
Contents

Preface	vi
Glossary of symbols	xiv
Acronyms and abbreviations	xv
Part I Foundations	
I The nature of theory	3
1.1 What is a theory?	3
1.1.1 Falsifiability	3
1.1.2 Comprehensiveness	4
1.1.3 Parsimony	4
1.1.4 Easier said than done	4
1.2 Ecology and physics	6
1.3 Types of theories	8
1.3.1 The role of mechanism in science	9
1.3.2 Mechanistic theories and models in ecology	11
1.3.3 Statistical theory and models in ecology	12
1.3.4 Neutral theories of ecology	12
1.3.5 Theories based on an optimization principle	13
1.3.6 State variable theories	14
1.3.7 Scaling theories	14
1.4 Why keep theory simple?	16
1.5 Exercises	17
2 The logic of inference	19
2.1 Expanding prior knowledge	20
2.2 Sought knowledge can often be cast in the form of unknown probability distributions	21

2.3	Prior knowledge often constrains the sought-after distributions	22
2.4	We always seek the least-biased distribution	22
2.5	Exercises	23

Part II Macroecology

3	Scaling metrics and macroecology	27
3.1	Thinking like a macroecologist	27
3.1.1	Questioning like a macroecologist	27
3.1.2	Censusing like a macroecologist	28
3.2	Metrics for the macroecologist	29
3.2.1	Units of analysis	30
3.3	The meaning of the metrics	32
3.3.1	Species-level spatial abundance distribution	33
3.3.2	Range-area relationship	35
3.3.3	Species-level commonality	37
3.3.4	Intra-specific energy distribution	39
3.3.5	Dispersal distributions	40
3.3.6	The species-abundance distribution (SAD)	41
3.3.7	Species-area relationship (SAR)	41
3.3.8	The endemics-area relationship (EAR)	46
3.3.9	Community commonality	46
3.3.10	Community energy distribution	47
3.3.11	Energy- and mass-abundance relationships	47
3.3.12	Link distribution in a species network	51
3.3.13	Two other metrics: The inter-specific dispersal-abundance relationship and the metabolic scaling rule	52
3.4	Graphs and patterns	52
3.4.1	Species-level spatial-abundance distributions: $\Pi(n A, n_0, A_0)$	61
3.4.2	Range-area relationship: $B(A n_0, A_0)$	63
3.4.2.1	A note on the nomenclature of curvature	63
3.4.3	Species-level commonality: $C(A, D n_0, A_0)$	63
3.4.4	Intra-specific distribution of metabolic rates: $\Theta(\varepsilon n_0)$	65
3.4.5	Intra-specific distribution of dispersal distances: $\Delta(D)$	65
3.4.6	The species-abundance distribution: $\Phi(n S_0, N_0, A_0)$	66
3.4.7	The species-area relationship: $\bar{S}(A N_0, S_0, A_0)$	68
3.4.8	The endemics-area relationship: $\bar{E}(A N_0, S_0, A_0)$	73
3.4.9	Community-level commonality: $X(A, D N_0, S_0, A_0)$	73
3.4.10	Energy and mass distributions and energy- and mass-abundance relationships	75
3.4.11	$\Lambda(l S_0, L_0)$	76
3.4.12	$\varepsilon(m)$	77

3.5	Why do we care about the metrics?	78
3.5.1	Estimating biodiversity in large areas	78
3.5.2	Estimating extinction	79
3.5.3	Estimating abundance from sparse data	82
3.6	Exercises	83

4 Overview of macroecological models and theories 87

4.1	Purely statistical models	87
4.1.1	The Coleman model: Distinguishable individuals	87
4.1.2	Models of Indistinguishable Individuals	89
4.1.2.1	Generalized Laplace model	92
4.1.2.2	HEAP	93
4.1.3	The negative binomial distribution	95
4.1.4	The Poisson cluster model	97
4.2	Power-law models	97
4.2.1	Commonality under self-similarity	100
4.3	Other theories of the SAD and/or the SAR	102
4.3.1	Preston's theory	102
4.3.2	Hubbell's neutral theory of ecology	104
4.3.3	Niche-based models	105
4.3.4	Island biogeographic theory	108
4.4	Energy and mass distributions	109
4.5	Mass-abundance and energy-abundance relationships	110
4.6	Food web models	110
4.7	A note on confidence intervals for testing model goodness	111
4.8	Exercises	112

