

# Contents

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

Concepts 1

### 1.1 Overview of Ecology 2

Concept 1.1 Review 3

## Section I

### NATURAL HISTORY AND EVOLUTION

## Chapter 2 Life on Land 4

Concepts 4

Terrestrial Biomes 5

### 2.1 Large-Scale Patterns of Climatic Variation 6

Temperature, Atmospheric Circulation, and Precipitation 6

Climate Diagrams 8

Concept 2.1 Review 9

### 2.2 Soil: The Foundation of Terrestrial Biomes 9

Concept 2.2 Review 11

### 2.3 Natural History and Geography of Biomes 12

Tropical Rain Forest 12

Tropical Dry Forest 13

Tropical Savanna 14

Desert 17

Mediterranean Woodland and Shrubland 18

Temperate Grassland 21

Temperate Forest 22

Boreal Forest 24

Tundra 26

Mountains: Islands in the Sky 28

Concept 2.3 Review 29

## Chapter 3 Life in Water 31

Concepts 31

### 3.1 The Hydrologic Cycle 32

Concept 3.1 Review 32

### 3.2 The Natural History of Aquatic Environments 32

The Oceans 33

Life in Shallow Marine Waters: Kelp Forests and Coral Gardens 37

Marine Shores: Life Between High and Low Tides 40

Transitional Environments: Estuaries, Salt Marshes, Mangrove Forests, and Freshwater Wetlands 42

Rivers and Streams: Life Blood and Pulse of the Land 46

Lakes: Small Seas 50

Concept 3.2 Review 56

Applications: Biological Integrity—Assessing the Health of Aquatic Systems 56

Number of Species and Species Composition 56

Trophic Composition 56

Fish Abundance and Condition 56

A Test 56

## Chapter 4 Population Genetics and Natural Selection 58

Concepts 58

### 4.1 Variation Within Populations 60

Variation in a Widely Distributed Plant 61

Variation in Alpine Fish Populations 61

Concept 4.1 Review 63

### 4.2 Hardy-Weinberg Principle 64

Calculating Gene Frequencies 64

Concept 4.2 Review 66

### 4.3 The Process of Natural Selection 66

Stabilizing Selection 66

Directional Selection 67

Disruptive Selection 67

Concept 4.3 Review 68

### 4.4 Evolution by Natural Selection 68

Heritability: Essential for Evolution 68

Directional Selection: Adaptation by Soapberry Bugs to New Host Plants 69

Concept 4.4 Review 72

### 4.5 Change Due to Chance 72

Evidence of Genetic Drift in Chihuahua Spruce 72

Genetic Variation in Island Populations 73

Genetic Diversity and Butterfly Extinctions 74

Concept 4.5 Review 74

## Section II

### ADAPTATIONS TO THE ENVIRONMENT

## Chapter 5 Temperature Relations 75

Concepts 75

### 5.1 Microclimates 76

Altitude 76

|                                  |    |
|----------------------------------|----|
| Aspect                           | 77 |
| Vegetation                       | 77 |
| Color of the Ground              | 77 |
| Presence of Boulders and Burrows | 78 |
| Aquatic Temperatures             | 78 |
| Concept 5.1 Review               | 79 |

|                                                      |    |
|------------------------------------------------------|----|
| 5.2 Evolutionary Trade-Offs                          | 79 |
| The Principle of Allocation                          | 80 |
| Concept 5.2 Review                                   | 80 |
| 5.3 Temperature and Performance of Organisms         | 81 |
| Investigating the Evidence 1: Laboratory Experiments | 82 |
| Extreme Temperatures and Photosynthesis              | 83 |
| Temperature and Microbial Activity                   | 84 |
| Concept 5.3 Review                                   | 85 |
| 5.4 Regulating Body Temperature                      | 85 |
| Balancing Heat Gain against Heat Loss                | 85 |
| Temperature Regulation by Plants                     | 86 |
| Temperature Regulation by Ectothermic Animals        | 88 |
| Temperature Regulation by Endothermic Animals        | 90 |
| Temperature Regulation by Thermogenic Plants         | 94 |
| Concept 5.4 Review                                   | 95 |
| 5.5 Surviving Extreme Temperatures                   | 95 |
| Inactivity                                           | 95 |
| Reducing Metabolic Rate                              | 96 |
| Hibernation by a Tropical Species                    | 96 |
| Concept 5.5 Review                                   | 97 |

