

Contents

Preface xiii

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 3

Forest Canopy Research: A Physical and Scientific Frontier 6

Climatic and Ecological Change: Past and Future 6

Concept 1.2 Review 8

Investigating the Evidence 1: The Scientific Method—
Questions and Hypotheses 9

Section I

NATURAL HISTORY AND EVOLUTION

2 Life on Land 11

Concepts 11

Terrestrial Biomes 12

2.1 Large-Scale Patterns of Climatic Variation 13

Temperature, Atmospheric Circulation,
and Precipitation 13

Climate Diagrams 15

Concept 2.1 Review 16

2.2 Soil: The Foundation of Terrestrial Biomes 16

Investigating the Evidence 2: Determining
the Sample Mean 18

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

Mediterranean Woodland and Shrubland 27

Temperate Grassland 30

Temperate Forest 31

Boreal Forest 34

Tundra 35

Mountains: Islands in the Sky 38

Concept 2.3 Review 41

Applications: Climatic Variation and the Palmer Drought
Severity Index 41

3 Life in Water 45

Concepts 45

3.1 The Hydrologic Cycle 46

Concept 3.1 Review 46

3.2 The Natural History of Aquatic Environments 46

The Oceans 46

Life in Shallow Marine Waters: Kelp Forests
and Coral Gardens 51

Investigating the Evidence 3: Determining
the Sample Median 52

Marine Shores: Life between
High and Low Tides 55

Estuaries, Salt Marshes, and Mangrove
Forests 58

Rivers and Streams: Life Blood and Pulse
of the Land 62

Lakes: Small Seas 66

Concept 3.2 Review 72

Applications: Biological Integrity—Assessing the Health
of Aquatic Systems 72

Number of Species and Species Composition 72

Trophic Composition 73

Fish Abundance and Condition 73

A Test 73

4 Population Genetics and Natural Selection 77

Concepts 77

4.1 Variation Within Populations 79

Variation in a Widely Distributed Plant 79

Variation in Alpine Fish Populations 80

Concept 4.1 Review 82

4.2 Hardy-Weinberg 83

Calculating Gene Frequencies 83

Concept 4.2 Review 85

4.3 The Process of Natural Selection 85

Stabilizing Selection 85

Directional Selection 85

Disruptive Selection 86

Concept 4.3 Review 87

4.4 Evolution by Natural Selection 87

Heritability: Essential for Evolution 87

Investigating the Evidence 4: Variation in Data 88

Directional Selection: Rapid Adaptation by Soapberry Bugs
to New Host Plants 89

Concept 4.4 Review 92

- 4.5 Change Due to Chance 92
 - Evidence of Genetic Drift in Chihuahua Spruce 92
 - Genetic Variation in Island Populations 93
 - Genetic Diversity and Butterfly Extinctions 94
 - Concept 4.5 Review* 95

- Applications: Evolution and Agriculture 95
 - Evolution of Herbicide Resistance in Weeds 95

Section II

ADAPTATIONS TO THE ENVIRONMENT

5 Temperature Relations 99

Concepts 99

- 5.1 Microclimates 100
 - Altitude 100
 - Aspect 101
 - Vegetation 101
 - Color of the Ground 101
 - Presence of Boulders and Burrows 102
 - Aquatic Temperatures 102
 - Concept 5.1 Review* 103
- 5.2 Evolutionary Trade-Offs 103
 - The Principle of Allocation 103
 - Concept 5.2 Review* 104
- 5.3 Temperature and Performance of Organisms 104
 - Investigating the Evidence 5: Laboratory Experiments 106
 - Extreme Temperatures and Photosynthesis 106
 - Temperature and Microbial Activity 107
 - Concept 5.3 Review* 109
- 5.4 Regulating Body Temperature 109
 - Balancing Heat Gain against Heat Loss 109
 - Temperature Regulation by Plants 110
 - Temperature Regulation by Ectothermic Animals 112
 - Temperature Regulation by Endothermic Animals 113
 - Temperature Regulation by Thermogenic Plants 117
 - Concept 5.4 Review* 119
- 5.5 Surviving Extreme Temperatures 119
 - Inactivity 119
 - Reducing Metabolic Rate 120
 - Hibernation by a Tropical Species 121
 - Concept 5.5 Review* 121

