

Contents

Acknowledgments	xvii
List of Symbols	xix
Part I Preliminaries	
1 Introduction	3
2 Models and Theories	7
2.1 The usefulness of models	7
2.2 What models should model	8
2.3 The possibility of ecological theory	10
2.4 Theory-driven ecological research	11
3 Some Basic Concepts	13
3.1 Basic concepts of food-web studies	13
3.2 Physical quantities and dimensions	15
Part II Elements of Food-Web Models	
4 Energy and Biomass Budgets	19
4.1 Currencies of accounting	19
4.2 Rates and efficiencies	20
4.3 Energy budgets in food webs	21
5 Allometric Scaling Relationships Between Body Size and Physiological Rates	25
5.1 Scales and scaling	25
5.2 Allometric scaling	26
6 Population Dynamics	29
6.1 Basic considerations	29
6.1.1 Exponential population growth	29
6.1.2 Five complications	30
6.1.3 Environmental variability	31

6.2	Structured populations and density-dependence	32
6.2.1	The dilemma between species and stages	32
6.2.2	Explicitly stage-structured population dynamics	32
6.2.3	Communities of structured populations	35
6.3	The Quasi-Neutral Approximation	35
6.3.1	The emergence of food webs	35
6.3.2	<i>Rana catesbeiana</i> and its resources	35
6.3.3	Numerical test of the approximation	38
6.4	Reproductive value	40
6.4.1	The concept of reproductive value	40
6.4.2	The role of reproductive value in the QNA	40
6.4.3	Body mass as a proxy for reproductive value	40
7	From Trophic Interactions to Trophic Link Strengths	45
7.1	Functional and numerical responses	45
7.2	Three models for functional responses	46
7.2.1	Linear response	46
7.2.2	Type II response	46
7.2.3	Type II response with prey switching	47
7.2.4	Strengths and weaknesses of these models	48
7.3	Food webs as networks of trophic link strengths	48
7.3.1	The ontology of trophic link strengths	48
7.3.2	Variability of trophic link strengths	49
8	Trophic Niche Space and Trophic Traits	51
8.1	Topology and dimensionality of trophic niche space	52
8.1.1	Formal setting	52
8.1.2	Definition of trophic niche-space dimensionality	53
8.2	Examples and ecological interpretations	55
8.2.1	A minimal example	55
8.2.2	Is the definition of dimensionality reasonable?	55
8.2.3	Dependencies between vulnerability and foraging traits of a species	56
8.2.4	The range of phenotypes considered affects niche-space dimensionality	56
8.3	Determination of trophic niche-space dimensionality	58
8.3.1	Typical empirical data	58
8.3.2	Direct estimation of dimensionality	59
8.3.3	Iterative estimation of dimensionality	59
8.4	Identification of trophic traits	60
8.4.1	Formal setting	60
8.4.2	Dimensional reduction	62
8.5	The geometry of trophic niche space	65
8.5.1	Abstract trophic traits	65
8.5.2	Indeterminacy in abstract trophic traits	65
8.5.3	The D -dimensional niche space as a pseudo-Euclidean space	66
8.5.4	Linear transformations of abstract trophic traits	67
8.5.5	Non-linear transformations of abstract trophic traits	68
8.5.6	Standardization and interpretation of abstract trophic traits	69
8.5.7	A hypothesis and a convention	72
8.5.8	Getting oriented in trophic niche space	73
8.6	Conclusions	75

