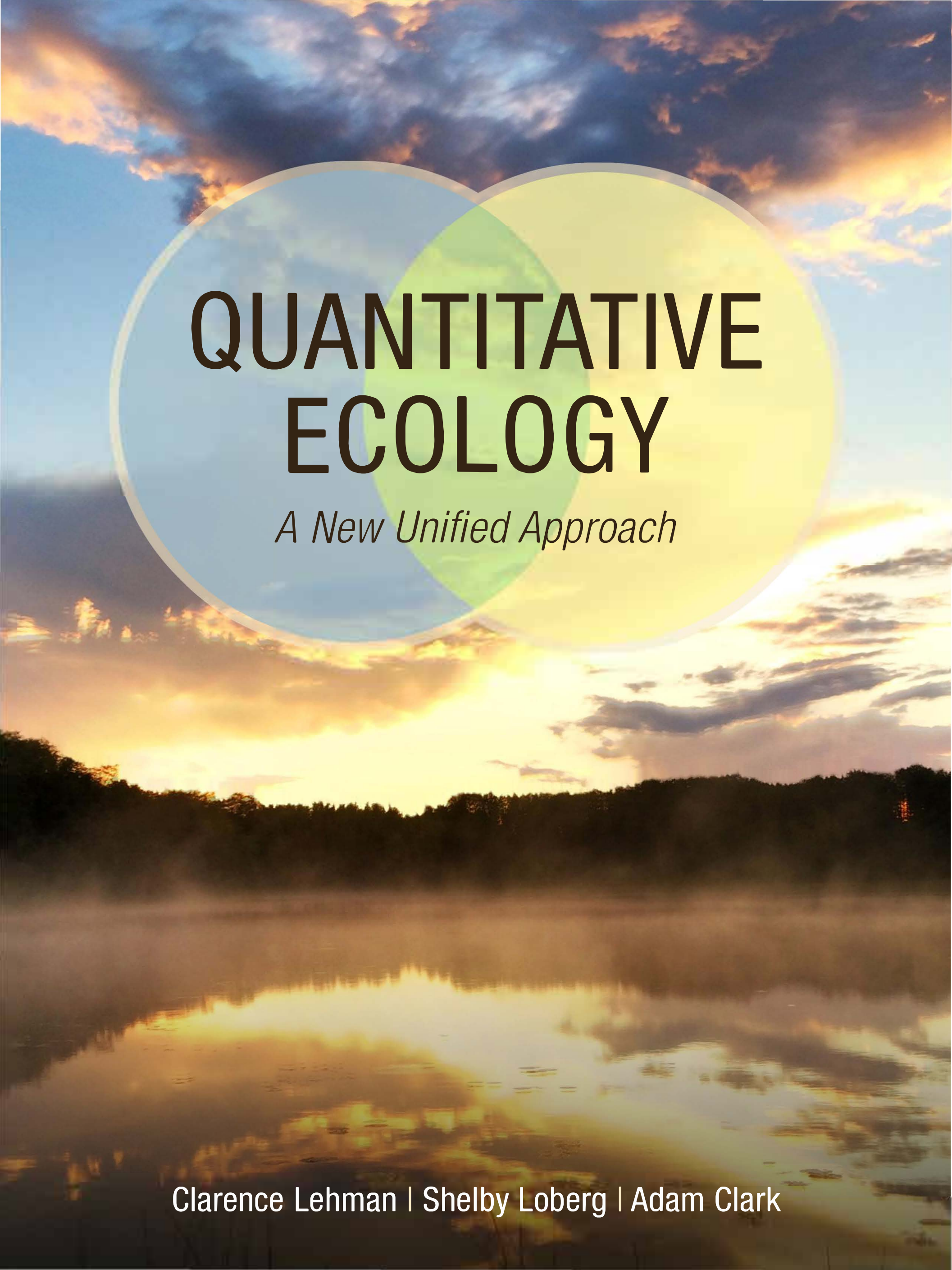

QUANTITATIVE ECOLOGY

A New Unified Approach

Clarence Lehman | Shelby Loberg | Adam Clark

Contents

	Preface	*ii*
	Ebook versus book	*iv*
	Background	
Chapter 1.	What is ecology?	2
1.1	Definitions of ecology	3
1.2	Ecology then and now	6
1.3	Methods of ecology	7
Chapter 2.	Ecological theory	10
2.1	Levels of ecology	10
2.2	Role of theory	12
2.3	What is a model?	14
2.4	Present state	16
	Single populations	
Chapter 3.	A basic population model	18
3.1	Characterizing populations	18
3.2	Bacterial growth	19
3.3	A first computer model	20
3.4	Program results	25
3.5	Darwin's elephants	27
Chapter 4.	Modeling a single population	30