- Applications: Local Extinction of a Land Snail in an Urban Heat Island 121

6 Water Relations 125

Concepts 125

- 6.1 Water Availability 126
 - Water Content of Air 127
 - Water Movement in Aquatic Environments 128

- Water Movement Between Soils and Plants 129
 - Concept 6.1 Review* 131

- 6.2 Water Regulation on Land 131
 - Water Acquisition by Animals 131
 - Water Acquisition by Plants 133
 - Water Conservation by Plants and Animals 134
 - Investigating the Evidence 6: Sample Size 136
 - Dissimilar Organisms with Similar Approaches to Desert Life 138
 - Two Arthropods with Opposite Approaches to Desert Life 139
 - Concept 6.2 Review* 142

- 6.3 Water and Salt Balance in Aquatic Environments 142
 - Marine Fish and Invertebrates 142
 - Freshwater Fish and Invertebrates 143
 - Concept 6.3 Review* 144

- Applications: Using Stable Isotopes to Study Water Uptake by Plants 144

- Stable Isotope Analysis 145
- Using Stable Isotopes to Identify Plant Water Sources 146

7 Energy and Nutrient Relations 149

Concepts 149

- 7.1 Photosynthetic Autotrophs 151
 - The Solar-Powered Biosphere 151
 - Concept 7.1 Review* 155
- 7.2 Chemosynthetic Autotrophs 155
 - Concept 7.2 Review* 155
- 7.3 Heterotrophs 155
 - Chemical Composition and Nutrient Requirements 155
 - Concept 7.3 Review* 162
- 7.4 Energy Limitation 162
 - Photon Flux and Photosynthetic Response Curves 163
 - 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
 - Investigating the Evidence 7: Scatter Plots and the Relationship between Variables 168
 - Concept 7.5 Review* 169

- Applications: Bioremediation—Using the Trophic Diversity of Bacteria to Solve Environmental Problems 169

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

8 Social Relations 173

Concepts 173

- 8.1 Mate Choice versus Predation 175
 - Mate Choice and Sexual Selection in Guppies 176
 - Concept 8.1 Review* 178

8.2	Mate Choice and Resource Provisioning	179
	<i>Concept 8.2 Review</i>	182
8.3	Nonrandom Mating in a Plant Population	182
	<i>Concept 8.3 Review</i>	184
8.4	Sociality	184
	Cooperative Breeders	184
	Investigating the Evidence 8: Estimating Heritability Using Regression Analysis	188
	<i>Concept 8.4 Review</i>	191
8.5	Eusociality	191
	Eusocial Species	191
	Evolution of Eusociality	193
	<i>Concept 8.5 Review</i>	195
Applications: Behavioral Ecology and Conservation 195		
	Tinbergen's Framework	195
	Environmental Enrichment and Development of Behavior	195

Section III POPULATION ECOLOGY

9	Population Distribution and Abundance	198
	Concepts	198
9.1	Distribution Limits	200
	Kangaroo Distributions and Climate	200
	A Tiger Beetle of Cold Climates	201
	Distributions of Plants along a Moisture-Temperature Gradient	202
	Distributions of Barnacles along an Intertidal Exposure Gradient	203
	<i>Concept 9.1 Review</i>	204
9.2	Patterns on Small Scales	204
	Scale, Distributions, and Mechanisms	205
	Distributions of Tropical Bee Colonies	205
	Distributions of Desert Shrubs	206
	<i>Concept 9.2 Review</i>	208
9.3	Patterns on Large Scales	208
	Bird Populations across North America	208
	Investigating the Evidence 9: Clumped, Random, and Regular Distributions	209
	Plant Distributions along Moisture Gradients	210
	<i>Concept 9.3 Review</i>	211
9.4	Organism Size and Population Density	212
	Animal Size and Population Density	212
	Plant Size and Population Density	212
	<i>Concept 9.4 Review</i>	213
Applications: Rarity and Vulnerability to Extinction 213		
	Seven Forms of Rarity and One of Abundance	214

