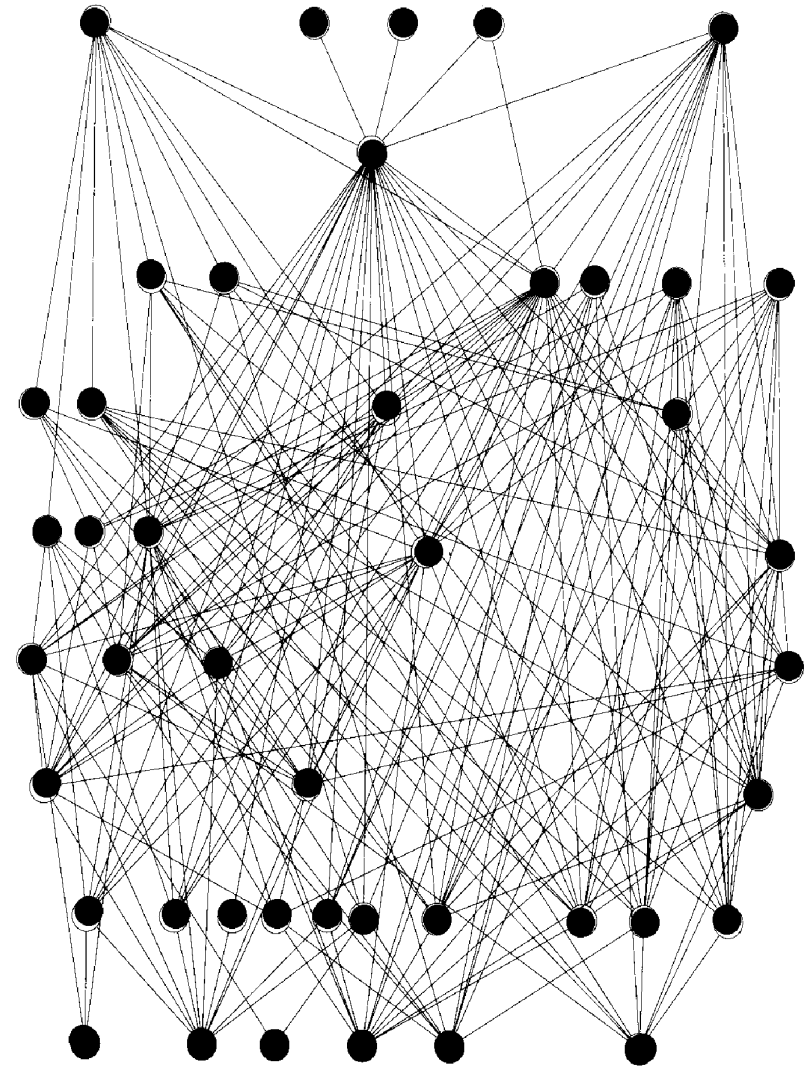
interconnected network, which is now altered and accommodates 45 circles; (3) the invader works its way into the network at the expense of others – one or more of the original 44 become extinct so that the system, now including the new species, contains 44 or fewer circles. It's impossible to say *a priori* which of these three possibilities will pertain.

Other questions come to mind: How does the system respond to the removal (extinction) of one or more species? Or to a change in a parameter, perhaps simulating a natural or anthropogenic disturbance? How did the ecosystem form? Is it permanent in the face of disturbances?

These and related questions are central to the science of ecology, and they are subjects of much of the current research under the general heading of theoretical *population ecology*.

The questions are easily posed, but the answers are not easily obtained. Certainly they are not intuitive. The most formidable obstacle is the complexity of real ecosystems. Even systems much smaller than the St. Martin Island case (already a relatively small example) are far too unwieldy for a systematic study, either by way of field studies or by way of mathematical models. While the connecting lines in a food web might be established, already a daunting task, obtaining functional relationships belonging to those lines, for use in mathematical models, is practically impossible for all but very simple cases.

Fortunately for my objectives, and those of others who work on theoretical ecosystem dynamics, it's not necessary to deal with such complicated webs. Instead, we work with simplified models and state our objectives as follows:



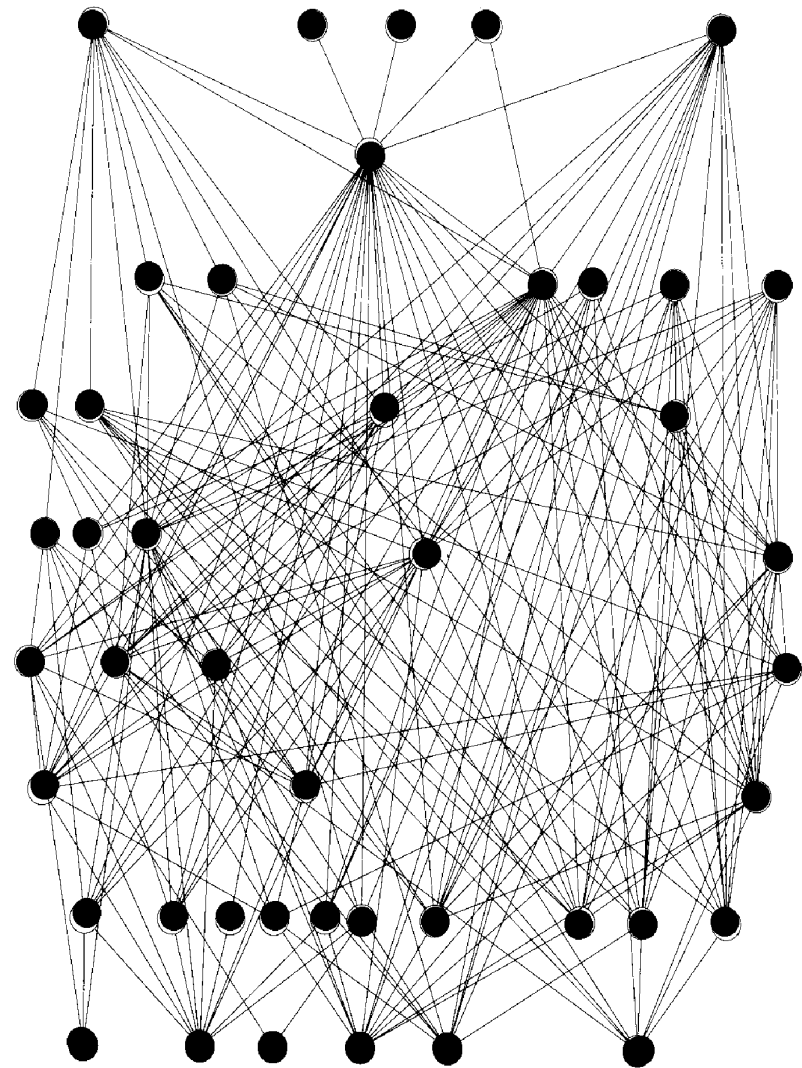
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The **primary objective** is to explore and elucidate the behavioral features of interacting species populations and ecosystems through the construction and analysis of mathematical models. A secondary objective, intertwined with the primary one, is to set out the modeling approaches and mathematical methods that can be used generally in studies of system dynamics.

