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A Primer of Ecology with R

 Springer

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*To my perfect parents, Martin and Ann,
to my loving wife, Julyan,
and to my wonderfully precocious kids, Tessa and Jack.*

Preface

Goals and audience

In spite of the presumptuous title, my goals for this book are modest. I wrote it as

- the manual I wish I had in graduate school, and
- a primer for our graduate course in Population and Community Ecology at Miami University¹

It is my hope that readers can enjoy the *ecological content* and ignore the R code, if they care to. Toward this end, I tried to make the code easy to ignore, by either putting boxes around it, or simply concentrating code in some sections and keeping it out of other sections.

It is also my hope that ecologists interested in learning R will have a rich yet gentle introduction to this amazing programming language. Toward that end, I have included some useful functions in an R package called **primer**. Like nearly all R packages, it is available through the R projects repositories, the CRAN mirrors. See the Appendix for an introduction to the R language.

I have a hard time learning something on my own, unless I can *do* something with the material. Learning ecology is no different, and I find that my students and I learn theory best when we write down formulae, manipulate them, and explore consequences of rearrangement. This typically starts with copying down, verbatim, an expression in a book or paper. Therefore, I encourage readers to take pencil to paper, and fingers to keyboard, and copy expressions they see in this book. After that, make sure that what I have done is correct by trying some of the same rearrangements and manipulations I have done. In addition, try things that aren't in the book — have fun.

A pedagogical suggestion

For centuries, musicians and composers have learned their craft in part by *copying by hand* the works of others. Physical embodiment of the musical notes

¹ Miami University is located in the Miami River valley in Oxford, Ohio, USA; the region is home to the Myaamia tribe that dwelled here prior to European occupation.

and their sequences helped them learn composition. I have it on great authority that most theoreticians (and other mathematicians) do the same thing — they start by copying down mathematical expressions. This physical process helps get the content under their skin and through their skull. I encourage you to do the same. Whether otherwise indicated or not, let the first assigned problem at the end of each chapter be to copy down, with a pencil and paper, the mathematical expression presented in that chapter. In my own self-guided learning, I have often taken this simple activity for granted and have discounted its value — to my own detriment. I am not surprised how often students also take this activity for granted, and similarly suffer the consequences. *Seeing* the logic of something is not always enough — sometimes we have to actually *recreate* the logic for ourselves.

Comparison to other texts

It may be useful to compare this book to others of a similar ilk. This book bears its closest similarities to two other wonderful primers: Gotelli's *A Primer of Ecology*, and Roughgarden's *Primer of Theoretical Ecology*. I am more familiar with these books than any other introductory texts, and I am greatly indebted to these authors for their contributions to my education and the discipline as a whole.

My book, geared toward graduate students, includes more advanced material than Gotelli's primer, but most of the ecological topics are similar. I attempt to start in the same place (e.g., "What is geometric growth?"), but I develop many of the ideas much further. Unlike Gotelli, I do not cover life tables at all, but rather, I devote an entire chapter to *demographic matrix models*. I include a chapter on community structure and diversity, including *multivariate distances*, *species-abundance distributions*, *species-area relations*, and *island biogeography*, as well as *diversity partitioning*. My book also includes code to implement most of the ideas, whereas Gotelli's primer does not.

This book also differs from Roughgarden's primer, in that I use the Open Source R programming language, rather than Matlab®, and I do not cover physiology or evolution. My philosophical approach is similar, however, as I tend to "talk" to the reader, and we fall down the rabbit hole together².

Aside from Gotelli and Roughgarden's books, this book bears similarity in content to several other wonderful introductions to mathematical ecology or biology. I could have cited repeatedly (and in some places did so) the following: Ellner and Guckenheimer (2006), Gurney and Nisbet (1998), Kingsland (1985), MacArthur (1972), Magurran (2004), May (2001), Morin (1999), Otto and Day (2006), and Vandermeer and Goldberg (2007). Still others exist, but I have not yet had the good fortune to dig too deeply into them.