10	Population Dynamics	218
	Concepts	218
10.1	Dispersal	219
	Dispersal of Expanding Populations	220
	Range Changes in Response to Climate Change	221
	Dispersal in Response to Changing Food Supply	222
	Dispersal in Rivers and Streams	223
	<i>Concept 10.1 Review</i>	224
10.2	Metapopulations	224
	A Metapopulation of an Alpine Butterfly	224
	Dispersal within a Metapopulation of Lesser Kestrels	225
	<i>Concept 10.2 Review</i>	226
10.3	Patterns of Survival	226
	Estimating Patterns of Survival	226
	High Survival among the Young	227
	Constant Rates of Survival	229
	High Mortality among the Young	229
	Three Types of Survivorship Curves	230
	<i>Concept 10.3 Review</i>	230
10.4	Age Distribution	230
	Contrasting Tree Populations	230
	A Dynamic Population in a Variable Climate	231
	<i>Concept 10.4 Review</i>	232
10.5	Rates of Population Change	232
	Estimating Rates for an Annual Plant	232
	Estimating Rates When Generations Overlap	234
	<i>Concept 10.5 Review</i>	235
	Investigating the Evidence 10: Hypotheses and Statistical Significance	236
Applications: Using Population Dynamics to Assess the Impact of Pollutants 236		

11	Population Growth	241
	Concepts	241
11.1	Geometric and Exponential Population Growth	242
	Geometric Growth	242
	Exponential Growth	243
	Exponential Growth in Nature	244
	<i>Concept 11.1 Review</i>	245
11.2	Logistic Population Growth	245
	<i>Concept 11.2 Review</i>	248
11.3	Limits to Population Growth	248
	Environment and Birth and Death among Darwin's Finches	248
	Investigating the Evidence 11: Frequency of Alternative Phenotypes in a Population	250
	<i>Concept 11.3 Review</i>	252
Applications: The Human Population 252		
	Distribution and Abundance	253
	Population Dynamics	254
	Population Growth	255

12 Life Histories 258

Concepts 258

- 12.1 Offspring Number versus Size 259
 - Egg Size and Number in Fish 260
 - Seed Size and Number in Plants 261
 - Seed Size and Seedling Performance 263
 - Concept 12.1 Review* 265
 - 12.2 Adult Survival and Reproductive Allocation 266
 - Life History Variation among Species 266
 - Life History Variation within Species 267
 - Concept 12.2 Review* 270
 - 12.3 Life History Classification 270
 - r* and *K* Selection 270
 - Plant Life Histories 271
 - Investigating the Evidence 12: A Statistical Test for Distribution Pattern 272
 - Opportunistic, Equilibrium, and Periodic Life Histories 274
 - Lifetime Reproductive Effort and Relative Offspring Size: Two Central Variables? 275
 - Concept 12.3 Review* 276
- Applications: Using Life History Information to Restore Riparian Forests 277

Section IV INTERACTIONS

13 Competition 282

Concepts 282

- 13.1 Intraspecific Competition 284
 - Intraspecific Competition among Plants 284
 - Intraspecific Competition among Planthoppers 285
 - Interference Competition among Terrestrial Isopods 285
 - Concept 13.1 Review* 286
- 13.2 Competitive Exclusion and Niches 286
 - The Feeding Niches of Darwin's Finches 286
 - The Habitat Niche of a Salt Marsh Grass 287
 - Concept 13.2 Review* 288
- 13.3 Mathematical and Laboratory Models 289
 - Modeling Interspecific Competition 289
 - Laboratory Models of Competition 291
 - Concept 13.3 Review* 292
- 13.4 Competition and Niches 292
 - Niches and Competition Among Plants 292
 - Niche Overlap and Competition between Barnacles 293
 - Competition and the Habitat of a Salt Marsh Grass 294
 - Competition and the Niches of Small Rodents 294
 - Character Displacement 296
 - Evidence for Competition in Nature 298
 - Investigating the Evidence 13: Field Experiments 299
 - Concept 13.4 Review* 300

