

The cover features a photograph of a moose standing in a lake, with a forest of trees in autumn colors and mountains in the background. The moose is dark brown with large, light-colored antlers. The water is blue, and the rocks in the foreground are grey. The background shows a dense forest of trees with yellow, orange, and green foliage, and a mountain range under a hazy sky.

Ecology

Concepts & Applications

Fourth Edition

Manuel C. Molles Jr.

McGraw-Hill International Edition



Chapter 1 Introduction: *What Is Ecology?* 1

- Overview of Ecology 2
- The Ecology of Forest Birds: Using Field Studies to Test Theory 3
- Forest Nutrient Budgets: Inventories and Large-Scale Experiments 5
- Vegetation Change: Information from Pollen Records and Modeling 7
- The Nature and Scope of Ecology 8
- Investigating the Evidence 1: The Scientific Method—Questions and Hypotheses** 9

Section I NATURAL HISTORY

Chapter 2 Life on Land 12

- Terrestrial Biomes 14

Concepts 14

2.1 Large-Scale Patterns of Climatic Variation 14

- Temperature, Atmospheric Circulation, and Precipitation 15
- Climate Diagrams 16
- Concept 2.1 Review* 19

Investigating the Evidence 2: Determining the Sample Mean 19

2.2 Soil: The Foundation of Terrestrial Biomes 20

- Concept 2.2 Review* 21

2.3 Natural History and Geography of Biomes 21

- Tropical Rain Forest 21
- Tropical Dry Forest 23
- Tropical Savanna 25
- Desert 27
- Mediterranean Woodland and Shrubland 30
- Temperate Grassland 32
- Temperate Forest 33
- Boreal Forest 36
- Tundra 37
- Mountains: Islands in the Sky 40
- Concept 2.3 Review* 43

Applications: Climatic Variation and the Palmer Drought Severity Index 43

Chapter 3 Life in Water 47

Concepts 48

3.1 The Hydrologic Cycle 48

- Concept 3.1 Review* 49

3.2 The Natural History of Aquatic Environments 49

- The Oceans 49
- Life in Shallow Marine Waters: Kelp Forests and Coral Gardens 54

Investigating the Evidence 3: Determining the Sample Median 55

- Marine Shores: Life Between High and Low Tides 59
- Estuaries, Salt Marshes, and Mangrove Forests 62
- Rivers and Streams: Life Blood and Pulse of the Land 67
- Lakes: Small Seas 71
- Concept 3.2 Review* 77

Applications: Biological Integrity—Assessing the Health of Aquatic Systems 77

- Number of Species and Species Composition 77
- Trophic Composition 77
- Fish Abundance and Condition 77
- A Test 77

Section II INDIVIDUALS

Chapter 4 Temperature Relations 82

Concepts 83

4.1 Microclimates 83

- Altitude 83
- Aspect 84
- Vegetation 84
- Color of the Ground 85
- Presence of Boulders and Burrows 85
- Aquatic Temperatures 85
- Concept 4.1 Review* 86

4.2 Temperature and Performance of Organisms 87

- Temperature and Animal Performance 87
- Investigating the Evidence 4: Laboratory Experiments** 88
- Extreme Temperatures and Photosynthesis 89
- Temperature and Microbial Activity 90
- Concept 4.2 Review* 91

- 4.3 Regulating Body Temperature 91**
 Balancing Heat Gain Against Heat Loss 91
 Temperature Regulation by Plants 92
 Temperature Regulation by Ectothermic Animals 94
 Temperature Regulation by Endothermic Animals 96
 Temperature Regulation by Thermogenic Plants 99
Concept 4.3 Review 101
- 4.4 Surviving Extreme Temperatures 101**
 Inactivity 101
 Reducing Metabolic Rate 101
 Hibernation by a Tropical Species 103
Concept 4.4 Review 103
- Applications: Climatic Warming and the Local
 Extinction of a Land Snail 103**