Part III The maximum entropy principle

5 Entropy, information, and the concept of maximum entropy 117

5.1	Thermodynamic entropy	117
5.2	Information theory and information entropy	121
5.3	MaxEnt	123

6 MaxEnt at work 130

6.1	What if MaxEnt doesn't work?	130
6.2	Some examples of constraints and distributions	131
6.3	Uses of MaxEnt	133
6.3.1	Image resolution	133

6.3.2	Climate envelopes	133
6.3.3	Economics	134
6.3.4	Food webs and other networks	135
6.3.5	Classical and non-equilibrium thermodynamics and mechanics	135
6.3.6	Macroecology	136
6.4	Exercises	136

Part IV Macroecology and MaxEnt

7	The maximum entropy theory of ecology (METE)	141
7.1	The entities and the state variables	141
7.2	The structure of METE	142
7.2.1	Abundance and energy distributions	142
7.2.2	Species-level spatial distributions across multiple scales	146
7.3	Solutions: $R(n, \epsilon)$ and the metrics derived from it	146
7.3.1	Rank distributions for $\Psi(\epsilon)$, $\Theta(\epsilon)$, and $\Phi(n)$	152
7.3.2	Implications: extreme values of n and ϵ	153
7.3.3	Predicted forms of other energy and mass metrics	155
7.4	Solutions: $\Pi(n)$ and the metrics derived from it	157
7.5	The predicted species–area relationship	162
7.5.1	Predicting the SAR: Method 1	163
7.5.2	The special case of $\bar{S}(A)$ for $1 - A/A_0 \ll 1$	166
7.6	The endemics–area relationship	167
7.7	The predicted collector's curve	168
7.8	When should energy-equivalence and the Damuth relationship hold?	169
7.9	Miscellaneous predictions	173
7.10	Summary of predictions	174
7.11	Exercises	175
8	Testing METE	177
8.1	A general perspective on theory evaluation	177
8.2	Datasets	178
8.2.1	Some warnings regarding censusing procedures	180
8.3	The species-level spatial abundance distribution	180
8.3.1	A note on use of an alternative entropy measure	186
8.4	The community-level species–abundance distribution	186
8.5	The species–area and endemics–area relationships	190
8.6	The distribution of metabolic rates	193
8.7	Patterns in the failures of METE	196
8.8	Exercises	197

Part V A wider perspective**9 Applications to conservation 201**

- 9.1 Scaling up species' richness 201
- 9.2 Inferring abundance from presence-absence data 202
- 9.3 Estimating extinction under habitat loss 202
- 9.4 Inferring associations between habitat characteristics
and species occurrence 203
- 9.5 Exercises 206

10 Connections to other theories 208

- 10.1 METE and the Hubbell neutral theory 208
- 10.2 METE and metabolic scaling theories 209
- 10.3 METE and food web theory 210
- 10.4 Other applications of MaxEnt in macroecology 210
- 10.5 Exercise 212

11 Future directions 213

- 11.1 Incorporating spatial correlations into METE 213
 - 11.1.1 Method 1: Correlations from consistency constraints 213
 - 11.1.2 Method 2: A Bayesian approach to correlations 216
- 11.2 Understanding the structure of food webs 218
- 11.3 Toward a dynamic METE 218
- 11.4 Exercises 225

Epilogue: Is a comprehensive unified theory of ecology possible? What might it look like? 229**Appendix A: Access to plant census data from a serpentine grassland 232****Appendix B: A fractal model 233****Appendix C: Predicting the SAR: An alternative approach 240****References 244****Index 253**