Applications: Competition between Native and Invasive Species 300

14 Exploitative Interactions: Predation, Herbivory, Parasitism, and Disease 303

Concepts 303

- 14.1 Complex Interactions 304
 - Parasites and Pathogens that Manipulate Host Behavior 304
 - The Entangling of Exploitation with Competition 306
 - Concept 14.1 Review* 308
- 14.2 Exploitation and Abundance 308
 - A Herbivorous Stream Insect and Its Algal Food 308
 - Bats, Birds, and Herbivory in a Tropical Forest 309
 - A Pathogenic Parasite, a Predator, and Its Prey 311
 - Concept 14.2 Review* 312
- 14.3 Dynamics 312
 - Cycles of Abundance in Snowshoe Hares and Their Predators 312
 - Investigating the Evidence 14: Standard Error of the Mean 314
 - Experimental Test of Food and Predation Impacts 316
 - Population Cycles in Mathematical and Laboratory Models 316
 - Concept 14.3 Review* 319
- 14.4 Refuges 319
 - Refuges and Host Persistence in Laboratory and Mathematical Models 319
 - Exploited Organisms and Their Wide Variety of "Refuges" 321
 - Concept 14.4 Review* 325

Applications: The Value of Pest Control by Bats: A Case Study 325

15 Mutualism 329

Concepts 329

- 15.1 Plant Mutualisms 330
 - Plant Performance and Mycorrhizal Fungi 330
 - Ants and Swollen Thorn Acacias 334
 - A Temperate Plant Protection Mutualism 337
 - Concept 15.1 Review* 339
 - 15.2 Coral Mutualisms 340
 - Zooxanthellae and Corals 340
 - A Coral Protection Mutualism 340
 - Concept 15.2 Review* 342
 - 15.3 Evolution of Mutualism 342
 - Investigating the Evidence 15: Confidence Intervals 343
 - Facultative Ant-Plant Protection Mutualisms 345
 - Concept 15.3 Review* 345
- Applications: Mutualism and Humans 345
- Guiding Behavior 346

Section V

COMMUNITIES AND ECOSYSTEMS

16 Species Abundance and Diversity 350

Concepts 350

- 16.1 Species Abundance 351
 - The Lognormal Distribution 352
 - Concept 16.1 Review* 353
- 16.2 Species Diversity 353
 - A Quantitative Index of Species Diversity 353
 - Rank-Abundance Curves 354
 - Concept 16.2 Review* 355
- 16.3 Environmental Complexity 355
 - Forest Complexity and Bird Species Diversity 355
 - Investigating the Evidence 16: Estimating the Number of Species in Communities 356
 - Niches, Heterogeneity, and the Diversity of Algae and Plants 357
 - The Niches of Algae and Terrestrial Plants 358
 - Complexity in Plant Environments 358
 - Soil and Topographic Heterogeneity and the Diversity of Tropical Forest Trees 359
 - Algal and Plant Species Diversity and Increased Nutrient Availability 360
 - Nitrogen Enrichment and Ectomycorrhizal Fungus Diversity 360
 - Concept 16.3 Review* 362
- 16.4 Disturbance and Diversity 362
 - The Nature of Equilibrium 362
 - The Nature and Sources of Disturbance 362
 - The Intermediate Disturbance Hypothesis 362
 - Disturbance and Diversity in the Intertidal Zone 363
 - Disturbance and Diversity in Temperate Grasslands 364
 - Concept 16.4 Review* 365