From the vantage point of those objectives, the picture on the right is a schematic front for a mathematical model. In its simplest form, the model consists of a system of 44 coupled ordinary differential equations, presumably nonlinear, each expressing a material balance for one species. The subjects of species extinctions and dynamic responses to disturbances immediately relate, from this vantage point, to the application of bifurcation theory and methods of stability analysis and simulations for the study of stationary (steady) states, attractors, and trajectories in the state space of species masses or populations.

As you will see through subsequent chapters, those who pursue the stated objectives and apply a rather common set of analytical and computational methods to studies of model food webs and ecosystems strike it rich. Even simple models yield a remarkable assortment of fascinating dynamic features – seemingly of every imaginable description. And it's frosting on the cake that these features give meaningful insights into the behavior of the real systems that the models are intended to mimic.

The models used in chapters to follow are of the make-believe variety. They are **study models** that are used to address, in a systematic way, the questions that I've raised and, importantly, to develop and illustrate the approach to finding the answers – sophisticated enough yet simple enough for those purposes.

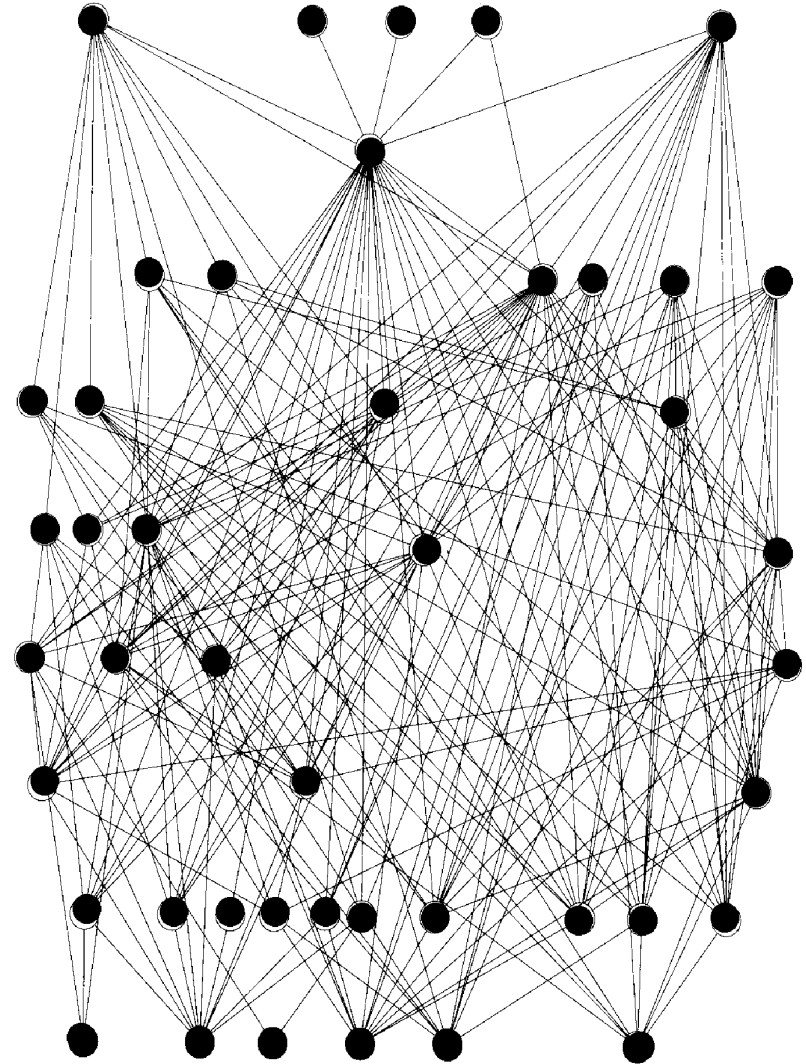


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Don't expect, however, that general theorems will result. Every ecosystem is different. Expect instead to have a scrapbook of pictures in the form of bifurcation diagrams, phase portraits, and transient responses, that represent a large variety of behavioral features arguably covering the entire spectrum of possible events. Expect also to have familiarity and experience with the general approach of constructing mathematical models and with general methods of analysis and simulations. Coming out of it all will be a framework on which a theoretical study of any given ecosystem can be built – a framework that steers your thinking, points out what to expect, and sets down a procedure for working it out.

All of this reinforces my statement in the *Prologue* that the emphasis throughout reflects my strong interest in mathematical models, analysis, and simulations. Readers, especially those with biological backgrounds, will find deficiencies, in many instances, in the biological/ecological interpretation of models and results, empirical examples, and field/laboratory data. Such material can be found in a number of other works, including Hastings (1997), Roughgarden (1998), Gotelli (2001), and Rockwood (2006). For example, each chapter in the book by Gotelli (2001) concludes with a section on empirical examples.

I'll defer a further description of objectives and of the arrangement of material in this book to the subsection immediately following. There I extend this introduction to present and describe a model ecosystem that will be the basis for study throughout.



