

Brief Contents

	1 Introduction to Ecology: Historical Foundations and Developing Frontiers	1
Section I	Natural History and Evolution	11
	2 Life on Land	11
	3 Life in Water	44
	4 Population Genetics and Natural Selection	78
Section II	Adaptations to the Environment	101
	5 Temperature Relations	101
	6 Water Relations	127
	7 Energy and Nutrient Relations	149
	8 Social Relations	172
Section III	Population Ecology	196
	9 Population Distribution and Abundance	196
	10 Population Dynamics	215
	11 Population Growth	237
	12 Life Histories	253
Section IV	Interactions	275
	13 Species Interactions and Competition	275
	14 Exploitative Interactions: Predation, Herbivory, Parasitism, and Disease	297
	15 Mutualism	323
Section V	Communities and Ecosystems	343
	16 Species Abundance and Diversity	343
	17 Species Interactions and Community Structure	362
	18 Primary and Secondary Production	381
	19 Nutrient Cycling and Retention	401
	20 Succession and Stability	421
Section VI	Large-Scale Ecology	443
	21 Landscape Ecology	443
	22 Geographic Ecology	466
	23 Global Ecology	488
	Appendix A Investigating the Evidence	511
	Appendix B Statistical Tables	538

Contents

Preface xiii

Chapter 1 Introduction to Ecology: Historical Foundations and Developing Frontiers 1

Concepts 1

1.1 Overview of Ecology 2

Concept 1.1 Review 3

1.2 Sampling Ecological Research 3

The Ecology of Forest Birds: Old Tools and New 4

Forest Canopy Research: A Physical and Scientific
Frontier 6

Climatic and Ecological Change: Past and Future 7

Concept 1.2 Review 8

Applications: Ecology Can Inform Environmental Law and
Policy 9

Section I

NATURAL HISTORY AND EVOLUTION

Chapter 2 Life on Land 11

Concepts 11

Terrestrial Biomes and the Importance of Plants 12

2.1 Large-Scale Patterns of Climatic Variation 14

Temperature, Atmospheric Circulation, and Precipitation 14

Climate Diagrams 16

Concept 2.1 Review 16

2.2 Other Factors That Shape Terrestrial Biomes 17

Concept 2.2 Review 19

2.3 Natural History and Geography of Biomes 19

Tropical Rain Forest 19

Tropical Dry Forest 21

Tropical Savanna 23

Desert 25

Woodland and Shrubland 27

Temperate Grassland 29

Temperate Forest 31

Boreal Forest 32

Tundra 35

Mountains: A Diversity of Biomes 37

Concept 2.3 Review 40

Applications: Finer Scale Climatic Variation Over Time
and Space 40

Chapter 3 Life in Water 44

Concepts 44

Aquatic Biomes and How They Differ 45

3.1 Water Cycling 47

The Hydrologic Cycle 47

The Effects of Wind and Temperature 47

Concept 3.1 Review 48

3.2 The Natural History of Aquatic Environments 49

The Oceans 49

Life in Shallow Marine Waters: Kelp Forests and Coral
Gardens 54

Marine Shores: Life Between High and Low Tides 57

Transitional Environments: Estuaries, Salt Marshes,
Mangrove Forests, and Freshwater Wetlands 59

Rivers and Streams: Life Blood and Pulse of the Land 64

Lakes: Small Seas 69

Concept 3.2 Review 73

Applications: Biological Integrity—Assessing the Health
of Aquatic Systems 73

Number of Species and Species Composition 74

Trophic Composition 74

Fish Abundance and Condition 74

A Test 74

Chapter 4 Population Genetics and Natural Selection 78

Concepts 78

4.1 Variation Within Populations 81

Variation in a Widely Distributed Plant 81

Variation in Alpine Fish Populations 83

Concept 4.1 Review 84

4.2 Hardy-Weinberg Principle 84

Calculating Gene Frequencies 84

Concept 4.2 Review 86

4.3 The Process of Natural Selection 87

Stabilizing Selection 87

Directional Selection 87

Disruptive Selection 88

Concept 4.3 Review 88

4.4 Evolution by Natural Selection 88

Heritability: Essential for Evolution 89

Directional Selection: Adaptation by Soapberry Bugs to
New Host Plants 90

Concept 4.4 Review 92

- 4.5 Change Due to Chance 92
 Evidence of Genetic Drift in Island Crickets 93
 Genetic Diversity and Butterfly Extinctions 95
Concept 4.5 Review 96
 Applications: Evolution and Agriculture 96
 Evolution of Herbicide Resistance in Weeds 97