Applications: Disturbance by Humans 365

- Urban Diversity 365

17 Species Interactions and Community Structure 370

Concepts 370

- 17.1 Community Webs 372
 - Detailed Food Webs Reveal Great Complexity 372
 - Strong Interactions and Food Web Structure 372
 - Concept 17.1 Review* 374
- 17.2 Indirect Interactions 374
 - Indirect Commensalism 374
 - Apparent Competition 374
 - Concept 17.2 Review* 376
- 17.3 Keystone Species 376
 - Food Web Structure and Species Diversity 376
 - Experimental Removal of Sea Stars 378
 - Snail Effects on Algal Diversity 378

Fish as Keystone Species in River Food Webs 381

Investigating the Evidence 17: Using Confidence Intervals to Compare Populations 382

Concept 17.3 Review 384

- 17.4 Mutualistic Keystones 384
 - A Cleaner Fish as a Keystone Species 384
 - Seed Dispersal Mutualists as Keystone Species 385
 - Concept 17.4 Review* 386

Applications: Human Modification of Food Webs 386

- The Empty Forest: Hunters and Tropical Rain Forest Animal Communities 386
- Ants and Agriculture: Keystone Predators for Pest Control 387

18 Primary Production and Energy Flow 390

Concepts 390

- 18.1 Patterns of Terrestrial Primary Production 392
 - Actual Evapotranspiration and Terrestrial Primary Production 392
 - Soil Fertility and Terrestrial Primary Production 393
 - Concept 18.1 Review* 394
- 18.2 Patterns of Aquatic Primary Production 394
 - Patterns and Models 394
 - Whole Lake Experiments on Primary Production 395
 - Global Patterns of Marine Primary Production 395
 - Concept 18.2 Review* 396
- 18.3 Consumer Influences 397
 - Piscivores, Planktivores, and Lake Primary Production 397
 - Grazing by Large Mammals and Primary Production on the Serengeti 399
 - Concept 18.3 Review* 401
- 18.4 Trophic Levels 401
 - A Trophic Dynamic View of Ecosystems 401
 - Investigating the Evidence 18: Comparing Two Populations with the *t*-Test 402
 - Energy Flow in a Temperate Deciduous Forest 402
 - Concept 18.4 Review* 404

Applications: Using Stable Isotope Analysis to Trace Energy Flow through Ecosystems 405

- Trophic Levels of Tropical River Fish 405
- Using Stable Isotopes to Identify Sources of Energy in a Salt Marsh 406
- Food Habits of Prehistoric Human Populations 407

19 Nutrient Cycling and Retention 410

Concepts 410

- 19.1 Nutrient Cycles 411
 - The Phosphorus Cycle 412
 - The Nitrogen Cycle 412
 - The Carbon Cycle 414
 - Concept 19.1 Review* 415

19.2	Rates of Decomposition	415
	Decomposition in Two Mediterranean Woodland Ecosystems	415
	Decomposition in Two Temperate Forest Ecosystems	416
	Decomposition in Aquatic Ecosystems	418
	Investigating the Evidence 19: Assumptions for Statistical Tests	419
	<i>Concept 19.2 Review</i>	420
19.3	Organisms and Nutrients	420
	Nutrient Cycling in Streams and Lakes	420
	Animals and Nutrient Cycling in Terrestrial Ecosystems	422
	Plants and the Nutrient Dynamics of Ecosystems	423
	<i>Concept 19.3 Review</i>	424
19.4	Disturbance and Nutrients	424
	Disturbance and Nutrient Loss from Forests	425
	Flooding and Nutrient Export by Streams	425
	<i>Concept 19.4 Review</i>	427
	Applications: Altering Aquatic and Terrestrial Ecosystems	427