## Chapter 6 Water Relations 98

Concepts 98

|                                                             |     |
|-------------------------------------------------------------|-----|
| 6.1 Water Availability                                      | 100 |
| Water Content of Air                                        | 100 |
| Water Movement in Aquatic Environments                      | 101 |
| Water Movement between Soils and Plants                     | 102 |
| Concept 6.1 Review                                          | 103 |
| 6.2 Water Regulation on Land                                | 104 |
| Water Acquisition by Animals                                | 104 |
| Water Acquisition by Plants                                 | 106 |
| Water Conservation by Plants and Animals                    | 107 |
| Dissimilar Organisms with Similar Approaches to Desert Life | 110 |
| Two Arthropods with Opposite Approaches to Desert Life      | 112 |
| Concept 6.2 Review                                          | 114 |
| 6.3 Water and Salt Balance in Aquatic Environments          | 114 |
| Marine Fish and Invertebrates                               | 114 |
| Freshwater Fish and Invertebrates                           | 115 |
| Concept 6.3 Review                                          | 117 |

## Chapter 7 Energy and Nutrient Relations 118

Concepts 118

|                                                |     |
|------------------------------------------------|-----|
| 7.1 Photosynthetic Autotrophs                  | 120 |
| The Solar-Powered Biosphere                    | 120 |
| Concept 7.1 Review                             | 124 |
| 7.2 Chemosynthetic Autotrophs                  | 124 |
| Concept 7.2 Review                             | 124 |
| 7.3 Heterotrophs                               | 124 |
| Chemical Composition and Nutrient Requirements | 125 |
| Concept 7.3 Review                             | 132 |
| 7.4 Energy Limitation                          | 132 |
| Photon Flux and Photosynthetic Response Curves | 132 |
| Food Density and Animal Functional Response    | 133 |
| Concept 7.4 Review                             | 134 |
| 7.5 Optimal Foraging Theory                    | 134 |
| Testing Optimal Foraging Theory                | 135 |
| Optimal Foraging by Plants                     | 136 |
| Concept 7.5 Review                             | 137 |

## Chapter 8 Social Relations 138

Concepts 138

|                                                                                 |     |
|---------------------------------------------------------------------------------|-----|
| 8.1 Mate Choice versus Predation                                                | 140 |
| Mate Choice and Sexual Selection in Guppies                                     | 141 |
| Concept 8.1 Review                                                              | 144 |
| 8.2 Mate Choice and Resource Provisioning                                       | 144 |
| Concept 8.2 Review                                                              | 147 |
| 8.3 Nonrandom Mating in a Plant Population                                      | 147 |
| Concept 8.3 Review                                                              | 149 |
| 8.4 Sociality                                                                   | 149 |
| Cooperative Breeders                                                            | 150 |
| Investigating the Evidence 2: Estimating Heritability Using Regression Analysis | 153 |
| Concept 8.4 Review                                                              | 156 |
| 8.5 Eusociality                                                                 | 156 |
| Eusocial Species                                                                | 156 |
| Evolution of Eusociality                                                        | 158 |
| Concept 8.5 Review                                                              | 160 |

## Section III

### POPULATION ECOLOGY

## Chapter 9 Population Distribution and Abundance 161

Concepts 161

|                                                                  |     |
|------------------------------------------------------------------|-----|
| 9.1 Distribution Limits                                          | 163 |
| Kangaroo Distributions and Climate                               | 163 |
| A Tiger Beetle of Cold Climates                                  | 164 |
| Distributions of Plants Along a Moisture-Temperature Gradient    | 165 |
| Distributions of Barnacles Along an Intertidal Exposure Gradient | 166 |