Section II

ADAPTATIONS TO THE ENVIRONMENT

Chapter 5 Temperature Relations 101

- Concepts 101
 5.1 Microclimates 102
 Altitude 102
 Aspect 103
 Vegetation 103
 Color of the Ground 103
 Presence of Boulders and Burrows 104
 Aquatic Temperatures 104
Concept 5.1 Review 105
 5.2 Evolutionary Trade-Offs 105
 The Principle of Allocation 106
Concept 5.2 Review 106
 5.3 Temperature and Performance of Organisms 107
 Extreme Temperatures and Photosynthesis 108
 Temperature and Microbial Activity 109
Concept 5.3 Review 110
 5.4 Regulating Body Temperature 110
 Balancing Heat Gain Against Heat Loss 110
 Temperature Regulation by Plants 111
 Temperature Regulation by Ectothermic Animals 113
 Temperature Regulation by Endothermic Animals 115
 Temperature Regulation by Thermogenic Plants 119
Concept 5.4 Review 120
 5.5 Surviving Extreme Temperatures 120
 Inactivity 120
 Reducing Metabolic Rate 121
 Hibernation by a Tropical Species 121
Concept 5.5 Review 121
 Applications: Local Extinction of a Land Snail in an Urban Heat Island 123

Chapter 6 Water Relations 127

- Concepts 127
 6.1 Water Availability 129
 Water Content of Air 129
 Water Movement in Aquatic Environments 130
 Water Movement Between Soils and Plants 131
Concept 6.1 Review 132
 6.2 Water Regulation on Land 133
 Water Acquisition by Animals 133

- Water Acquisition by Plants 135
 Water Conservation by Plants and Animals 136
 Dissimilar Organisms with Similar Approaches to Desert Life 139
 Two Arthropods with Opposite Approaches to Desert Life 141

Concept 6.2 Review 143

- 6.3 Water and Salt Balance in Aquatic Environments 143
 Marine Fish and Invertebrates 143
 Freshwater Fish and Invertebrates 145
Concept 6.3 Review 146

Applications: Using Stable Isotopes to Study Water Uptake by Plants 146

- Stable Isotope Analysis 146
 Using Stable Isotopes to Identify Plant Water Sources 147

Chapter 7 Energy and Nutrient Relations 149

- Concepts 149
 7.1 Photosynthetic Autotrophs 150
 The Solar-Powered Biosphere 150
Concept 7.1 Review 154
 7.2 Chemosynthetic Autotrophs 154
Concept 7.2 Review 156
 7.3 Heterotrophs 156
 Chemical Composition and Nutrient Requirements 156
Concept 7.3 Review 162
 7.4 Energy Limitation 162
 Photon Flux and Photosynthetic Response Curves 162
 Food Density and Animal Functional Response 164
Concept 7.4 Review 165
 7.5 Optimal Foraging Theory 165
 Testing Optimal Foraging Theory 165
 Optimal Foraging by Plants 166
Concept 7.5 Review 168

Applications: Bioremediation—Using the Trophic Diversity of Bacteria to Solve Environmental Problems 168

- Leaking Underground Storage Tanks 168
 Cyanide and Nitrates in Mine Spoils 169

Chapter 8 Social Relations 172

- Concepts 172
 8.1 Mate Choice versus Predation 174
 Mate Choice and Sexual Selection in Guppies 175
Concept 8.1 Review 178
 8.2 Mate Choice and Resource Provisioning 178
Concept 8.2 Review 181
 8.3 Nonrandom Mating in a Plant Population 181
Concept 8.3 Review 183
 8.4 Sociality 183
 Cooperative Breeders 184
Concept 8.4 Review 188