20 Succession and Stability 431

	Concepts	431
20.1	Community Changes during Succession	433
	Primary Succession at Glacier Bay	433
	Secondary Succession in Temperate Forests	434
	Succession in Rocky Intertidal Communities	435
	Succession in Stream Communities	435
	<i>Concept 20.1 Review</i>	436
20.2	Ecosystem Changes during Succession	436
	Ecosystem Changes at Glacier Bay	436
	Four Million Years of Ecosystem Change	438
	Recovery of Nutrient Retention following Disturbance	439
	Succession and Stream Ecosystem Properties	441
	<i>Concept 20.2 Review</i>	442
20.3	Mechanisms of Succession	442
	Facilitation	442
	Tolerance	442
	Inhibition	442
	Successional Mechanisms in the Rocky Intertidal Zone	443
	Successional Mechanisms in Forests	445
	<i>Concept 20.3 Review</i>	446
20.4	Community and Ecosystem Stability	446
	Some Definitions	446
	Lessons from the Park Grass Experiment	446
	Replicate Disturbances and Desert Stream Stability	447
	<i>Concept 20.4 Review</i>	449
	Investigating the Evidence 20: Variation around the Median	450
	Applications: Using Repeat Photography to Detect Long-Term Change	450

Section VI LARGE-SCALE ECOLOGY

21 Landscape Ecology 456

	Concepts	456
21.1	Landscape Structure	458
	The Structure of Six Landscapes in Ohio	458
	The Fractal Geometry of Landscapes	460
	<i>Concept 21.1 Review</i>	461
21.2	Landscape Processes	461
	Landscape Structure and the Dispersal of Mammals	462
	Habitat Patch Size and Isolation and the Density of Butterfly Populations	463
	Habitat Corridors and Movement of Organisms	464
	Landscape Position and Lake Chemistry	465
	Investigating the Evidence 21: Comparison of Two Samples Using a Rank Sum Test	466
	<i>Concept 21.2 Review</i>	467
21.3	Origins of Landscape Structure and Change	467
	Geological Processes, Climate, and Landscape Structure	467
	Organisms and Landscape Structure	470
	Fire and the Structure of a Mediterranean Landscape	474
	<i>Concept 21.3 Review</i>	475
	Applications: Restoring a Riverine Landscape	475
	Riverine Restoration: The Kissimmee River	475

22 Geographic Ecology 481

	Concepts	481
22.1	Area, Isolation, and Species Richness	483
	Sampling Area and Number of Species	483
	Island Area and Species Richness	483
	Island Isolation and Species Richness	484
	<i>Concept 22.1 Review</i>	486
22.2	The Equilibrium Model of Island Biogeography	486
	Species Turnover on Islands	487
	Experimental Island Biogeography	488
	Colonization of New Islands by Plants	489
	Manipulating Island Area	490
	Island Biogeography Update	491
	<i>Concept 22.2 Review</i>	491
22.3	Latitudinal Gradients in Species Richness	491
	Area and Latitudinal Gradients in Species Richness	493
	Continental Area and Species Richness	494
	<i>Concept 22.3 Review</i>	495
22.4	Historical and Regional Influences	495
	Exceptional Patterns of Diversity	495
	Investigating the Evidence 22: Sample Size Revisited	496
	Historical and Regional Explanations	497
	<i>Concept 22.4 Review</i>	498
	Applications: Global Positioning Systems, Remote Sensing, and Geographic Information Systems	498

Global Positioning Systems	499
Remote Sensing	499
Geographic Information Systems	501
23 Global Ecology	504
Concepts	504
The Atmospheric Envelope and the Greenhouse Earth	505
23.1 A Global System	506
The Historical Thread	506
El Niño and La Niña	507
El Niño and Marine Populations	508
El Niño and the Great Salt Lake	510
El Niño and Terrestrial Populations in Australia	511
<i>Concept 23.1 Review</i>	513
23.2 Human Activity and the Global Nitrogen Cycle	513
<i>Concept 23.2 Review</i>	514
23.3 Changes in Land Cover	514
Tropical Deforestation	514
<i>Concept 23.3 Review</i>	517
23.4 Human Influence on Atmospheric Composition	517
Investigating the Evidence 23: Discovering What's Been Discovered	518
Depletion and Recovery of the Ozone Layer	521
The Future	522
<i>Concept 23.4 Review</i>	523
Applications: Cooperative Research Networks for Global Ecology	523
Appendix Statistical Tables	527
Glossary	531
References	541
Credits	552
Index	553