9 Community Turnover and Evolution	77
9.1 The spatial scale of interest	77
9.2 How communities evolve	78
9.3 The mutation-for-dispersion trick	79
9.4 Mutation-for-dispersion in a neutral food-web model	80
10 The Population-Dynamical Matching Model	81
Part III Mechanisms and Processes	
11 Basic Characterizations of Link-Strength Distributions	87
11.1 Modelling the distribution of logarithmic link strengths	88
11.1.1 General normally distributed trophic traits	88
11.1.2 Isotropically distributed trophic traits	91
11.2 High-dimensional trophic niche spaces	93
11.2.1 Understanding link strengths in high-dimensional trophic niche spaces	93
11.2.2 Log-normal probability distributions	94
11.2.3 The limit of log-normally distributed trophic link strength	95
11.2.4 Correlations between trophic link strengths	96
11.2.5 The distribution of the strengths of observable links	97
11.2.6 The probability of observing links (connectance)	99
11.2.7 Estimation of link-strength spread and Pareto exponent	100
11.2.8 Empirical examples	101
12 Diet Partitioning	103
12.1 The diet partitioning function	103
12.1.1 Relation to the probability distribution of diet proportions	105
12.1.2 Another probabilistic interpretation of the DPF	106
12.1.3 The normalization property of the DPF	106
12.1.4 Empirical determination of the DPF	107
12.2 Modelling the DPF	107
12.2.1 Formal setting	107
12.2.2 Diet ratios	108
12.2.3 The DPF for high-dimensional trophic niche spaces	109
12.2.4 Gini-Simpson dietary diversity	110
12.2.5 Dependence of the DPF on niche-space dimensionality	112
12.3 Comparison with data	113
12.4 Conclusions	114
13 Multivariate Link-Strength Distributions and Phylogenetic Patterns	117
13.1 Modelling phylogenetic structure in trophic traits	118
13.1.1 Phylogenetic correlations among logarithmic link strengths	120
13.1.2 Phylogenetic correlations among link strengths	121
13.1.3 Phylogenetic patterns in binary food webs	122
13.2 The matching model	123
13.2.1 A simple model for phylogenetic structure in food webs	123
13.2.2 Definition of the matching model	124

13.2.3	Sampling steady-state matching model food webs	124
13.2.4	Alternatives to the matching model	126
13.3	Characteristics of phylogenetically structured food webs	126
13.3.1	Graphical representation of food-web topologies	127
13.3.2	Standard parameter values	127
13.3.3	Intervality	128
13.3.4	Intervality and trophic niche-space dimensionality	129
13.3.5	Degree distributions	131
13.3.6	Other phylogenetic patterns	134
13.3.7	Is phylogeny just a nuisance?	135
14	A Framework Theory for Community Assembly	137
14.1	Ecological communities as dynamical systems	137
14.2	Existence, positivity, stability, and permanence	138
14.3	Generic bifurcations in community dynamics and their ecological phenomenology	139
14.3.1	General concepts	139
14.3.2	Saddle-node bifurcations	140
14.3.3	Hopf bifurcations	142
14.3.4	Transcritical bifurcations	142
14.3.5	Bifurcations of complicated attractors	144
14.4	Comparison with observations	144
14.4.1	Extirpations and invasions proceed slowly	145
14.4.2	The logistic equation works quite well	145
14.4.3	IUCN Red-List criteria highlight specific extinction scenarios	147
14.4.4	Conclusion	148
14.5	Invasion fitness and harvesting resistance	148
14.5.1	Invasion fitness	148
14.5.2	Harvesting resistance: definition	149
14.5.3	Harvesting resistance: interpretation	149
14.5.4	Harvesting resistance: computation	151
14.5.5	Interpretation of $h \rightarrow 0$	152
14.6	Community assembly and stochastic species packing	152
14.6.1	Community saturation and species packing	152
14.6.2	Invasion probability	154
14.6.3	The steady-state distribution of harvesting resistance	157
14.6.4	The scenario of stochastic species packing	158
14.6.5	A numerical example	160
14.6.6	Biodiversity and ecosystem functioning	162
15	Competition in Food Webs	165
15.1	Basic concepts	166
15.1.1	Modes of competition	166
15.1.2	Interactions in communities	166
15.2	Competition in two-level food webs	167
15.2.1	The Lotka-Volterra two-level food-web model	168
15.2.2	Computation of the equilibrium point	168
15.2.3	Direct competition among producers	169
15.2.4	Resource-mediated competition in two-level food webs	169
15.2.5	Consumer-mediated competition in two-level food webs	170
15.3	Competition in arbitrary food webs	173