*Concept 9.1 Review* 167

## 9.2 Patterns on Small Scales 167

Scale, Distributions, and Mechanisms 168

Distributions of Tropical Bee Colonies 168

Distributions of Desert Shrubs 169

*Concept 9.2 Review* 171

## 9.3 Patterns on Large Scales 171

Bird Populations Across North America 171

Investigating the Evidence 3: Clumped, Random,  
and Regular Distributions 172

Plant Distributions Along Moisture Gradients 173

*Concept 9.3 Review* 174

## 9.4 Organism Size and Population Density 175

Animal Size and Population Density 175

Plant Size and Population Density 175

*Concept 9.4 Review* 176Applications: Rarity and Vulnerability  
to Extinction 177

Seven Forms of Rarity and One of Abundance 177

**Chapter 10 Population Dynamics 180**

Concepts 180

## 10.1 Dispersal 182

Dispersal of Expanding Populations 182

Range Changes in Response to Climate Change 183

Dispersal in Response to Changing Food Supply 184

Dispersal in Rivers and Streams 185

*Concept 10.1 Review* 186

## 10.2 Metapopulations 186

A Metapopulation of an Alpine Butterfly 187

Dispersal Within a Metapopulation of Lesser Kestrels 188

*Concept 10.2 Review* 189

## 10.3 Patterns of Survival 189

Estimating Patterns of Survival 189

High Survival Among the Young 189

Constant Rates of Survival 191

High Mortality Among the Young 192

Three Types of Survivorship Curves 192

*Concept 10.3 Review* 193

## 10.4 Age Distribution 193

Contrasting Tree Populations 193

A Dynamic Population in a Variable Climate 194

*Concept 10.4 Review* 195

## 10.5 Rates of Population Change 195

Estimating Rates for an Annual Plant 195

Estimating Rates When Generations Overlap 196

*Concept 10.5 Review* 198**Chapter 11 Population Growth 199**

Concepts 199

11.1 Geometric and Exponential Population  
Growth 200

Geometric Growth 200

Exponential Growth 201

Exponential Growth in Nature 202

*Concept 11.1 Review* 203

## 11.2 Logistic Population Growth 204

*Concept 11.2 Review* 206

## 11.3 Limits to Population Growth 206

Environment and Birth and Death Among Darwin's  
Finches 207*Concept 11.3 Review* 209**Chapter 12 Life Histories 210**

Concepts 210

## 12.1 Offspring Number Versus Size 211

Egg Size and Number in Fish 212

Seed Size and Number in Plants 214

Seed Size and Seedling Performance 215

*Concept 12.1 Review* 217

## 12.2 Adult Survival and Reproductive Allocation 218

Life History Variation Among Species 218

Life History Variation Within Species 219

*Concept 12.2 Review* 222

## 12.3 Life History Classification 222

*r* and *K* Selection 222

Plant Life Histories 223

Investigating the Evidence 4: A Statistical Test  
for Distribution Pattern 224Opportunistic, Equilibrium, and Periodic Life  
Histories 226Lifetime Reproductive Effort and Relative Offspring Size:  
Two Central Variables? 227*Concept 12.3 Review* 228**Section IV  
INTERACTIONS****Chapter 13 Competition 230**

Concepts 230

- 13.1 Intraspecific Competition 232  
 Intraspecific Competition Among Plants 232  
 Intraspecific Competition Among Planthoppers 233  
 Interference Competition Among Terrestrial Isopods 233  
*Concept 13.1 Review* 234
- 13.2 Competitive Exclusion and Niches 234  
 The Feeding Niches of Darwin's Finches 234  
 The Habitat Niche of a Salt Marsh Grass 236  
*Concept 13.2 Review* 237
- 13.3 Mathematical and Laboratory Models 237  
 Modeling Interspecific Competition 237  
 Laboratory Models of Competition 239  
*Concept 13.3 Review* 240
- 13.4 Competition and Niches 240  
 Niches and Competition Among Plants 241  
 Niche Overlap and Competition between Barnacles 241  
 Competition and the Habitat of a Salt Marsh Grass 243  
 Competition and the Niches of Small Rodents 243  
 Character Displacement 244  
 Evidence for Competition in Nature 246  
 Investigating the Evidence 5: Field Experiments 247  
*Concept 13.4 Review* 248