Acknowledgements

I am indebted to Scott Meiners and his colleagues for their generous sharing of data, metadata, and statistical summaries from the Buell-Small Succession

² From *Alice's Adventures in Wonderland* (1865), L. Carroll (C. L. Dodgson).

Study (<http://www.ecostudies.org/bss/>), a 50+ year study of secondary succession (supported in part by NSF grant DEB-0424605) in the North American temperate deciduous forest biome. I would like to thank Stephen Ellner for Ross's Bombay plague death data and for R code and insight over the past few years. I am also indebted to Tom Crist and his colleagues for sharing some of their moth data (work supported by The Nature Conservancy Ecosystem Research Program, and NSF DEB-0235369).

I am grateful for the generosity of early reviewers and readers, each of whom has contributed much to the quality of this work: Jeremy Ash, Tom Crist, David Gorchov, Raphael Herrera-Herrera, Thomas Petzoldt, James Vonesh, as well as several anonymous reviewers, and the students of our Population and Community Ecology class. I am also grateful for the many conversations and emails shared with four wonderful mathematicians and theoreticians: Jayanth Banavar, Ben Bolker, Stephen Ellner, Amit Shukla, and Steve Wright — I never have a conversation with these people without learning something. I have been particularly fortunate to have team-taught Population and Community Ecology at Miami University with two wonderful scientists and educators, David Gorchov and Thomas Crist. Only with this experience, of working closely with these colleagues, have I been able to attempt this book. It should go without saying, but I will emphasize, that the mistakes in this book are mine, and there would be many more but for the sharp eyes and insightful minds of many other people.

I am also deeply indebted to the R Core Development Team for creating, maintaining and pushing forward the R programming language and environment [173]. Like the air I breathe, I cannot imagine my (professional) life without it. I would especially like to thank Friedrich Leisch for the development of *Sweave*, which makes literate programming easy [106]. Because I rely on Aquamacs, ESS, L^AT_EX, and a host of other Open Source programs, I am deeply grateful to those who create and distribute these amazing tools.

A few other R packages bear special mention. First, Ben Bolker's text [13] and packages for modeling ecological data (*bbmle* and *emdbook*) are broadly applicable. Second, Thomas Petzoldt's and Karsten Rinke's *simecol* package provides a general computational architecture for ecological models, and implements many wonderful examples [158]. Much of what is done in this primer (especially in chapters 1, 3–6, 8) can be done with *simecol*, and sometimes done better. Third, Robin Hankin's *untb* package is an excellent resource for exploring ecological neutral theory (chapter 10) [69]. Last, I relied heavily on the *deSolve* [190] and *vegan* packages [151].

Last, and most importantly, I would like to thank those to whom this book is dedicated, whose love and senses of humor make it all worthwhile.

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Oxford, OH, USA, Earth
February, 2009

Contents

Part I Single Species Populations

1	Simple Density-independent Growth	3
1.1	A Very Specific Definition	4
1.2	A Simple Example	5
1.3	Exploring Population Growth	5
1.3.1	Projecting population into the future	7
1.3.2	Effects of initial population size	8
1.3.3	Effects of different per capita growth rates	10
1.3.4	Average growth rate	10
1.4	Continuous Exponential Growth	13
1.4.1	Motivating continuous exponential growth	14
1.4.2	Deriving the time derivative	16
1.4.3	Doubling (and tripling) time	17
1.4.4	Relating λ and r	18
1.5	Comments on Simple Density-independent Growth Models	19
1.6	Modeling with Data: Simulated Dynamics	20
1.6.1	Data-based approaches	21
1.6.2	Looking at and collecting the data	21
1.6.3	One simulation	23
1.6.4	Multiple simulations	24
1.6.5	Many simulations, with a function	26
1.6.6	Analyzing results	27
1.7	Summary	31
	Problems	31
2	Density-independent Demography	33
2.1	A Hypothetical Example	34
2.1.1	The population projection matrix	36
2.1.2	A brief primer on matrices	36
2.1.3	Population projection	37
2.1.4	Population growth	39