15.3.1	The general Lotka-Volterra food-web model	173
15.3.2	The competition matrix for general food webs	174
15.3.3	The L-R-P formalism	176
15.3.4	Ecological interpretations of the matrices L , R , and P	176
15.3.5	Formal computation of the equilibrium point	177
15.3.6	Consumer-mediated competition in general food webs	178
15.3.7	Consumer-mediated competitive exclusion	179
15.3.8	Conclusions	179
16	Mean-Field Theory of Resource-Mediated Competition	181
16.1	Transition to scaled variables	182
16.1.1	The competitive overlap matrix	182
16.1.2	Free abundances	183
16.2	The extended mean-field theory of competitive exclusion	184
16.2.1	Assumptions	184
16.2.2	Separation of means and residuals	186
16.2.3	Mean-field theory for the mean scaled abundance	187
16.2.4	Mean-field theory for the variance of scaled abundance	188
16.2.5	The coefficient of variation of scaled abundance	190
16.2.6	Related theories	191
17	Resource-Mediated Competition and Assembly	193
17.1	Preparation	193
17.1.1	Scaled vs. unscaled variables and parameters	193
17.1.2	Mean-field vs. framework theory	195
17.2	Stochastic species packing under asymmetric competition	197
17.2.1	Species richness and distribution of invasion fitness (Part I)	198
17.2.2	Community response to invasion	199
17.2.3	Sensitivity of residents to invaders	200
17.2.4	Species richness and distribution of invasion fitness (Part II)	203
17.2.5	Random walks of abundances driven by invasions	204
17.2.6	Further discussion of the scenario	206
17.3	Stochastic species packing with competition symmetry	207
17.3.1	Community assembly with perfectly symmetric competition	207
17.3.2	Community assembly under nearly perfectly symmetric competition	209
17.3.3	Outline of mechanism limiting competition avoidance	211
17.3.4	The distribution of invasion fitness	212
17.3.5	Competition between residents and invaders	213
17.3.6	Balance of scaled biomass during assembly	214
17.3.7	Competition avoidance	215
17.3.8	Numerical test of the theory	216
18	Random-Matrix Competition Theory	221
18.1	Asymmetric competition	221
18.1.1	Girko's Law	221
18.1.2	Application to competitive overlap matrices	223
18.1.3	Implications for sensitivity to invaders	223
18.1.4	Relation to mean-field theory	224
18.2	Stability vs. feasibility limits to species richness	225

18.2.1	The result of May (1972)	225
18.2.2	Comparison of stability and feasibility criteria	225
18.3	Partially and fully symmetric competition	226
18.4	Sparse overlap matrices	228
18.4.1	Sparse competition	228
18.4.2	Eigenvalue distributions for sparse matrices	228
18.5	Resource overlap matrices	230
18.5.1	Diffuse resource competition	230
18.5.2	Sparse resource competition: the basic problem	232
18.5.3	The effect of trophic niche-space geometry	235
18.5.4	Competition among highly specialized consumers	237
18.5.5	Resource competition for varying ratios of producer to consumer richness	237
18.5.6	Competition for competing resources	239
18.6	Comparison with data	242
18.6.1	Gall-inducing insects on plants	242
18.6.2	Freshwater ecosystems	243
18.6.3	The North Sea	244
18.6.4	Conclusions	244
19	Species Richness, Size and Trophic Level	247
19.1	Predator-prey mass ratios	247
19.2	Modelling the joint distribution of size, trophic level, and species richness	249
19.2.1	Initial considerations	249
19.2.2	Model definition	251
19.2.3	Model simulation and comparison with data	252
20	Consumer-Mediated Competition and Assembly	255
20.1	A two-level food-web assembly model	256
20.2	Analytic characterization of the model steady state	257
20.2.1	Mechanism controlling producer richness	257
20.2.2	Other characteristics of the model steady state	259
20.3	Dependence of invader impacts on dietary diversity	262
20.3.1	Formal setting	262
20.3.2	Invadability condition	263
20.3.3	Extirpation of resources during invasion	263
20.3.4	Extirpation of resources through consumer-mediated competition	264
20.3.5	Synthesis	264
20.4	Evolution of base attack rates	266
20.4.1	Motivation	266
20.4.2	Model definition	267
20.4.3	Numerical demonstration of attack rate evolution	267
20.4.4	Attack-rate evolution and prudent predation	268
21	Food Chains and Size Spectra	271
21.1	Concepts	271
21.1.1	Community size spectra	271
21.1.2	Species size spectra	273
21.2	Power-law food chains	274
21.2.1	Infinitely long power-law food chains	274