## Chapter 14 Exploitative Interactions: Predation, Herbivory, Parasitism, and Disease 249

- Concepts 249
- 14.1 Complex Interactions 250  
 Parasites and Pathogens that Manipulate Host Behavior 250  
 The Entangling of Exploitation with Competition 253  
*Concept 14.1 Review* 254
- 14.2 Exploitation and Abundance 254  
 A Herbivorous Stream Insect and Its Algal Food 254  
 Bats, Birds, and Herbivory in a Tropical Forest 255  
 A Pathogenic Parasite, a Predator, and Its Prey 257  
*Concept 14.2 Review* 258
- 14.3 Dynamics 258  
 Cycles of Abundance in Snowshoe Hares and Their Predators 258  
 Experimental Test of Food and Predation Impacts 260  
 Population Cycles in Mathematical and Laboratory Models 261  
*Concept 14.3 Review* 264
- 14.4 Refuges 264  
 Refuges and Host Persistence in Laboratory and Mathematical Models 264  
 Exploited Organisms and Their Wide Variety of "Refuges" 266  
*Concept 14.4 Review* 268
- 14.5 Ratio-Dependent Models of Functional Response 268  
 Alternative Model for Trophic Ecology 268

- Evidence for Ratio-Dependent Predation 269  
*Concept 14.5 Review* 271

## Chapter 15 Mutualism 272

- Concepts 272
- 15.1 Plant Mutualisms 273  
 Plant Performance and Mycorrhizal Fungi 274  
 Ants and Swollen Thorn Acacias 277  
 A Temperate Plant Protection Mutualism 281  
*Concept 15.1 Review* 282
- 15.2 Coral Mutualisms 282  
 Zooxanthellae and Corals 283  
 A Coral Protection Mutualism 283  
*Concept 15.2 Review* 285
- 15.3 Evolution of Mutualism 285  
 Facultative Ant-Plant Protection Mutualisms 287  
*Concept 15.3 Review* 288

## Section V

### COMMUNITIES AND ECOSYSTEMS

## Chapter 16 Species Abundance and Diversity 289

- Concepts 289
- 16.1 Species Abundance 291  
 The Lognormal Distribution 291  
*Concept 16.1 Review* 292
- 16.2 Species Diversity 292  
 A Quantitative Index of Species Diversity 292  
 Rank-Abundance Curves 293  
*Concept 16.2 Review* 294
- 16.3 Environmental Complexity 294  
 Forest Complexity and Bird Species Diversity 295  
 Investigating the Evidence 6: Estimating the Number of Species in Communities 296  
 Niches, Heterogeneity, and the Diversity of Algae and Plants 297  
 The Niches of Algae and Terrestrial Plants 297  
 Complexity in Plant Environments 298  
 Soil and Topographic Heterogeneity and the Diversity of Tropical Forest Trees 298  
 Algal and Plant Species Diversity and Increased Nutrient Availability 300  
 Nitrogen Enrichment and Ectomycorrhizal Fungus Diversity 300  
*Concept 16.3 Review* 301
- 16.4 Disturbance and Diversity 301  
 The Nature and Sources of Disturbance 301  
 The Intermediate Disturbance Hypothesis 301  
 Disturbance and Diversity in the Intertidal Zone 302

|                                                   |     |
|---------------------------------------------------|-----|
| Disturbance and Diversity in Temperate Grasslands | 302 |
| <i>Concept 16.4 Review</i>                        | 304 |