8.5 Eusociality 189

Eusocial Species 189

Evolution of Eusociality 191

Concept 8.5 Review 192

Applications: Behavioral Ecology and Conservation 193

Tinbergen's Framework 193

Environmental Enrichment and Development of
Behavior 193

Section III

POPULATION ECOLOGY

Chapter 9 Population Distribution and
Abundance 196

Concepts 196

9.1 Distribution Limits 198

Kangaroo Distributions and Climate 198

A Tiger Beetle of Cold Climates 199

Distributions of Plants Along a Moisture-Temperature
Gradient 200Distributions of Barnacles Along an Intertidal Exposure
Gradient 201*Concept 9.1 Review* 202

9.2 Patterns on Small Scales 202

Scale, Distributions, and Mechanisms 203

Distributions of Tropical Bee Colonies 203

Distributions of Desert Shrubs 204

Concept 9.2 Review 206

9.3 Patterns on Large Scales 206

Bird Populations Across North America 206

Plant Distributions Along Moisture Gradients 207

Concept 9.3 Review 208

9.4 Organism Size and Population Density 209

Animal Size and Population Density 209

Plant Size and Population Density 209

Concept 9.4 Review 210

Applications: Rarity and Vulnerability to Extinction 211

Seven Forms of Rarity and One of Abundance 211

Chapter 10 Population Dynamics 215

Concepts 215

10.1 Dispersal 217

Dispersal of Expanding Populations 217

Range Changes in Response to Climate Change 218

Dispersal in Response to Changing Food Supply 219

Dispersal in Rivers and Streams 220

Concept 10.1 Review 221

10.2 Metapopulations 221

A Metapopulation of an Alpine Butterfly 222

Dispersal Within a Metapopulation of Lesser Kestrels 223

Concept 10.2 Review 224

10.3 Patterns of Survival 224

Estimating Patterns of Survival 224

High Survival Among the Young 224

Constant Rates of Survival 226

High Mortality Among the Young 227

Three Types of Survivorship Curves 227

Concept 10.3 Review 228

10.4 Age Distribution 228

Contrasting Tree Populations 228

A Dynamic Population in a Variable Climate 229

Concept 10.4 Review 230

10.5 Rates of Population Change 230

Estimating Rates for an Annual Plant 230

Estimating Rates When Generations Overlap 231

Concept 10.5 Review 233Applications: Changes in Species Distributions in Response to
Climate Warming 233

Chapter 11 Population Growth 237

Concepts 237

11.1 Geometric and Exponential Population Growth 238

Geometric Growth 238

Exponential Growth 239

Exponential Growth in Nature 240

Concept 11.1 Review 241

11.2 Logistic Population Growth 242

Concept 11.2 Review 244

11.3 Limits to Population Growth 244

Environment and Birth and Death Among Darwin's
Finches 245*Concept 11.3 Review* 247

Applications: The Human Population 247

Distribution and Abundance 248

Population Dynamics 249

Population Growth 250

Chapter 12 Life Histories 253

Concepts 253

12.1 Offspring Number versus Size 254

Egg Size and Number in Fish 255

Seed Size and Number in Plants 257

Seed Size and Seedling Performance 258

Concept 12.1 Review 260

12.2 Adult Survival and Reproductive Allocation 261

Life History Variation Among Species 261

Life History Variation within Species 263

Concept 12.2 Review 265

12.3 Life History Classification 265

r and *K* Selection 265

Plant Life Histories 266

Opportunistic, Equilibrium, and Periodic Life
Histories 267

- Lifetime Reproductive Effort and Relative Offspring Size:
Two Central Variables? 269
Concept 12.3 Review 271

Applications: Climate Change and Timing of Reproduction and Migration 271

- Altered Plant Phenology 271
Animal Phenology 272

Section IV

INTERACTIONS

Chapter 13 Species Interactions and Competition 275

- Concepts 275
Competitive Interactions Are Diverse 277
- 13.1 Intraspecific Competition 278
Intraspecific Competition Among Plants 278
Intraspecific Competition Among Planthoppers 279
Interference Competition Among Terrestrial Isopods 280
Concept 13.1 Review 280
- 13.2 Competitive Exclusion and Niches 280
The Feeding Niches of Darwin's Finches 281
Competition for Caterpillars 282
Concept 13.2 Review 283
- 13.3 Mathematical and Laboratory Models 283
Modeling Interspecific Competition 284
Laboratory Models of Competition 285
Concept 13.3 Review 287
- 13.4 Competition and Niches 287
Niches and Competition Among Plants 287
Niche Overlap and Competition Between Barnacles 288
Competition and the Habitat of a Salt Marsh Grass 288
Competition and the Niches of Small Rodents 289
Character Displacement 291
Evidence for Competition in Nature 293
Concept 13.4 Review 293
- Applications: Competition Between Native and Invasive Species 294