21.2.2	Top-down and bottom-up control	276
21.2.3	Power law-food chains of finite lengths and their stability to pulse perturbations	278
21.2.4	Food chains as approximations for size spectra	279
21.2.5	Adaptation of attack rates	281
21.3	Food chains with non-linear functional responses	281
21.3.1	Loss of stability with density-independent consumption	282
21.3.2	Linearization of a generalized food chain model	283
21.3.3	Linear responses to press perturbations	284
21.3.4	Linear stability to pulse perturbations	285
21.4	What are the mechanisms controlling the scaling laws?	290
21.4.1	Arguments for biological constraints on transfer efficiency	290
21.4.2	Arguments for stability constraints on transfer efficiency	291
21.4.3	Arguments for ecological constraints on biomass imbalance	291
21.4.4	Arguments for mechanical constraints on PPMR	292
21.4.5	Arguments for dynamical constraints on PPMR	293
21.4.6	Conclusions	293
21.5	Scavengers and detritivores	294
21.5.1	The general argument	294
21.5.2	The microbial loop and other detrital channels	294
22	Structure and Dynamics of PDMM Model Communities	297
22.1	PDMM model definition	298
22.1.1	Model states	298
22.1.2	Species sampling and community assembly	298
22.1.3	Population dynamics	301
22.2	PDMM simulations	303
22.2.1	Trophic niche space and phylogenetic correlations	304
22.2.2	Steady state and invasion fitness	307
22.2.3	Diet partitioning	309
22.2.4	Resource-mediated competition	310
22.2.5	Distribution of species over body sizes and trophic levels	311
22.2.6	The size spectrum and related distributions	312
22.3	The PDMM with evolving attack rates	314
22.3.1	Modelling and tracking evolving attack rates in the PDMM	314
22.3.2	Time series of species richness, aggressivity and dietary diversity	315
22.3.3	Mutual regulation of aggressivity and dietary diversity	316
22.4	Conclusions	318

Part IV Implications

23	Scientific Implications	323
23.1	Main mechanisms identified by the theory	323
23.1.1	Two trades – one currency	323
23.1.2	Resource-mediated competition	324
23.1.3	Randomness and structure in food webs	324
23.1.4	Consumer-mediated competition and attack-rate evolution	325
23.2	Testable assumptions and predictions	325
23.2.1	Link-strength distributions and trophic niche-space geometry	325
23.2.2	Diet-partitioning statistics and sampling curves	325

23.2.3	Prey switching	326
23.2.4	Adapted attack rates	326
23.2.5	Community assembly and turnover	326
23.2.6	Patterns in link-strength matrices	327
23.3	Some unsolved problems	327
23.3.1	Large plants	327
23.3.2	Interactions between modes of competition	327
23.3.3	Absolute species richness: the role of viruses	327
23.3.4	The role of prey switching for community structure	328
23.3.5	The role of phylogenetic correlations for community dynamics	328
23.3.6	Fundamental constraints determining size-spectrum slopes	328
23.3.7	Community assembly with non-trivial attractors	328
23.3.8	Solution of the Riccati Equation for resource competition	328
23.3.9	Eigenvalues of competition matrices	329
23.3.10	Geometry and topology of trophic niche space	329
23.4	The future of community ecology	329
24	Conservation Implications	331
24.1	Assessing biodiversity	331
24.1.1	Quantifying biodiversity	331
24.1.2	Biodiversity supporting biodiversity	331
24.1.3	Assessing community turnover	332
24.2	Modelling ecological communities	333
24.2.1	Unpredictability of long-term community responses	333
24.2.2	Short-term predictions of community responses	334
24.2.3	Coarse-grained and stochastic community models	334
24.3	Managing biodiversity	334
Appendix A		337
A.1	Mathematical concepts, formulae, and jargon	337
A.1.1	Sums	337
A.1.2	Complex numbers	338
A.1.3	Vectors and matrices	339
A.1.4	Sets and functions	343
A.1.5	Differential calculus	343
A.1.6	Integrals	344
A.1.7	Differential equations	345
A.1.8	Random variables and expectation values	346
Bibliography		349
Index		365