## Chapter 17 Species Interactions and Community Structure 305

|                                               |     |
|-----------------------------------------------|-----|
| Concepts                                      | 305 |
| 17.1 Community Webs                           | 307 |
| Detailed Food Webs Reveal Great Complexity    | 307 |
| Strong Interactions and Food Web Structure    | 307 |
| <i>Concept 17.1 Review</i>                    | 308 |
| 17.2 Indirect Interactions                    | 309 |
| Indirect Commensalism                         | 309 |
| Apparent Competition                          | 309 |
| <i>Concept 17.2 Review</i>                    | 311 |
| 17.3 Keystone Species                         | 311 |
| Food Web Structure and Species Diversity      | 312 |
| Experimental Removal of Sea Stars             | 313 |
| Snail Effects on Algal Diversity              | 314 |
| Fish as Keystone Species in River Food Webs   | 316 |
| <i>Concept 17.3 Review</i>                    | 318 |
| 17.4 Mutualistic Keystones                    | 318 |
| A Cleaner Fish as a Keystone Species          | 318 |
| Seed Dispersal Mutualists as Keystone Species | 319 |
| <i>Concept 17.4 Review</i>                    | 320 |

## Chapter 18 Primary and Secondary Production 321

|                                                                  |     |
|------------------------------------------------------------------|-----|
| Concepts                                                         | 321 |
| 18.1 Patterns of Terrestrial Primary Production                  | 323 |
| Actual Evapotranspiration and Terrestrial Primary Production     | 323 |
| Soil Fertility and Terrestrial Primary Production                | 324 |
| <i>Concept 18.1 Review</i>                                       | 325 |
| 18.2 Patterns of Aquatic Primary Production                      | 325 |
| Patterns and Models                                              | 325 |
| Whole Lake Experiments on Primary Production                     | 326 |
| Global Patterns of Marine Primary Production                     | 326 |
| <i>Concept 18.2 Review</i>                                       | 327 |
| 18.3 Primary Producer Diversity                                  | 328 |
| Terrestrial Plant Diversity and Primary Production               | 328 |
| Algal Diversity and Aquatic Primary Production                   | 329 |
| <i>Concept 18.3 Review</i>                                       | 329 |
| 18.4 Consumer Influences                                         | 330 |
| Piscivores, Planktivores, and Lake Primary Production            | 330 |
| Grazing by Large Mammals and Primary Production on the Serengeti | 332 |
| <i>Concept 18.4 Review</i>                                       | 334 |
| 18.5 Secondary Production                                        | 334 |

|                                                     |     |
|-----------------------------------------------------|-----|
| A Trophic Dynamic View of Ecosystems                | 335 |
| Linking Primary Production and Secondary Production | 336 |
| <i>Concept 18.5 Review</i>                          | 337 |

## Chapter 19 Nutrient Cycling and Retention 338

|                                                           |     |
|-----------------------------------------------------------|-----|
| Concepts                                                  | 338 |
| 19.1 Nutrient Cycles                                      | 339 |
| The Phosphorus Cycle                                      | 340 |
| The Nitrogen Cycle                                        | 341 |
| The Carbon Cycle                                          | 342 |
| <i>Concept 19.1 Review</i>                                | 343 |
| 19.2 Rates of Decomposition                               | 343 |
| Decomposition in Two Mediterranean Woodland Ecosystems    | 343 |
| Decomposition in Two Temperate Forest Ecosystems          | 344 |
| Decomposition in Aquatic Ecosystems                       | 346 |
| <i>Concept 19.2 Review</i>                                | 347 |
| 19.3 Organisms and Nutrients                              | 347 |
| Nutrient Cycling in Streams and Lakes                     | 347 |
| Animals and Nutrient Cycling in Terrestrial Ecosystems    | 349 |
| Plants and the Nutrient Dynamics of Ecosystems            | 351 |
| <i>Concept 19.3 Review</i>                                | 352 |
| 19.4 Disturbance and Nutrients                            | 352 |
| Disturbance and Nutrient Loss from Forests                | 352 |
| Flooding and Nutrient Export by Streams                   | 353 |
| <i>Concept 19.4 Review</i>                                | 354 |
| Applications: Altering Aquatic and Terrestrial Ecosystems | 355 |