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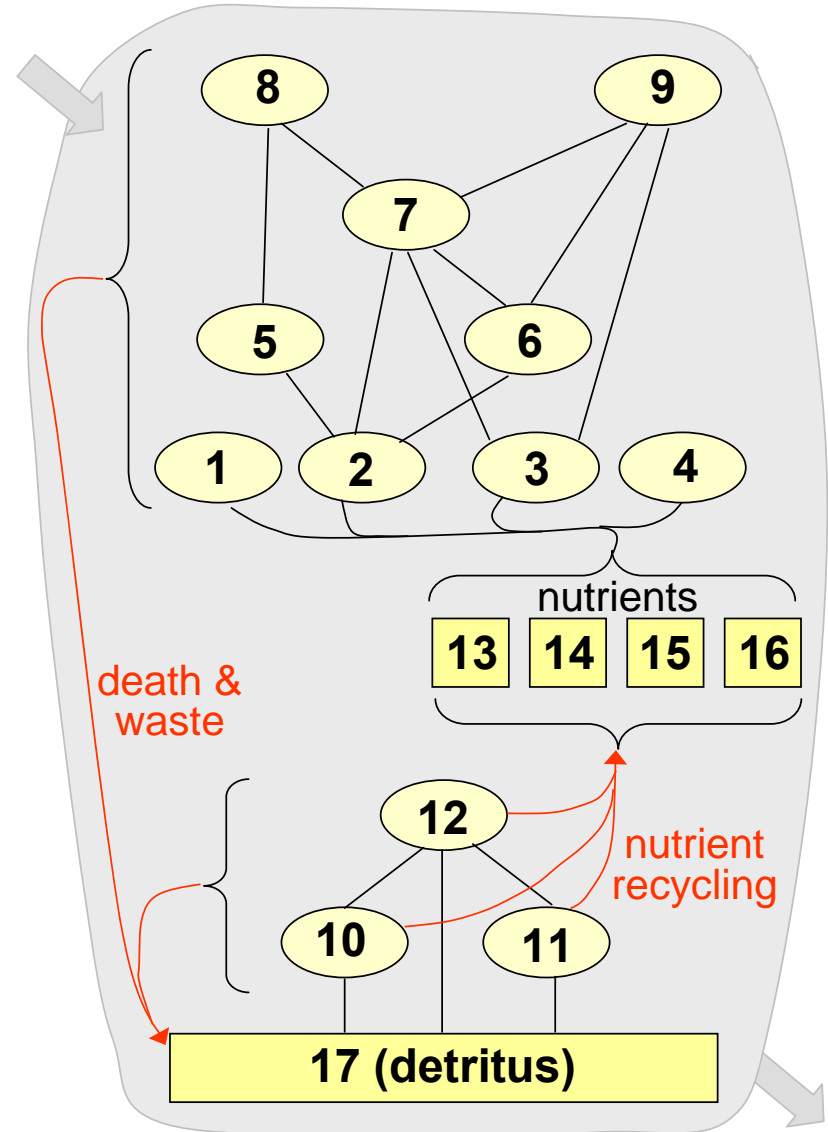
The working model

The schematic diagram on the right is my creation of a model ecosystem – a model from which nearly all cases in the chapters to follow (particularly Chapters 2 through 8) will be drawn.

I emphasize that this is a model – more specifically, I call it a *study model* because it exists solely to provide insights into the behavior of real systems and generally to pursue the objectives stated in the previous section. It serves that purpose because, as I explain below, it contains most of the essential features of all real ecosystems. It obviously involves a much simpler food web than the real one shown in the previous section, yet it is still too involved to analyze immediately in one fell swoop. We'll work into it by considering a number of subcases or fragments, each with increasing complexity. More about that later; first let me paint the setting by giving a description of the full system.

The ovals in the picture represent populations of living species. Those numbered 1 through 4 are basal species or producers (plants) at the lowest trophic level. They grow by photosynthesis, consuming inorganic nutrients (represented by square boxes numbered 13 through 16) in the process. Shown at three higher trophic levels, species 5 through 9 are consumers (animals), growing as predators consuming other living species, their prey. Further subdivided, the group of consumers consists of herbivores (5 and 6), or grazers, consuming plants only; a carnivore (8), that consumes only other animals; and omnivores (7 and 9) that consume both plants and animals.

Dead species and organic wastes form a detritus reservoir, the rectangular box 17 at the bottom. A secondary food web of detritivores and decomposers, represented in the figure by species 10, 11, and 12 (such as fungi, bacteria, termites, lice, earthworms) feed on the detritus, and on each other as the lines show, in the



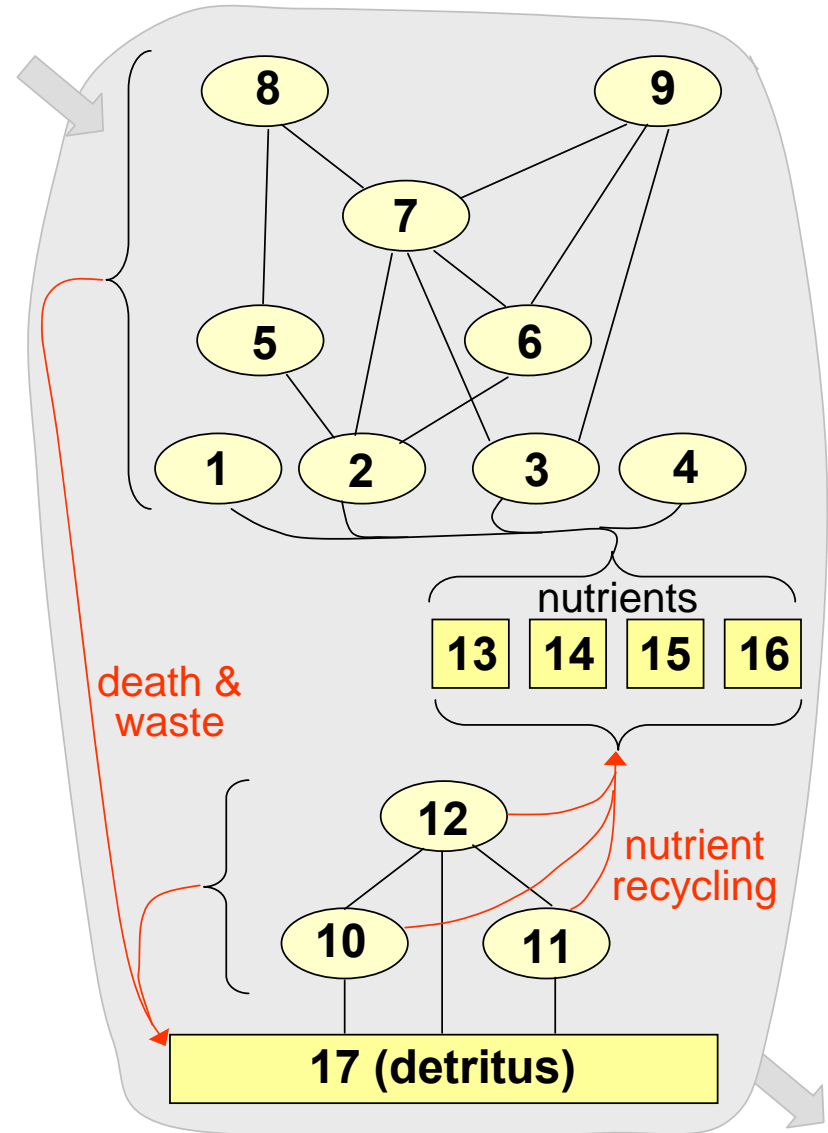
decaying process that mineralizes the detritus and regenerates the nutrients in four boxes numbered 13 through 16.

Some or all of the species that share a trophic level, such as 1, 2, 3, and 4, or 10 and 12, or 5 and 6, or 8 and 9, are generally competitors for resources at lower levels. Thus species 5 and 6 compete for their single food source, species 2. And 1, 2, 3, and 4 compete with each other for the nutrients.