- 6.2 Energy Limitation 146**
 Photon Flux and Photosynthetic Response Curves 146
 Food Density and Animal Functional Response 146
Concept 6.2 Review 148
- 6.3 Optimal Foraging Theory 148**
 Testing Optimal Foraging Theory 148
 Optimal Foraging by Plants 150
Investigating the Evidence 6: Variation in Data 151
Concept 6.3 Review 152
- Applications: Bioremediation—Using the Trophic
 Diversity of Bacteria to Solve Environmental
 Problems 152**
 Leaking Underground Storage Tanks 153
 Cyanide and Nitrates in Mine Spoils 153

Chapter 5 Water Relations 108

Concepts 110

- 5.1 Water Availability 110**
 Water Content of Air 110
 Water Movement in Aquatic Environments 111
 Water Movement Between Soils and Plants 112
Concept 5.1 Review 114
- 5.2 Water Regulation on Land 114**
 Water Acquisition by Animals 115
 Water Acquisition by Plants 116
 Water Conservation by Plants and Animals 118
Investigating the Evidence 5: Sample Size 119
 Dissimilar Organisms with Similar Approaches
 to Desert Life 122
 Two Arthropods with Opposite Approaches to
 Desert Life 122
Concept 5.2 Review 124
- 5.3 Water and Salt Balance in Aquatic
 Environments 126**
 Marine Fish and Invertebrates 126
 Freshwater Fish and Invertebrates 126
Concept 5.3 Review 128
- Applications: Using Stable Isotopes to Study Water
 Uptake by Plants 129**
 Stable Isotope Analysis 129
 Using Stable Isotopes to Identify Plant Water
 Sources 129

Chapter 6 Energy and Nutrient Relations 133

Concepts 134

- 6.1 Energy Sources 134**
 Photosynthesis 135
 Heterotrophs 139
 Chemosynthesis 144
Concept 6.1 Review 145

Chapter 7 Social Relations 157

Concepts 159

- 7.1 Mate Choice 160**
 Mate Choice and Sexual Selection in Guppies 160
 Mate Choice Among Scorpionflies 164
 Nonrandom Mating Among Wild Radish 167
Concept 7.1 Review 169
- 7.2 Sociality 169**
 Cooperative Breeders 170
**Investigating the Evidence 7: Scatter Plots and the
 Relationship Between Variables 172**
Concept 7.2 Review 175
- 7.3 Eusociality 175**
 Eusocial Species 175
 Evolution of Eusociality 177
Concept 7.3 Review 179
- Applications: Behavioral Ecology and Conservation 179**
 Tinbergen's Framework 179
 Environmental Enrichment and Development of
 Behavior 179

Section III

POPULATION ECOLOGY

Chapter 8 Population Genetics and Natural Selection 184

Concepts 186

- 8.1 Variation Within Populations 187**
 Variation in Plant Populations 187
 Variation in Animal Populations 190
Concept 8.1 Review 192
- 8.2 Hardy-Weinberg 193**
 Calculating Gene Frequencies 193
Concept 8.2 Review 195

- 8.3 The Process of Natural Selection 195**
 Stabilizing Selection 195
 Directional Selection 196
 Disruptive Selection 197
Concept 8.3 Review 197
- 8.4 Evolution by Natural Selection 197**
 Evolution by Natural Selection and Genetic Variation 197
Investigating the Evidence 8: Estimating Heritability Using Regression Analysis 198
 Adaptive Change in Colonizing Lizards 198
 Rapid Adaptation by Soapberry Bugs to New Host Plants 200
Concept 8.4 Review 202
- 8.5 Change Due to Chance 202**
 Evidence of Genetic Drift in Chihuahua Spruce 202
 Genetic Variation in Island Populations 203
 Genetic Diversity and Butterfly Extinctions 204
Concept 8.5 Review 205
- Applications: Estimating Genetic Variation in Populations 205**
 Molecular Approaches to Genetic Variation 205