Chapter 14 Exploitative Interactions: Predation, Herbivory, Parasitism, and Disease 297

- Concepts 297
- 14.1 Exploitation and Abundance 298
A Herbivorous Stream Insect and Its Algal Food 298
Bats, Birds, and Herbivory in a Tropical Forest 299
A Pathogenic Parasite, a Predator, and Its Prey 301
Concept 14.1 Review 302

- 14.2 Dynamics 302
Cycles of Abundance in Snowshoe Hares and Their Predators 302
Experimental Test of Food and Predation Impacts 304
Population Cycles in Mathematical and Laboratory Models 305
Concept 14.2 Review 308
- 14.3 Refuges 308
Refuges and Host Persistence in Laboratory and Mathematical Models 308
Exploited Organisms and Their Wide Variety of "Refuges" 310
Concept 14.3 Review 312
- 14.4 Ratio-Dependent Models of Functional Response 312
Alternative Model for Trophic Ecology 312
Evidence for Ratio-Dependent Predation 313
Concept 14.4 Review 315
- 14.5 Complex Interactions 315
Parasites and Pathogens That Manipulate Host Behavior 315
The Entangling of Exploitation with Competition 318
Concept 14.5 Review 319
- Applications: The Value of Pest Control by Bats: A Case Study 319

Chapter 15 Mutualism 323

- Concepts 323
- 15.1 Plant Mutualisms 324
Plant Performance and Mycorrhizal Fungi 325
Ants and Swollen Thorn Acacias 328
A Temperate Plant Protection Mutualism 332
Concept 15.1 Review 333
- 15.2 Coral Mutualisms 333
Zooxanthellae and Corals 334
A Coral Protection Mutualism 334
Concept 15.2 Review 336
- 15.3 Evolution of Mutualism 336
Facultative Ant-Plant Protection Mutualisms 338
Concept 15.3 Review 339
- Applications: Mutualism and Humans 339
Guiding Behavior 339

Section V

COMMUNITIES AND ECOSYSTEMS

Chapter 16 Species Abundance and Diversity 343

- Concepts 343
- 16.1 Species Abundance 345
The Lognormal Distribution 345
Concept 16.1 Review 346

- 16.2 Species Diversity 346
 A Quantitative Index of Species Diversity 346
 Rank-Abundance Curves 347
Concept 16.2 Review 348
- 16.3 Environmental Complexity 348
 Forest Complexity and Bird Species Diversity 348
 Niches, Heterogeneity, and the Diversity of Algae and Plants 349
 The Niches of Algae and Terrestrial Plants 350
 Complexity in Plant Environments 351
 Soil and Topographic Heterogeneity and the Diversity of Tropical Forest Trees 351
 Nutrient Enrichment Can Reduce Environmental Complexity 352
 Nitrogen Enrichment and Ectomycorrhizal Fungus Diversity 353
Concept 16.3 Review 354
- 16.4 Disturbance and Diversity 354
 The Nature and Sources of Disturbance 354
 The Intermediate Disturbance Hypothesis 354
 Disturbance and Diversity in the Intertidal Zone 355
 Disturbance and Diversity in Temperate Grasslands 355
Concept 16.4 Review 357
- Applications: Disturbance by Humans 357
 Urban Diversity 358