Thus our working model consists of an interconnected community of producers and consumers at four trophic levels rendered sustainable by a nutrient regeneration process involving a secondary community of decomposers and detritivores – all defining elements of an ecosystem. Interconnections are such that a change in the mass content of any oval or box affects that of all of the others.

Notice that there is an arrow in the picture at the upper left, indicating an entry of material into the system, and another at the lower right indicating removal. In the absence of those flows, the system is closed. As such, the total mass, living plus nonliving, is constant, and no species can survive indefinitely by itself. (Why not?) The total earth's biosphere – the global ecosystem – is an example of a closed system. Others may be practically closed (Biosphere II?), and reasonably modeled as such, but most real systems are open. For example, the flows might be streams carrying nutrients and organisms to and from an aquatic ecosystem in a lake. Or they might be forced flows in a laboratory chemostat – a continuous stirred tank reactor (CSTR) to a chemical engineer. You'll see more about chemostats through the chapters ahead.

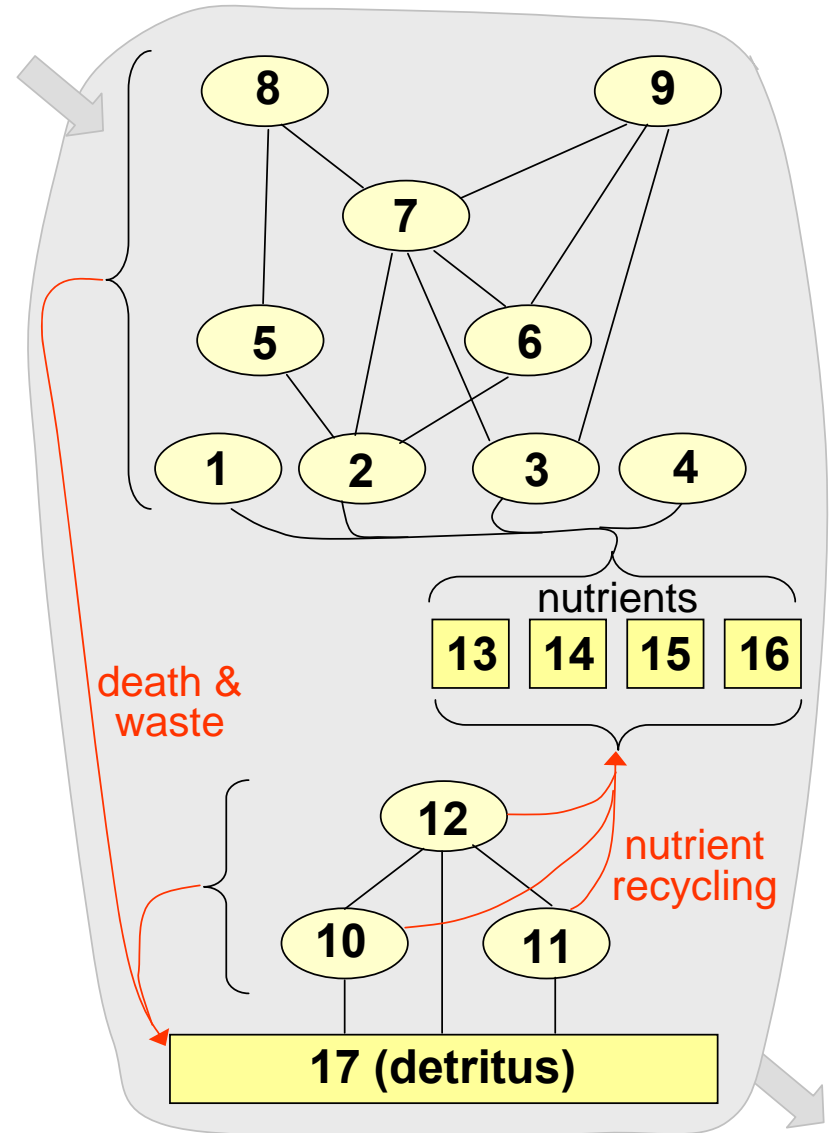
The arrows in and out should actually be viewed more generally as the injection or removal of any ecosystem mass from or to the surroundings. They might apply to a single oval, for example, representing the harvesting of a particular species or the deliberate injection of a nonindigenous species.



Two incidental points: To be more representative of realistic systems, the top and bottom webs should be connected by consumers from the top feeding on decomposers from the bottom (e.g., robins eating earthworms). The connectedness then would resemble that of the web on [page 1.2](#). But since that feature will not be incorporated in models to follow, I'm opting for consistency and clarity by not including it here. Second, the model does not account for the fact that some nutrients are naturally recycled through abiotic processes for use in inorganic form, independent of the detritus/decomposer process. A familiar example is carbon dioxide, produced by species respiration and used directly in photosynthesis by the producers.

Which oval represents human beings? Perhaps 9, an omnivore without predators? That may have been so tens of thousands of years ago, but *Homo sapiens*, from the time of the agricultural revolution, at least, some 10,000 years ago, don't fit well into food web activities with other living species. We humans destroy other species not simply for food but because they might interfere with our life style or because we consider them pests – wolves, moles, mice, rats, insects, weeds, etc. If we need more space, we take it from the habitats of other species. We develop medicines and procedures to affect our own natural death rate. We control our food availability. In short, we don't live by the rules that seem to apply rather generally to other species. Humans are best viewed as disturbances to an ecosystem, affecting the resources and the death and birth rates of others. Or if the population dynamics of humans is the object of study, one should consider a stand-alone oval – a single species – which, in fact, is the subject of Chapter 2.

Admittedly being repetitious, I emphasize that this is a simplified representation of real ecosystems, designed in keeping with our objectives. We would need a few million ovals to represent all known species on the earth – and there are probably many million more that are not yet known. Yet don't you agree that this diagram portrays a splendid machine? – albeit not nearly as marvelous as nature's real thing.