2.2	Analyzing the Projection Matrix	40
2.2.1	Eigenanalysis	41
2.2.2	Finite rate of increase – λ	42
2.2.3	Stable stage distribution	44
2.2.4	Reproductive value	45
2.2.5	Sensitivity and elasticity	46
2.2.6	More demographic model details	48
2.3	Confronting Demographic Models with Data	49
2.3.1	An Example: <i>Chamaedorea</i> palm demography	49
2.3.2	Strategy	50
2.3.3	Preliminary data management	51
2.3.4	Estimating projection matrix	52
2.3.5	Eigenanalyses	54
2.3.6	Bootstrapping a demographic matrix	55
2.3.7	The demographic analysis	56
2.4	Summary	59
	Problems	59
3	Density-dependent Growth	61
3.1	Discrete Density-dependent Growth	62
3.1.1	Motivation	62
3.1.2	Relations between growth rates and density	64
3.1.3	Effect of initial population size on growth dynamics	66
3.1.4	Effects of α	68
3.1.5	Effects of r_d	69
3.2	Continuous Density Dependent Growth	75
3.2.1	Generalizing and resimplifying the logistic model	76
3.2.2	Equilibria of the continuous logistic growth model	79
3.2.3	Dynamics around the equilibria — stability	79
3.2.4	Dynamics	85
3.3	Other Forms of Density-dependence	86
3.4	Maximum Sustained Yield	89
3.5	Fitting Models to Data	92
3.5.1	The role of resources in altering population interactions within a simple food web	92
3.5.2	Initial data exploration	93
3.5.3	A time-implicit approach	95
3.5.4	A time-explicit approach	101
3.6	Summary	107
	Problems	107
4	Populations in Space	111
4.1	Source-sink Dynamics	112
4.2	Two Types of Metapopulations	114
4.3	Related Models	117
4.3.1	The classic Levins model	117
4.3.2	Propagule rain	118

4.3.3	The rescue effect and the core-satellite model	120
4.4	Parallels with Logistic Growth	123
4.5	Habitat Destruction	125
4.6	Core-Satellite Simulations	128
4.7	Summary	132
	Problems	132

Part II Two-species Interactions

5	Lotka–Volterra Interspecific Competition	135
5.1	Discrete and Continuous Time Models	136
5.1.1	Discrete time model	136
5.1.2	Effects of α	137
5.1.3	Continuous time model	139
5.2	Equilibria	140
5.2.1	Isoclines	141
5.2.2	Finding equilibria	143
5.3	Dynamics at the Equilibria	146
5.3.1	Determine the equilibria	146
5.3.2	Create the Jacobian matrix	148
5.3.3	Solve the Jacobian at an equilibrium	149
5.3.4	Use the Jacobian matrix	150
5.3.5	Three interesting equilibria	151
5.4	Return Time and the Effect of r	155
5.5	Summary	157
	Problems	158
6	Enemy–Victim Interactions	161
6.1	Predators and Prey	162
6.1.1	Lotka–Volterra model	162
6.1.2	Stability analysis for Lotka–Volterra	168
6.1.3	Rosenzweig–MacArthur model	171
6.1.4	The paradox of enrichment	177
6.2	Space, Hosts, and Parasitoids	179
6.2.1	Independent and random attacks	180
6.2.2	Aggregation leads to coexistence	185
6.2.3	Stability of host–parasitoid dynamics	188
6.3	Disease	192
6.3.1	SIR with frequency–dependent transmission	195
6.3.2	SIR with population dynamics	200
6.3.3	Modeling data from Bombay	202
6.4	Summary	206
	Problems	207