Chapter 17 Species Interactions and Community Structure 362

- Concepts 362
- 17.1 Community Webs 364
 Detailed Food Webs Reveal Great Complexity 364
 Strong Interactions and Food Web Structure 364
Concept 17.1 Review 365
- 17.2 Indirect Interactions 366
 Indirect Commensalism 366
 Apparent Competition 366
Concept 17.2 Review 368
- 17.3 Keystone Species 368
 Food Web Structure and Species Diversity 369
 Experimental Removal of Sea Stars 370
 Snail Effects on Algal Diversity 370
 Fish as Keystone Species in River Food Webs 373
Concept 17.3 Review 375
- 17.4 Mutualistic Keystones 375
 A Cleaner Fish as a Keystone Species 375
 Seed Dispersal Mutualists as Keystone Species 376
Concept 17.4 Review 377
- Applications: Human Modification of Food Webs 377
 The Empty Forest: Hunters and Tropical Rain Forest Animal Communities 377
 Ants and Agriculture: Keystone Predators for Pest Control 378

Chapter 18 Primary and Secondary Production 381

- Concepts 381
- 18.1 Patterns of Terrestrial Primary Production 383
 Actual Evapotranspiration and Terrestrial Primary Production 383
 Soil Fertility and Terrestrial Primary Production 384
Concept 18.1 Review 385
- 18.2 Patterns of Aquatic Primary Production 385
 Patterns and Models 385
 Whole-Lake Experiments on Primary Production 386
 Global Patterns of Marine Primary Production 386
Concept 18.2 Review 387
- 18.3 Primary Producer Diversity 388
 Terrestrial Plant Diversity and Primary Production 388
 Algal Diversity and Aquatic Primary Production 389
Concept 18.3 Review 389
- 18.4 Consumer Influences 390
 Piscivores, Planktivores, and Lake Primary Production 390
 Grazing by Large Mammals and Primary Production on the Serengeti 392
Concept 18.4 Review 394
- 18.5 Secondary Production 394
 A Trophic Dynamic View of Ecosystems 395
 Linking Primary Production and Secondary Production 396
Concept 18.5 Review 397
- Applications: Using Stable Isotope Analysis to Study Feeding Habits 397
 Using Stable Isotopes to Identify Sources of Energy in a Salt Marsh 398

Chapter 19 Nutrient Cycling and Retention 401

- Concepts 401
- 19.1 Nutrient Cycles 402
 The Phosphorus Cycle 403
 The Nitrogen Cycle 404
 The Carbon Cycle 405
Concept 19.1 Review 406
- 19.2 Rates of Decomposition 406
 Decomposition in Two Mediterranean Woodland Ecosystems 406
 Decomposition in Two Temperate Forest Ecosystems 407
 Decomposition in Aquatic Ecosystems 409
Concept 19.2 Review 410
- 19.3 Organisms and Nutrients 410
 Nutrient Cycling in Streams and Lakes 410
 Animals and Nutrient Cycling in Terrestrial Ecosystems 413
 Plants and the Nutrient Dynamics of Ecosystems 414
Concept 19.3 Review 415

- 19.4 Disturbance and Nutrients 415
 - Disturbance and Nutrient Loss from Forests 415
 - Flooding and Nutrient Export by Streams 416
 - Concept 19.4 Review 417

Applications: Altering Aquatic and Terrestrial
Ecosystems 417

Chapter 20 Succession and Stability 421

Concepts 421

- 20.1 Community Changes During Succession 423
 - Primary Succession at Glacier Bay 423
 - Secondary Succession in Temperate Forests 424
 - Succession in Rocky Intertidal Communities 425
 - Succession in Stream Communities 426
 - Concept 20.1 Review 427
- 20.2 Ecosystem Changes During Succession 427
 - Ecosystem Changes at Glacier Bay 427
 - Four Million Years of Ecosystem Change 427
 - Succession and Stream Ecosystem Properties 429
 - Concept 20.2 Review 431
- 20.3 Mechanisms of Succession 431
 - Facilitation 431
 - Tolerance 431
 - Inhibition 431
 - Successional Mechanisms in the Rocky Intertidal Zone 431
 - Successional Mechanisms in Forests 434
 - Concept 20.3 Review 435
- 20.4 Community and Ecosystem Stability 435
 - Lessons from the Park Grass Experiment 435
 - Replicate Disturbances and Desert Stream Stability 437
 - Concept 20.4 Review 438