Mathematical models and methods

– just a nibble

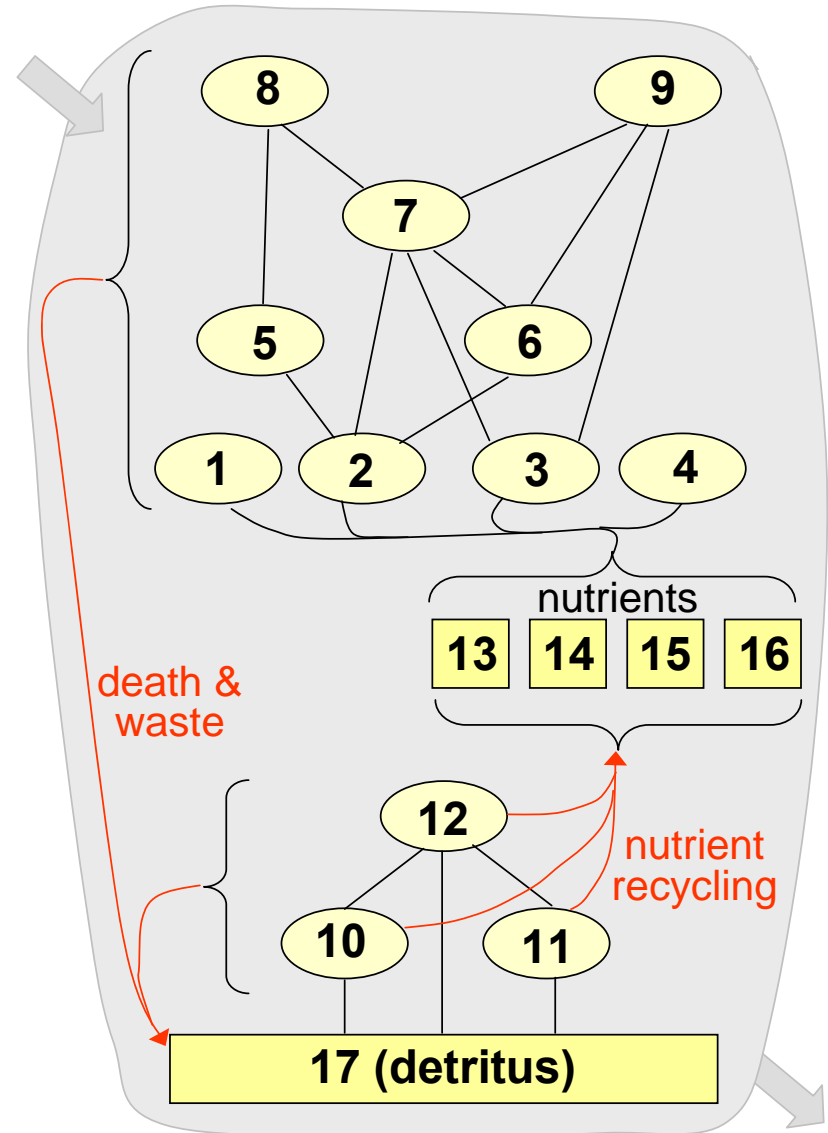
My intention here is to preview briefly in general terms the mathematical models, methods, and assumptions that will be pervasive in chapters to follow. Perhaps I can best accomplish that by presenting and explaining the following equation, which describes the population change of an arbitrarily selected species in the system – species 6.

$$\frac{dm_6}{dt} = \underbrace{(s_6 - h_6)}_{\text{net rate of growth}} + \underbrace{[\Gamma_{6,2}(m_6, m_2)]}_{\text{rate of exchange with (in from - out to) the surroundings}} + \underbrace{[\Lambda_{6,7}(m_6, m_7) + \Lambda_{6,9}(m_6, m_9)]}_{\text{rate of growth by consumption of 2}} - \underbrace{d_6 m_6}_{\text{rate of loss due to consumption by 7 and 9}} - \underbrace{d_6 m_6}_{\text{rate of natural death}}$$

1 - 1

As the labels beneath the terms indicate, the equation accounts for the rate of change of the mass (the derivative with respect to time on the left) of species 6 in terms of the difference between those rate processes for the formation and those for the depletion of the species mass. Each term has units of mass/time.

In similar fashion, we can write a differential equation for each oval (species) and box in the figure – 17 such equations in all – but we'll need only this one for my immediate purposes of introduction.



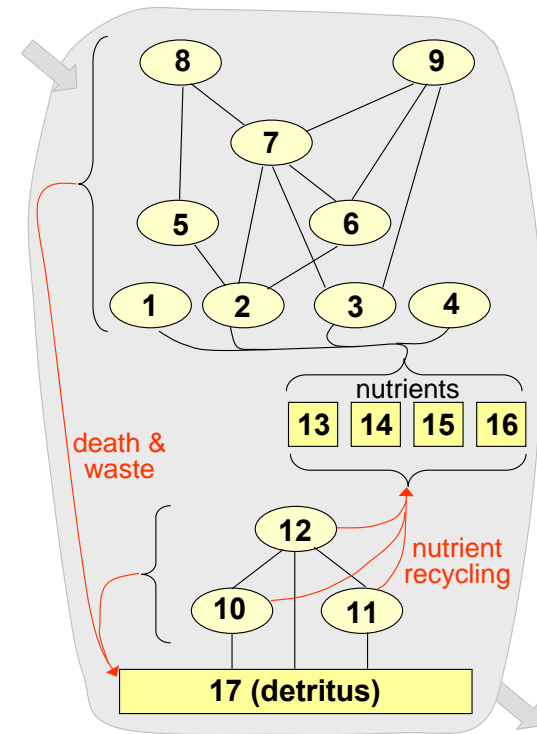
I'll define symbols here, and at the same time call your attention to the button labeled "notation" which will appear on the navigation bar at the bottom of every page. A click on that button will take you to a list that defines the notation used in this chapter. I've tried to keep the nomenclature as consistent as possible from one chapter to the next.

Obviously, t stands for time and m for mass, more conveniently for mass density in some cases. The subscript, 6 in this case, identifies the species or component of the system.

In the first term on the right, s and h are the rates of supplying and harvesting, respectively; schematically represented by the arrows from and to the surroundings. In cases for which these rates are in bulk flow, as with an organism flowing in and out of a chemostat, for example, the term is simply $D(m_{f6} - m_6)$, where m_{f6} and m_6 are mass densities of species 6 in the influent and effluent streams, respectively. D is the dilution rate (i.e., q/V , the reciprocal of the residence time); V is the volume of the system; q is a volumetric flow rate.

The last term on the right accounts for the mortality of the species – natural death as opposed to death by consumption by predators. That rate is assumed to be proportional to the mass of species 6, the proportionality constant, d_6 , or rate constant, is the specific mortality rate.