Part III Special Topics

7	An Introduction to Food Webs	211
7.1	Food Web Characteristics	211
7.2	Food chain length — an emergent property	214
7.2.1	Multi-species Lotka–Volterra notation	214
7.2.2	Background	214
7.3	Implementing Pimm and Lawton’s Methods	217
7.4	Shortening the Chain	221
7.5	Adding Omnivory	222
7.5.1	Comparing Chain A versus B	223
7.6	Re-evaluating Take-Home Messages	225
7.7	Summary	226
	Problems	226
8	Multiple Basins of Attraction	227
8.1	Introduction	227
8.1.1	Alternate stable states	227
8.1.2	Multiple basins of attraction	228
8.2	Lotka–Volterra Competition and MBA	230
8.2.1	Working through Lotka–Volterra MBA	232
8.3	Resource Competition and MBA	234
8.3.1	Working through resource competition	237
8.4	Intraguild Predation	242
8.4.1	The simplest Lotka–Volterra model of IGP	243
8.4.2	Lotka–Volterra model of IGP with resource competition	243
8.4.3	Working through an example of intraguild predation	245
8.4.4	Effects of relative abundance	247
8.4.5	Effects of absolute abundance	248
8.4.6	Explanation	249
8.5	Summary	252
	Problems	252
9	Competition, Colonization, and Temporal Niche Partitioning	255
9.1	Competition–colonization Tradeoff	255
9.2	Adding Reality: Finite Rates of Competitive Exclusion	266
9.3	Storage effect	275
9.3.1	Building a simulation of the storage effect	276
9.4	Summary	282
	Problems	283
10	Community Composition and Diversity	285
10.1	Species Composition	286
10.1.1	Measures of abundance	286
10.1.2	Distance	287
10.1.3	Similarity	290

10.2	Diversity	291
10.2.1	Measurements of variety	292
10.2.2	Rarefaction and total species richness	297
10.3	Distributions.....	299
10.3.1	Log-normal distribution	300
10.3.2	Other distributions	301
10.3.3	Pattern <i>vs.</i> process	305
10.4	Neutral Theory of Biodiversity and Biogeography.....	306
10.4.1	Different flavors of neutral communities	310
10.4.2	Investigating neutral communities	312
10.4.3	Symmetry and the rare species advantage	317
10.5	Diversity Partitioning	318
10.5.1	An example of diversity partitioning	321
10.5.2	Species–area relations	323
10.5.3	Partitioning species–area relations	330
10.6	Summary.....	332
	Problems	332
A	A Brief Introduction to R.....	335
A.1	Strengths of R/S	335
A.2	The R Graphical User Interface (GUI)	336
A.3	Where is R?	338
A.4	Starting at the Very Beginning	338
B	Programming in R	341
B.1	Help	341
B.2	Assignment	342
B.3	Data Structures	343
B.3.1	Vectors	343
B.3.2	Getting information about vectors	344
B.3.3	Extraction and missing values.....	347
B.3.4	Matrices	348
B.3.5	Data frames	352
B.3.6	Lists	354
B.3.7	Data frames are also lists	355
B.4	Functions	356
B.4.1	Writing your own functions	357
B.5	Sorting.....	358
B.6	Iterated Actions: the apply Family and Loops	359
B.6.1	Iterations of independent actions	359
B.6.2	Dependent iterations.....	360
B.7	Rearranging and Aggregating Data Frames	361
B.7.1	Rearranging or reshaping data	361
B.7.2	Summarizing by groups	362
B.8	Getting Data out of and into the Workspace	363
B.9	Probability Distributions and Randomization	364
B.10	Numerical integration of ordinary differential equations.....	366

B.11 Numerical Optimization	369
B.12 Derivatives	373
B.13 Graphics	374
B.13.1 <code>plot</code>	374
B.13.2 Adding points, lines and text to a plot	374
B.13.3 More than one response variable	375
B.13.4 Controlling Graphics Devices	377
B.13.5 Creating a Graphics File	378
B.14 Graphical displays that show distributions	378
B.15 Eigenanalysis	380
B.16 Eigenanalysis of demographic versus Jacobian matrices	380
B.17 Symbols used in this book	382
References	385
Index	397