Chapter 9 Population Distribution and Abundance 210

Concepts 212

- 9.1 Distribution Limits 212**
 Kangaroo Distributions and Climate 212
 A Tiger Beetle of Cold Climates 213
 Distributions of Plants Along a Moisture-Temperature Gradient 214
 Distributions of Barnacles Along an Intertidal Exposure Gradient 215
Concept 9.1 Review 216
- 9.2 Patterns on Small Scales 216**
 Scale, Distributions, and Mechanisms 217
 Distributions of Tropical Bee Colonies 217
 Distributions of Desert Shrubs 218
Concept 9.2 Review 220
- 9.3 Patterns on Large Scales 220**
 Bird Populations Across North America 220
Investigating the Evidence 9: Clumped, Random, and Regular Distributions 221
 Plant Distributions Along Moisture Gradients 223
Concept 9.3 Review 224
- 9.4 Organism Size and Population Density 224**
 Animal Size and Population Density 224
 Plant Size and Population Density 225
Concept 9.4 Review 226
- Applications: Rarity and Vulnerability to Extinction 226**
 Seven Forms of Rarity and One of Abundance 226

Chapter 10 Population Dynamics 231

Concepts 233

- 10.1 Dispersal 233**
 Dispersal of Expanding Populations 233
 Range Changes in Response to Climate Change 234
 Dispersal in Response to Changing Food Supply 235
 Dispersal in Rivers and Streams 236
Concept 10.1 Review 237
- 10.2 Metapopulations 237**
 A Metapopulation of an Alpine Butterfly 237
 Dispersal Within a Metapopulation of Lesser Kestrels 239
Concept 10.2 Review 239
- 10.3 Patterns of Survival 239**
 Estimating Patterns of Survival 240
 High Survival Among the Young 240
 Constant Rates of Survival 241
 High Mortality Among the Young 241
 Three Types of Survivorship Curves 243
Concept 10.3 Review 243
- 10.4 Age Distribution 243**
 Stable and Declining Tree Populations 244
 A Dynamic Population in a Variable Climate 244
Concept 10.4 Review 245
- 10.5 Rates of Population Change 245**
 Estimating Rates for an Annual Plant 246
 Estimating Rates When Generations Overlap 247
Concept 10.5 Review 249
- Investigating the Evidence 10: Hypotheses and Statistical Significance 249**
- Applications: Using Population Dynamics to Assess the Impact of Pollutants 250**

Chapter 11 Population Growth 254

Concepts 255

- 11.1 Geometric and Exponential Population Growth 255**
 Geometric Growth 256
 Exponential Growth 257
 Exponential Growth in Nature 257
Concept 11.1 Review 259
- 11.2 Logistic Population Growth 259**
Concept 11.2 Review 261
- 11.3 Limits to Population Growth 261**
Investigating the Evidence 11: Frequency of Alternative Phenotypes in a Population 262
 Environment and Birth and Death Among Galápagos Finches 262
Concept 11.3 Review 266
- Applications: The Human Population 266**
 Distribution and Abundance 266
 Population Dynamics 267
 Population Growth 268