Sandwiched between the first and last terms on the right are the functions $\Gamma_{6,2}$, $\Lambda_{6,7}$ and $\Lambda_{6,9}$ describing the interactions of species 6 with other species in the network – its rate of growth by consumption of prey and its rate of loss to predators. I'll have more to say about those functions as we proceed through the chapters ahead, but all we need to know for now is that they are generally expressed in terms of the mass of the interacting species and that they are generally nonlinear.



$$\underbrace{\frac{dm_6}{dt}}_{\text{net rate of growth}} = \underbrace{(s_6 - h_6)}_{\text{rate of exchange with (in from - out to) the surroundings}} + \underbrace{\left[\Gamma_{6,2}(m_6, m_2) \right]}_{\text{rate of growth by consumption of 2}} - \underbrace{\left[\Lambda_{6,7}(m_6, m_7) + \Lambda_{6,9}(m_6, m_9) \right]}_{\text{rate of loss due to consumption by 7 and 9}} - \underbrace{d_6 m_6}_{\text{rate of natural death}} \quad 1 - 1$$

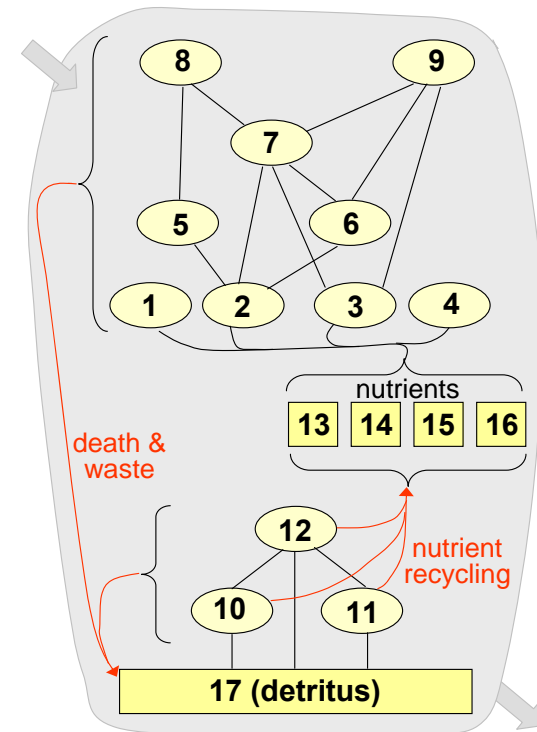
Notice that the derivative on the left and the absence of a space variable, x , y , or z , imply that m_6 is uniformly distributed throughout the space of the system. I'll say more about that assumption and others shortly.

The key descriptors of models of this type, which dominate the first eight chapters, are these: *continuous time*, *intraspecies uniformity*, *spatial uniformity*, and *determinism*. Each of these requires further comment. Let me say first that this type of model with those descriptors dominates the literature on ecosystem dynamics, including my presentations in the chapters to follow. The exceptions, as far as I've seen, consider systems with only a few species.

The alternative to a continuous time variable is a discrete representation wherein time is incremented in steps. This is a convenient representation in models for which intraspecies age distributions are considered or in which successive generations do not overlap. Time will be a continuous variable in our models except for a few examples in Chapters 2 and 9.

A tacit assumption in equation 1-1 is that every individual in the population of any species is identical to the others of that species. There is no intraspecies variability; such features as age and sex differences are ignored. We'll deal with a few cases in Chapter 2 for which this assumption cannot be invoked. For all others, our purposes will be served by assuming intraspecies uniformity.

The assumption of spatial uniformity is manifested in equation 1-1 by the fact that no location or position variable is involved. This can be a hard one to swallow since we can see spatial variation everywhere around us. Let's say that spatial variation is a detail, to a first approximation at least, in studies of the overall dynamics of interacting species. We'll consider this assumption further in Chapter 9 and introduce alternative models.



$$\underbrace{\frac{dm_6}{dt}}_{\text{net rate of growth}} = \underbrace{(s_6 - h_6)}_{\text{rate of exchange with (in from - out to) the surroundings}} + \underbrace{\left[\Gamma_{6,2}(m_6, m_2) \right]}_{\text{rate of growth by consumption of 2}} - \underbrace{\left[\Lambda_{6,7}(m_6, m_7) + \Lambda_{6,9}(m_6, m_9) \right]}_{\text{rate of loss due to consumption by 7 and 9}} - \underbrace{d_6 m_6}_{\text{rate of natural death}} \quad 1-1$$

Equation 1-1 is deterministic, meaning that terms are specified in a precise form as opposed to a probabilistic form – as in stochastic models. I'll relax that assumption also in the Chapter 9. Meanwhile we'll work with deterministic models.

All of these assumptions, and others yet to be stated as we proceed, are plausible and justified for our stated purpose – that is, to gain insights into the dynamics of communities of species through the formulation and study of mathematical models. We could relax any or all of them and compose a commensurate set of governing equations. But we would find the set to be large, unwieldy, and intractable. The question is: Do the assumptions introduce artifacts or spurious results that render useless the insight that we set out to gain? Let's assume not, since they are commonplace, but unfortunately the question often cannot be answered.

Need I point out that the equations (17 of them in the full set) are coupled? Just as the schematic picture tells us that a change in any one species population causes a ripple of changes throughout the entire ecosystem, so also are the state variables, the masses in the ovals and boxes, linked mathematically. No one equation can be solved independently of the others. Furthermore, as I've already indicated, the system is nonlinear. As such, it defies an analytical solution – with very few exceptions.

Our pattern of study will be repeated, for the most part, from one model to the next. Stated briefly, it will involve a study of steady-state (stationary) solutions (obtained after setting all time derivatives to zero), an inquiry into the stability of stationary states by application of linear stability analysis, and an examination of large-scale transient behavior by way of computer simulations. All of that is best described as we go along.

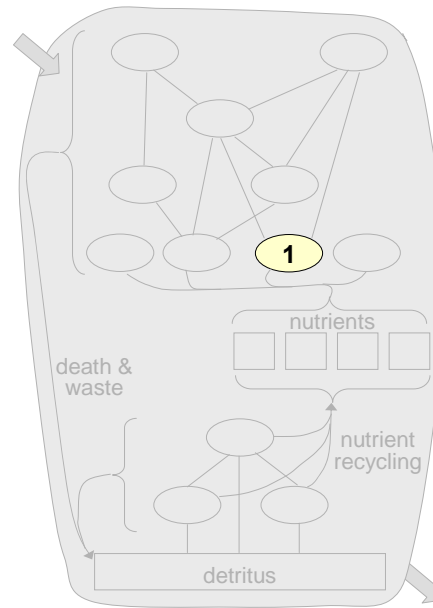
Enough for the time being about models, equations and methods. Before we embark on exploring all of this, I'll conclude this chapter with a final section that gives a picture and a succinct statement of what's coming in each of the chapters ahead. The overall progression from one chapter to the next is toward increasing complexity in one way or another. The chapters form a scaffold, rising from the case of a single species in Chapter 2, to the full ecosystem in Chapter 8. I've designed each chapter purposely to add something new to your scrapbook.