4.1	Density-independent growth	30
4.2	Density-enhanced growth	35
4.3	Density-limited growth	39
4.4	Parameter combinations	42
4.5	Generalization	45
Chapter 5.	Differential and difference forms	47
5.1	A mathematical view	51
5.2	Exponential solution	52
5.3	Logistic solution	54
5.4	Orthologistic solution	55
Chapter 6.	Human population growth	57
6.1	Phenomological graph	58
6.2	Biological–ecological graph	60
6.3	A global transition	62
Chapter 7.	Chaos and randomness	68
7.1	Depicting population growth	69
7.2	Hypothetical insect data	71
7.3	Sensitive dependence	76
7.4	Dampening of chaos	78
7.5	Bifurcation diagram	83
7.6	Properties	83

Models of two species

Chapter 8. Theory of interactions 86
8.1 Dynamics of two interacting species . . 86
8.2 Code for two species 95
8.3 Summary of interactions 97

Chapter 9. Embodied by natural selection 98
9.1 Mutualisms 98
9.2 Herbivory 103
9.3 Predation 105
9.4 Predatory plants 107
9.5 Defense 108
9.6 Competition 110

Chapter 10. Phase space 112
10.1 Surface generating the flow 118
10.2 Eigenvectors and eigenvalues 122
10.3 A phase space example 132

Chapter 11. State spaces 138

Chapter 12. Predator and prey 148
12.1 Further examples of predation 148
12.2 Ecological communities are complex . . 152
12.3 Predator–prey model 153
12.4 Phase space 159
12.5 Assumptions of the basic model 165
12.6 Independent carrying capacities 166
12.7 Predator satiation and starvation . . . 167
12.8 Effects of space 173

Chapter 13. Humans as predators 176

13.1 Consciously controlled predation 179
13.2 Stochastic modelling 185
13.3 Present situation 187

Chapter 14. Humans as prey 189
14.1 Portals 190
14.2 Pathogen mobility 192
14.3 Disease more generally 199
14.4 The strange case of polio 201
14.5 Modern disease trends 207
14.6 An ancient plague perhaps vanishing . 208

Chapter 15. Theory of disease 215
15.1 New terminology 215
15.2 The SIR flowchart 216
15.3 The SIR equations 219
15.4 The SI equations 220
15.5 The I equation 221
15.6 Analysis of the I model 225
15.7 The rsN model again 227
15.8 Application to an actual outbreak . . . 228
15.9 Conflicting ethics 239

Chapter 16. Competition 243
16.1 The niche concept 244
16.2 Resource competition 249
16.3 Competitive exclusion 255
16.4 Succession 260
16.5 Single-resource phase space 265
16.6 Multiple resource phase space 270
16.7 Lotka–Volterra formulation 279

Chapter 17. Mutualism 286
17.1 Phase diagrams 295
17.2 Quasi-species 297
17.3 Our own species 298

Chapter 18. Higher-order models 303
18.1 One-species examples 303
18.2 Two-species blending 306
18.3 A way of organizing 308

Chapter 1
What is ecology?

Winston Churchill* pointed out that "All the great things are simple, and many can be expressed in a single word—freedom, justice, honor, duty, mercy, hope." Should we try to define these? Can we define them?

We should at least try to define our subject, ecology; many textbooks start with definitions. But first, for background, consider how we might define life. Marvin Minsky* was an artificial intelligence researcher and computer scientist who thought about definitions. When is an object alive? Think about viruses, genes, self-reproducing machines—no one has really been able to give a good definition of "living" that satisfies in general. Some things are clearly living—mice—and some clearly are not—rocks. Lists of what makes something living used to appear in textbooks:

(1) Self-reproducing
(2) Responds to stimuli
(3) Metabolizes
(4) Made of protoplasm—protein, carbohydrates, DNA.

But (1) puts out the mule, (2) and (3) put out the spore, while if those conditions are dropped, (4) will admit the frankfurter. One can go on to extend the list with more careful qualifications, but questions remain until the list grows to include special mention of everything we can think of.

1.1 Definitions of ecology

With caveats in mind, consider definitions of ecology. In the 1860s, Ernst Haeckel,⋆ combined the term *oikos*—a place to live, home, habitat—with *logia*—discourse, study—to coin the word "ecology." In the 1890s Ellen Richards⋆ included humans and harmony, quite a modern view. Variations over the years are shown in Table 1.1.