Chapter 12 Life Histories 272

Concepts 273

12.1 Offspring Number Versus Size 274

Egg Size and Number in Fish 274

Seed Size and Number in Plants 276

Concept 12.1 Review 280

12.2 Adult Survival and Reproductive Allocation 280

Life History Variation Among Species 280

Life History Variation Within Species 281

Concept 12.2 Review 284

12.3 Life History Classification 284

r and K Selection 284

Plant Life Histories 285

Investigating the Evidence 12: A Statistical Test for Distribution Pattern 286

Opportunistic, Equilibrium, and Periodic Life Histories 288

Reproductive Effort, Offspring Size, and Benefit-Cost Ratios 290

Concept 12.3 Review 291

Applications: Using Life History Information to Restore Riparian Forests 291

Section

INTERACTIONS

Chapter 13 Competition 298

Concepts 300

13.1 Intraspecific Competition 300

Intraspecific Competition Among Plants 300

Intraspecific Competition Among Planthoppers 301

Interference Competition Among Terrestrial Isopods 302

Concept 13.1 Review 302

13.2 Niches 302

The Feeding Niches of Galápagos Finches 303

The Habitat Niche of a Salt Marsh Grass 304

Concept 13.2 Review 305

13.3 Mathematical and Laboratory Models 305

Modeling Interspecific Competition 305

Laboratory Models of Competition 307

Concept 13.3 Review 309

13.4 Competition and Niches 309

Niches and Competition Among Plants 309

Niche Overlap and Competition Between Barnacles 310

Competition and the Habitat of a Salt Marsh Grass 311

Competition and the Niches of Small Rodents 311

Character Displacement 312

Investigating the Evidence 13: Field Experiments 315

Evidence for Competition in Nature 316

Concept 13.4 Review 316

Applications: Competition Between Native and Invasive Species 316

Chapter 14 Exploitative Interactions: Predation, Herbivory, Parasitism, and Disease 320

Concepts 321

14.1 Complex Interactions 321

Parasites and Pathogens That Manipulate Host Behavior 322

The Entangling of Exploitation with Competition 324

Concept 14.1 Review 325

14.2 Exploitation and Abundance 325

A Herbivorous Stream Insect and Its Algal Food 325

An Introduced Cactus and a Herbivorous Moth 327

A Pathogenic Parasite, a Predator, and Its Prey 328

Investigating the Evidence 14: Standard Error of the Mean 330

Concept 14.2 Review 330

14.3 Dynamics 330

Cycles of Abundance in Snowshoe Hares and Their Predators 331

Experimental Test of Food and Predation Impacts 333

Population Cycles in Mathematical and Laboratory Models 334

Concept 14.3 Review 336

14.4 Refuges 337

Refuges and Host Persistence in Laboratory and Mathematical Models 337

Exploited Organisms and Their Wide Variety of "Refuges" 338

Concept 14.4 Review 342

Applications: Using Predators to Control a Parasite 343

Chapter 15 Mutualism 347

Concepts 349

15.1 Plant Mutualisms 349

Plant Performance and Mycorrhizal Fungi 349

Ants and Swollen Thorn Acacias 352

A Temperate Plant Protection Mutualism 355

Concept 15.1 Review 356

15.2 Coral Mutualisms 357

Zooxanthellae and Corals 357

A Coral Protection Mutualism 358

Concept 15.2 Review 359

15.3 Evolution of Mutualism 359

Investigating the Evidence 15: Confidence Intervals 360

Facultative Ant-Plant Protection Mutualisms 362

Concept 15.3 Review 363

Applications: Mutualism and Humans 363

The Honeyguide 363

Guiding Behavior 364

Section

COMMUNITIES AND ECOSYSTEMS**Chapter 16 Species Abundance and Diversity 370****Concepts 372****16.1 Species Abundance 372**

The Lognormal Distribution 372

*Concept 16.1 Review 373***16.2 Species Diversity 373**

A Quantitative Index of Species Diversity 374

Rank-Abundance Curves 374

Investigating the Evidence 16: Estimating the Number of Species in Communities 376*Concept 16.2 Review 377***16.3 Environmental Complexity 377**

Forest Complexity and Bird Species Diversity 377

Niches, Heterogeneity, and the Diversity of Algae and Plants 378

The Niches of Algae and Terrestrial Plants 378

Complexity in Plant Environments 379

Soil and Topographic Heterogeneity and the Diversity of Tropical Forest Trees 379

Algal and Plant Species Diversity and Increased Nutrient Availability 380

Nitrogen Enrichment and Ectomycorrhizal Fungus Diversity 380

*Concept 16.3 Review 382***16.4 Disturbance and Diversity 382**

The Nature of Equilibrium 382

The Nature and Sources of Disturbance 382

The Intermediate Disturbance Hypothesis 383

Disturbance and Diversity in the Intertidal Zone 383

Disturbance and Diversity in Temperate Grasslands 384

*Concept 16.4 Review 385***Applications: Disturbance by Humans 385**

Human Disturbance: An Ancient Feature of the Biosphere 386

Disturbance by Humans and the Diversity of Chalk Grasslands 387

Chapter 17 Species Interactions and Community Structure 391**Concepts 392****17.1 Community Webs 392**