$$\underbrace{\frac{dm_6}{dt}}_{\text{net rate of growth}} = \underbrace{(s_6 - h_6)}_{\text{rate of exchange with (in from - out to) the surroundings}} + \underbrace{\left[\Gamma_{6,2}(m_6, m_2) \right]}_{\text{+ rate of growth by consumption of 2}}$$

$$- \underbrace{\left[\Lambda_{6,7}(m_6, m_7) + \Lambda_{6,9}(m_6, m_9) \right]}_{\text{- rate of loss due to consumption by 7 and 9}} - \underbrace{d_6 m_6}_{\text{- rate of natural death}} \quad 1 - 1$$

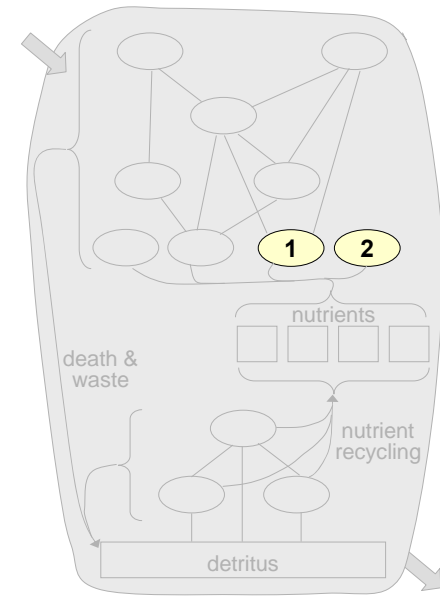
Coming attractions

As you page ahead, you will notice that the template above each chapter description highlights the subsystem on which that chapter focuses. Taken in sequence, each is a stage progressively adding and/or rearranging the highlighted ovals. The stages lead to Chapter 8, where the entire system lights up.



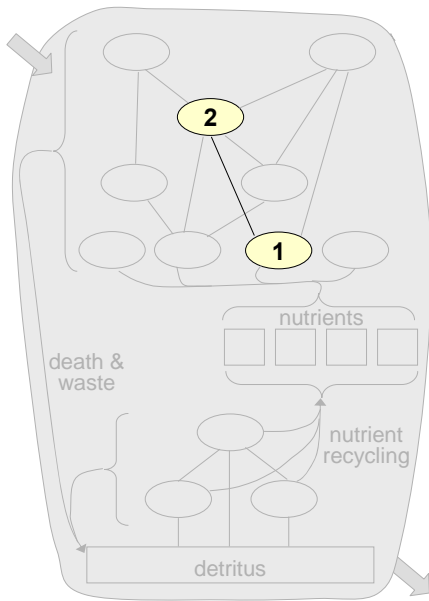
2. A single species

This, the simplest of subcases, serves to introduce such important concepts as: population explosion, carrying capacity, and stability. Further, it's the only occasion where we peer into the oval and account for intraspecies age and gender structure. Except for Chapter 9, it's the only place where we'll deal with a discrete-time model, exploited here to introduce oscillatory and chaotic behavior.



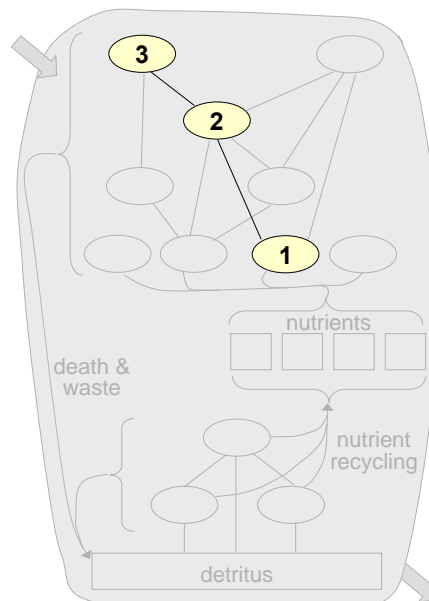
3. Competitors

Life in a food web is a struggle to survive among competitors and predators. Here I isolate two species that affect each other by vying for the same resource, but neither one consumes the other. Which species, if either, wins out? Can they coexist? In addressing such questions, I give attention to topics that are ubiquitous in subsequent chapters: multiple (alternate) steady (stationary) states, bifurcation theory, stability analysis, phase space representations, and simulations. I also touch on resource-based models to introduce the phenomenon of competitive exclusion, but I leave the meat of that story to Chapter 6.



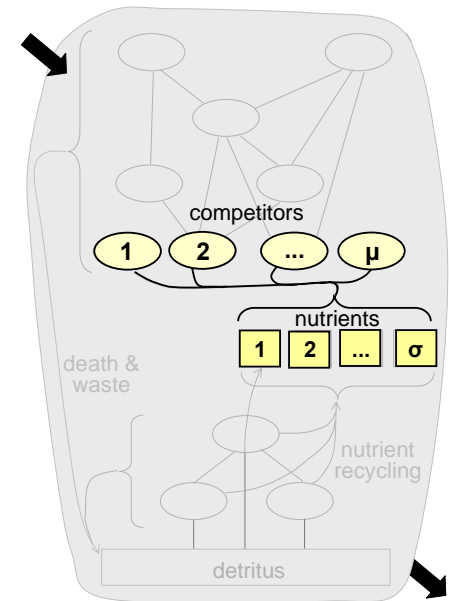
4. Predator-prey dynamics

In the classic predator-prey situation, the species under focus are not competitors, but one of them serves as the food source for the other. As in Chapter 3, we address questions of survival and coexistence. The new dynamic features are Hopf bifurcations and self-sustained oscillations – limit cycles in the phase plane. I introduce various forms of predator response functions in this chapter – that is, the functions Γ and Λ in [equation 1-1](#) – emphasizing Lotka-Volterra and Holling II forms that will be used hereafter.



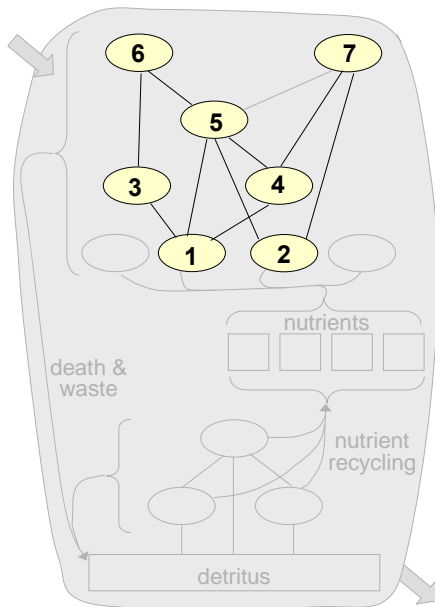
5. Food chains

We abandon the comfortable two-dimensional state space, the phase plane, of the previous two chapters and take our first serious leap into higher dimensions. To do that we adopt a model wherein the species are lined up vertically in a chain arrangement, one at each trophic level. I'll put the focus on a hexatrophic chain with Lotka-Volterra type interactions and on a tritrophic chain with Holling II type. For the latter, thanks to the nuances and complexities of the higher dimensionality, we find all sorts of new bifurcation features, along with an illustration of basins of attraction, and our first example of intrinsic chaos for a continuous-time model.