Haeckel	1860s	The total relations of an organism to its organic and inorganic environment
Richards	1890s	Living in harmony with the environment, first including family, then community, then the world and its resources
Elton	1920s	Scientific natural history
Odum	1960s	The study of the structure and function of nature, including the human species
Andrewartha	1960s	The scientific study of the distribution and abundance of organisms
Krebs		The scientific study of the interactions that determine the distribution and abundance of organisms
Molles	1990s	The study of relationships between organisms and the environment
Eilts	2010s	Life in context
Pope Francis	2015	The relationship between living organisms and the environment in which they develop

Table 1.1. *Various views of ecology.*

Each of these definitions has merit, but the first two and the last two are closest to the way the term is applied in this book. We humans have become prominent in ecology, locally to globally. No modern treatment of ecology is complete without a strong dose of anthropology.

The definition by Andrewartha has been widely quoted, but focusing merely on distribution and abundance reduces ecology to mapping, which is why Krebs modified this definition. The Pope's definition from his 2015 Encyclical includes the interesting idea of development, which can be taken to mean short-term development like embryogenesis and growth, plus long-term development like evolution. Overall, the definition by Eilts is perhaps the most general and engaging.

First and foremost, the most important concepts in ecology are about relationships, plus all of life, the whole environment, the processes of living and development, and, above all context. And in today's world, harmony. But also consider, "Poetry is the subject of the poem" (Wallace Stevens, 1937) and perhaps "Ecology is what ecologists do." With these in mind, we strive in the remainder of this book to define a theoretical form of ecology through examples and demonstrations, representative models and symbols, patterns and explanations, and lessons and caveats.

Figure 1.1. *The Rhind Papyrus, c. 1640 BC. One of the oldest known documents—and containing exercises from theoretical ecology!*

1.2 Ecology then and now

Our early hominin ancestors needed aspects of ecology. To find blueberries or other fruit, or where to dig wild onions, they had to know where these foods grew—their distribution and abundance. These parts of ecology have thus been part of life for hundreds of thousands of years. Ecology is connected with our species.

Some elements of the field of ecology were formalized more than 3000 years ago. The Rhind Papyrus (Figure 1.1) lists a number of ecological exercises for students—mathematics from ancient Egypt. Among these oldest ecological problems is this:

Number 27. If a mouse eat 521 ikats of grain each year and a cat kills 96 mice a year, in each of 24 barns, how many cats are required to control the destruction of stored grain?

This is a little problem in quantitative ecology! Even 36 centuries ago, mathematical ecology was part of life. Knowing how many grain bins determined how many cats were to be employed.

Today, ecology has become a glamour word. A product called "Ecogate," for example, is part of a central vacuum system that keeps sawdust and sanding dust from being tracked around. But why the word Ecogate? Dust collection *per se* has nothing to do with ecology. Advertisers, however, have found that consumers respond positively to the term.

The term "ecosystem" is frequently used in business and finance, but there it means a collection of companies, customers, and products and their interconnections. For better or worse, ecological terminology is expanding to other domains.

1.3 Methods of ecology

How do ecologists do ecology? Often, they start with observation, then move to theory—trying to fit observations together to make sense as a whole. Theory then leads to expectations, which in turn lead to experiments. Commonly, experiments aren't undertaken until there is some theory to be tested and understood.

(1) Observation
(2) Theory
(3) Experiment
(4) Serendipity

Observation, theory, and experiment, however, are not the whole story. A large part of science turns out to be serendipity—luck and chance—capitalizing on chance and doing something with it. One example is Alexander Fleming⋆, who discovered penicillin. Some of the bacterial cultures in his lab became contaminated with penicillium mold and the cultures died. That ruined his experiment.

He could have written a memo to the laboratory staff ordering "Always keep mold away from our bacterial cultures. It destroys the cultures and will ruin the hypotheses we are trying to test." But instead he capitalized on the serendipity, wondered what was happening, and found a substance in penicillium mold that kills bacteria. Fungi and bacteria have been archenemies for perhaps a billion years. Fleming's discovery has helped physicians actually *cure* disease, rather than being limited to diagnosing and prognosticating.

Following up on chance is, then, a large part of science. By the way, for an interesting paper, read the original 1929 report by Fleming about penicillium. It is so understated. He writes "the name 'penicillin' has been given to filtrates of broth cultures of the mould." No one had heard of the word before. Then he suggests that "it may be an efficient antiseptic." One of the greatest discoveries of all time and only, "it may be an efficient antiseptic."

Cedar Creek⋆ is a University of Minnesota research site about thirty miles north of the University's Saint Paul campus, and is one of the classic ecological research sites in the world. Pictured in Figure 1.2 is an experiment set up by Prof. David Tilman⋆ . While very carefully designed, it came about because of serendipity—the chance event of a deep two-year drought that altered the abundances of species in a particular way and triggered the idea for this experiment.

Keep your eyes open for such chance events; they can crop up anywhere.

Figure 1.2. *Observations and experiments testing theory at Cedar Creek⋆ . This entire experiment was established following up on serendipity.*