Applications: Ecological Succession Informing Ecological
Restoration 438

Applying Succession Concepts to Restoration 438

Section VI LARGE-SCALE ECOLOGY

Chapter 21 Landscape Ecology 443

Concepts 443

- 21.1 Landscape Structure 445
 - The Structure of Six Landscapes in Ohio 445
 - The Fractal Geometry of Landscapes 447
 - Concept 21.1 Review 448
- 21.2 Landscape Processes 448
 - Landscape Structure and the Dispersal of Mammals 449
 - Habitat Patch Size and Isolation and the Density of Butterfly Populations 450
 - Habitat Corridors and Movement of Organisms 451
 - Landscape Position and Lake Chemistry 452
 - Concept 21.2 Review 453

- 21.3 Origins of Landscape Structure and Change 453
 - Geological Processes, Climate, and Landscape Structure 454
 - Organisms and Landscape Structure 456
 - Fire and the Structure of a Mediterranean Landscape 460
 - Concept 21.3 Review 461

Applications: Landscape Approaches to Mitigating Urban Heat
Islands 461

Chapter 22 Geographic Ecology 466

Concepts 466

- 22.1 Area, Isolation, and Species Richness 468
 - Island Area and Species Richness 468
 - Island Isolation and Species Richness 470
 - Concept 22.1 Review 471
- 22.2 The Equilibrium Model of Island Biogeography 471
 - Species Turnover on Islands 472
 - Experimental Island Biogeography 473
 - Colonization of New Islands by Plants 474
 - Manipulating Island Area 475
 - Island Biogeography Update 476
 - Concept 22.2 Review 476
- 22.3 Latitudinal Gradients in Species Richness 476
 - Latitudinal Gradient Hypotheses 476
 - Area and Latitudinal Gradients in Species Richness 478
 - Continental Area and Species Richness 479
 - Concept 22.3 Review 480
- 22.4 Historical and Regional Influences 480
 - Exceptional Patterns of Diversity 480
 - Historical and Regional Explanations 481
 - Concept 22.4 Review 482

Applications: Global Positioning Systems, Remote Sensing, and
Geographic Information Systems 483

Global Positioning Systems 483

Remote Sensing 483

Geographic Information Systems 485

Chapter 23 Global Ecology 488

Concepts 488

The Atmospheric Envelope and the Greenhouse
Earth 489

- 23.1 A Global System 491
 - The Historical Thread 491
 - El Niño and La Niña 492
 - El Niño Southern Oscillation and Marine Populations 493
 - El Niño and the Great Salt Lake 495
 - El Niño and Terrestrial Populations in Australia 496
 - Concept 23.1 Review 497
- 23.2 Human Activity and the Global Nitrogen Cycle 497
 - Concept 23.2 Review 498
- 23.3 Changes in Land Cover 498
 - Tropical Deforestation 498
 - Concept 23.3 Review 502

23.4 Human Influence on Atmospheric Composition	502	12: A Statistical Test for Distribution Pattern	523
Depletion and Recovery of the Ozone Layer	505	13: Field Experiments	524
Concept 23.4 Review	506	14: Standard Error of the Mean	525
Applications: Impacts of Global Climate Change	506	15: Confidence Intervals	527
Shifts in Biodiversity and Widespread Extinction of Species	506	16: Estimating the Number of Species in Communities	528
Human Impacts of Climate Change	507	17: Using Confidence Intervals to Compare Populations	529
Appendix A Investigating the Evidence		18: Comparing Two Populations with the <i>t</i> -Test	530
1: The Scientific Method—Questions and Hypotheses	511	19: Assumptions for Statistical Tests	531
2: Determining the Sample Mean	512	20: Variation Around the Median	532
3: Determining the Sample Median	513	21: Comparison of Two Samples Using a Rank Sum Test	534
4: Variation in Data	514	22: Sample Size Revisited	535
5: Laboratory Experiments	515	23: Discovering What's Been Discovered	536
6: Sample Size	516	Appendix B Statistical Tables	538
7: Scatter Plots and the Relationship Between Variables	517	Glossary	542
8: Estimating Heritability Using Regression Analysis	518	References	552
9: Clumped, Random, and Regular Distributions	519	Index	564
10: Hypotheses and Statistical Significance	520		
11: Frequency of Alternative Phenotypes in a Population	521		