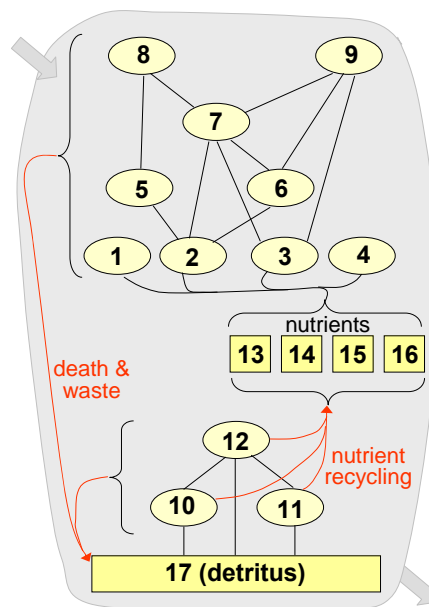
6. Competitors revisited

In this chapter we return to unfinished business of Chapter 3 – to the “rest of the story” about competitors. According to the so-called *principle of competitive exclusion*, species coexistence is not possible, except for transients, if the number, μ , of different species exceeds the number, σ , of different resources (nutrients). It's not an easily accepted principle, and there are loopholes. We'll see, as an example, that a larger number of species can coexist indefinitely on a smaller number of resources in an oscillatory state even though there is no steady-state solution in the interior of the state space.



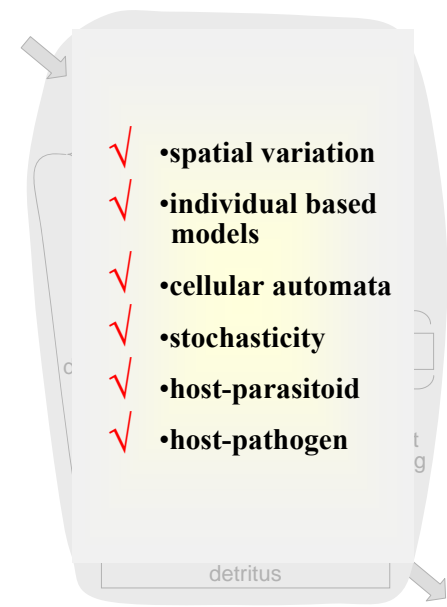
7. Large communities

This chapter begins by generalizing the material from earlier chapters and relating it to communities of arbitrary size. Following that, we explore the behavior of a specific example model involving 7 species at 4 trophic levels – an example that illustrates, through analysis and simulations, the expected and unexpected behavior of “large” interacting systems. You will see that building a large stable community is often very difficult. Destroying one, on the other hand, is always easy.



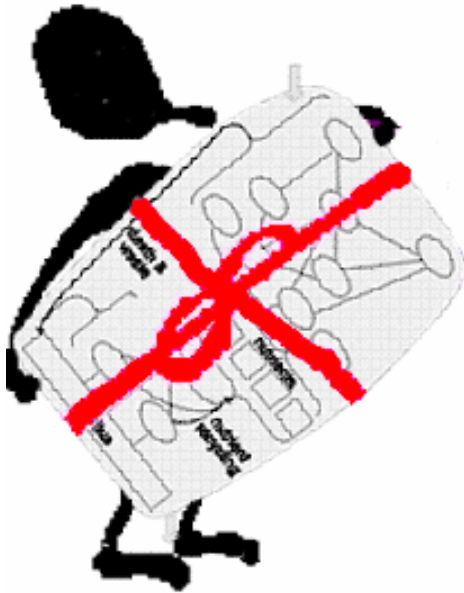
8. A virtual ecosystem

Finally, we inquire into the behavior of the whole bloody system – a working system of producers, consumers, detritus, detritivores, and nutrient recycling. I’ve already presented this make-believe world in this introductory chapter, and I bring things to a climax, in Chapter 8, by presenting and studying specific numerical examples. We’ll have cases for which it all works to give stable ecosystems, even when closed, but not easily by any means. Nature must have a simpler way.



9. Spatiotemporal models – and related topics

The subject matter listed above for this chapter amounts to an introductory exposure to a number of important topics that pertain to ecosystem dynamics but do not fit the pattern of the other chapters. The treatment in this chapter, while not exhaustive, serves to broaden the scope beyond the continuous-time, spatially uniform, deterministic models of earlier chapters. The emphasis is on spatial variations and stochasticity.



10. Wrapping up

My presentation of material is concluded with a few encapsulating paragraphs. The prevailing emphasis through preceding chapters has been on models, methods, simulations and resulting phenomena. By this time we will have seen an enormously rich assortment of steady-state and dynamic features – your scrapbooks should be chock full. But we could find ourselves mired forever in constructing and analyzing an endless assortment of different models. The objectives accomplished, it's time to conclude.

Left uncovered in those chapters is the entire area of *population genetics* – an area that considers the development of species and their interactions from an evolutionary perspective. Many books on ecology, including the aforementioned one by Roughgarden (1998), contain a chapter or more on population genetics. The interested reader can find books devoted to that subject. Those by Halliburton (2004), Hartl (2000), and Mayhew (2006) are examples of recent ones.

If you view the foregoing sequence of schematic representations in reverse, starting with that for Chapter 8 on the preceding page (or first with the St. Martin Island food web and then Chapters 8, 7, and so on) you might be reminded of Picasso's famous depiction of a bull (Pablo Picasso, 1945). That depiction is a series of eleven prints, each a stage in a process that takes a fully developed detailed bull down to a bare outline of its figure.

Picasso presented those prints to make a point about simplicity. He felt that in aspiring for complicated portrayals, humans were losing the understanding and appreciation that derives from simple ones.

That point applies aptly to the art of constructing mathematical models for purposes of learning and teaching. Let's keep it in mind.

Notation

- d rate coefficient for loss or death; d_6 , of species 6
- D dilution factor, q/V
- h harvesting rate; h_6 , of species 6
- m mass (or mass density) or population; m_i , of species i ; m_{fi} , of species i in an influent stream
- q volumetric flow rate
- s supply or inflow rate; s_6 , of species 6
- t time
- V volume of chemostat
- Γ function describing rate of species growth; $\Gamma_{6,2}$, of species 6 by consumption of species 2
- Λ function describing the rate of species loss by consumption; $\Lambda_{i,j}$, of species i by species j

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