Detailed Food Webs Reveal Great Complexity 392

Strong Interactions and Food Web Structure 394

*Concept 17.1 Review 394***17.2 Keystone Species 394**

Food Web Structure and Species Diversity 395

Experimental Removal of Sea Stars 396

Snail Effects on Algal Diversity 397

Fish as Keystone Species in River Food Webs 400

Investigating the Evidence 17: Using Confidence Intervals to Compare Populations 401*Concept 17.2 Review 403***17.3 Exotic Predators 403**

Introduced Fish: Predators That Simplify Aquatic Food Webs 403

*Concept 17.3 Review 405***17.4 Mutualistic Keystones 405**

A Cleaner Fish as a Keystone Species 405

Seed Dispersal Mutualists as Keystone Species 405

*Concept 17.4 Review 406***Applications: Humans as Keystone Species 406**

The Empty Forest: Hunters and Tropical Rain Forest Animal Communities 406

Ants and Agriculture: Keystone Predators for Pest Control 407

Chapter 18 Primary Production and Energy Flow 411**Concepts 413****18.1 Patterns of Terrestrial Primary Production 413**

Actual Evapotranspiration and Terrestrial Primary Production 413

Soil Fertility and Terrestrial Primary Production 414

*Concept 18.1 Review 415***18.2 Patterns of Aquatic Primary Production 415**

Patterns and Models 416

Whole Lake Experiments on Primary Production 416

Global Patterns of Marine Primary Production 417

*Concept 18.2 Review 418***18.3 Consumer Influences 418**

Piscivores, Planktivores, and Lake Primary Production 419

Grazing by Large Mammals and Primary Production on the Serengeti 421

Investigating the Evidence 18: Comparing Two Populations with the *t*-Test 422*Concept 18.3 Review 423***18.4 Trophic Levels 424**

A Trophic Dynamic View of Ecosystems 424

Energy Flow in a Temperate Deciduous Forest 424

*Concept 18.4 Review 426***Applications: Using Stable Isotope Analysis to Trace Energy Flow Through Ecosystems 426**

Trophic Levels of Tropical River Fish 426

Using Stable Isotopes to Identify Sources of Energy in a Salt Marsh 427

Food Habits of Prehistoric Human Populations 428

Chapter 19 Nutrient Cycling and Retention 432

- The Phosphorus Cycle 433
- The Nitrogen Cycle 434
- The Carbon Cycle 435

Concepts 436

19.1 Rates of Decomposition 436

- Decomposition in Two Mediterranean Woodland Ecosystems 436
- Decomposition in Two Temperate Forest Ecosystems 437
- Decomposition in Aquatic Ecosystems 439

Investigating the Evidence 19: Assumptions for Statistical Tests 441

Concept 19.1 Review 442

19.2 Organisms and Nutrients 442

- Nutrient Cycling in Streams 442
- Animals and Nutrient Cycling in Terrestrial Ecosystems 444
- Plants and the Nutrient Dynamics of Ecosystems 445
- Concept 19.2 Review 447*

19.3 Disturbance and Nutrients 447

- Disturbance and Nutrient Loss from the Hubbard Brook Experimental Forest 447
- Flooding and Nutrient Export by Streams 448
- Concept 19.3 Review 449*

Applications: Altering Aquatic and Terrestrial Ecosystems 449

Chapter 20 Succession and Stability 454

Concepts 456

20.1 Community Changes During Succession 456

- Primary Succession at Glacier Bay 456
- Secondary Succession in Temperate Forests 457
- Succession in Rocky Intertidal Communities 458
- Succession in Stream Communities 459
- Concept 20.1 Review 460*

20.2 Ecosystem Changes During Succession 460

- Ecosystem Changes at Glacier Bay 460
- Four Million Years of Ecosystem Change 461
- Recovery of Nutrient Retention Following Disturbance 463
- Succession and Stream Ecosystem Properties 464
- Concept 20.2 Review 465*