## Chapter 20 Succession and Stability 357

|                                                      |     |
|------------------------------------------------------|-----|
| Concepts                                             | 357 |
| 20.1 Community Changes During Succession             | 359 |
| Primary Succession at Glacier Bay                    | 359 |
| Secondary Succession in Temperate Forests            | 360 |
| Succession in Rocky Intertidal Communities           | 361 |
| Succession in Stream Communities                     | 361 |
| <i>Concept 20.1 Review</i>                           | 362 |
| 20.2 Ecosystem Changes During Succession             | 362 |
| Ecosystem Changes at Glacier Bay                     | 363 |
| Four Million Years of Ecosystem Change               | 363 |
| Recovery of Nutrient Retention Following Disturbance | 365 |
| Succession and Stream Ecosystem Properties           | 367 |
| <i>Concept 20.2 Review</i>                           | 368 |
| 20.3 Mechanisms of Succession                        | 368 |
| Facilitation                                         | 368 |
| Tolerance                                            | 368 |

- Inhibition 368
- Successional Mechanisms in the Rocky Intertidal Zone 369
- Successional Mechanisms in Forests 371
- Concept 20.3 Review* 372
- 20.4 Community and Ecosystem Stability 372
- Lessons from the Park Grass Experiment 373
- Replicate Disturbances and Desert Stream Stability 373
- Concept 20.4 Review* 375
- Investigating the Evidence 7: Variation Around the Median 376
- Applications: Ecological Succession Informing Ecological Restoration 376
- Applying Succession Concepts to Restoration 377

## Section VI

### LARGE-SCALE ECOLOGY

#### Chapter 21 Landscape Ecology 381

- Concepts 381
- 21.1 Landscape Structure 383
  - The Structure of Six Landscapes in Ohio 383
  - The Fractal Geometry of Landscapes 385
  - Concept 21.1 Review* 386
- 21.2 Landscape Processes 386
  - Landscape Structure and the Dispersal of Mammals 387
  - Habitat Patch Size and Isolation and the Density of Butterfly Populations 388
  - Habitat Corridors and Movement of Organisms 389
  - Landscape Position and Lake Chemistry 390
  - Investigating the Evidence 8: Comparison of Two Samples Using a Rank Sum Test 391
  - Concept 21.2 Review* 392
- 21.3 Origins of Landscape Structure and Change 392
  - Geological Processes, Climate, and Landscape Structure 393
  - Organisms and Landscape Structure 395
  - Fire and the Structure of a Mediterranean Landscape 399
  - Concept 21.3 Review* 400

#### Chapter 22 Geographic Ecology 401

- Concepts 401
- 22.1 Area, Isolation, and Species Richness 403
  - Island Area and Species Richness 403

- Island Isolation and Species Richness 405
- Concept 22.1 Review* 406
- 22.2 The Equilibrium Model of Island Biogeography 406
  - Species Turnover on Islands 407
  - Experimental Island Biogeography 408
  - Colonization of New Islands by Plants 409
  - Manipulating Island Area 410
  - Island Biogeography Update 411
  - Concept 22.2 Review* 411
- 22.3 Latitudinal Gradients in Species Richness 411
  - Latitudinal Gradient Hypotheses 411
  - Area and Latitudinal Gradients in Species Richness 413
  - Continental Area and Species Richness 414
  - Concept 22.3 Review* 415
- 22.4 Historical and Regional Influences 415
  - Exceptional Patterns of Diversity 415
  - Investigating the Evidence 9: Sample Size Revisited 416
  - Historical and Regional Explanations 417
  - Concept 22.4 Review* 418

#### Chapter 23 Global Ecology 419

- Concepts 419
- The Atmospheric Envelope and the Greenhouse Earth 420
- 23.1 A Global System 421
  - The Historical Thread 422
  - El Niño and La Niña 423
  - Concept 23.1 Review* 424
- 23.2 Human Activity and the Global Nitrogen Cycle 424
  - Concept 23.2 Review* 425
- 23.3 Changes in Land Cover 425
  - Tropical Deforestation 425
  - Concept 23.3 Review* 429
- 23.4 Human Influence on Atmospheric Composition 429
  - Depletion and Recovery of the Ozone Layer 431
  - Concept 23.4 Review* 432
- Applications: Impacts of Global Climate Change 433
  - Shifts in Biodiversity and Widespread Extinction of Species 433
  - Human Impacts of Climate Change 434

Glossary 435

Photo Credits 445