20.3 Mechanisms of Succession 465

- Successional Mechanisms in the Rocky Intertidal Zone 467
- Successional Mechanisms in Forests 468
- Concept 20.3 Review 469*

20.4 Community and Ecosystem Stability 469

- Some Definitions 470
- Lessons from the Park Grass Experiment 470
- Replicate Disturbances and Desert Stream Stability 471

Investigating the Evidence 20: Variation Around the Median 472

Concept 20.4 Review 474

Applications: Using Repeat Photography to Detect Long-Term Change 474

Section VI

LARGE-SCALE ECOLOGY

Chapter 21 Landscape Ecology 481

Concepts 483

21.1 Landscape Structure 483

- The Structure of Six Landscapes in Ohio 483
- The Fractal Geometry of Landscapes 485
- Concept 21.1 Review 486*

21.2 Landscape Processes 487

- Landscape Structure and the Dispersal of Mammals 487
- Habitat Patch Size and Isolation and the Density of Butterfly Populations 488
- Habitat Corridors and Movement of Organisms 489
- Landscape Position and Lake Chemistry 491

Investigating the Evidence 21: Comparison of Two Samples Using a Rank Sum Test 492

Concept 21.2 Review 493

21.3 Origins of Landscape Structure and Change 493

- Geological Processes, Climate, and Landscape Structure 493
- Organisms and Landscape Structure 495
- Fire and the Structure of a Mediterranean Landscape 499
- Concept 21.3 Review 500*

Applications: Restoring a Riverine Landscape 500

Riverine Restoration: The Kissimmee River 500

Chapter 22 Geographic Ecology 506

Concepts 508

22.1 Area, Isolation, and Species Richness 508

- Sampling Area and Number of Species 508
- Island Area and Species Richness 508
- Island Isolation and Species Richness 509
- Concept 22.1 Review 511*

22.2 The Equilibrium Model of Island Biogeography 511

- Species Turnover on Islands 513
- Experimental Island Biogeography 514
- Colonization of New Islands by Plants 515
- Manipulating Island Area 516
- Island Biogeography Update 516
- Concept 22.2 Review 516*

22.3 Latitudinal Gradients in Species Richness 517

- Area and Latitudinal Gradients in Species Richness 518

Continental Area and Species Richness	519
<i>Concept 22.3 Review</i>	520
22.4 Historical and Regional Influences	520
Exceptional Patterns of Diversity	520
Investigating the Evidence 22: Sample Size Revisited	521
<i>Historical and Regional Explanations</i>	522
<i>Concept 22.4 Review</i>	524
Applications: Global Positioning Systems, Remote Sensing, and Geographic Information Systems	524
Global Positioning Systems	524
Remote Sensing	524
Geographic Information Systems	526
Chapter 23 Global Ecology	530
The Atmospheric Envelope and the Greenhouse Earth	531
Concepts	532
23.1 A Global System	533
<i>The Historical Thread</i>	533
El Niño and La Niña	534
El Niño and Marine Populations	534
El Niño and the Great Salt Lake	537
El Niño and Terrestrial Populations in Australia	538
<i>Concept 23.1 Review</i>	539
23.2 Human Activity and the Global Nitrogen Cycle	539
<i>Concept 23.2 Review</i>	540
23.3 Changes in Land Cover	540
Tropical Deforestation	540
Investigating the Evidence 23: Discovering What's Been Discovered	544
<i>Concept 23.3 Review</i>	544
23.4 Human Influence on Atmospheric Composition	545
Depletion and Recovery of the Ozone Layer	548
The Future	548
<i>Concept 23.4 Review</i>	549
Applications: Cooperative Research Networks for Global Ecology	549
Appendix A Statistical Tables	554
Appendix B Answers to Concept Review Questions	558
Appendix C Answers to Critiquing the Evidence	567
Glossary	569
References	578
Credits	588
Index	589