



CRC Press  
Taylor & Francis Group

# UNDERSTANDING NATURE

## Ecology for a New Generation

Louise M. Weber



สำนักหอสมุด มหาวิทยาลัยเชียงใหม่

b 16707850  
O 1257695  
i 22688687

# Understanding Nature

## Ecology for a New Generation



Louise M. Weber

Department of Biology and Environmental Science, University of Saint Francis -  
Fort Wayne, USA



CRC Press

Taylor & Francis Group

Boca Raton London New York

CRC Press is an imprint of the  
Taylor & Francis Group, an **informa** business

# Contents

---

Acknowledgments	xix
About the Author	xxi
<b>1 Introduction</b>	<b>1</b>
A 21st-Century Response	1
The Goals of This Book	2
Ecology's Magic Glasses	3
What Is Ecology?	3
What Became of the Early Nature Study Movement?	6
Today's Nature Study	7
The Strategy for This Book	7
Closing Arguments	7
References	8
<b>2 We stand on their shoulders</b>	<b>9</b>
Introduction	9
Natural History Meets Traditional Ecological Knowledge	10
The Wolf, the Raven	11
The History of SEK	11
The Renaissance and Natural History	12
1700s – Age of Exploration and Natural History	13
Linnaeus	13
1800s – Age of Evolution	13
Gilbert White	13
Charles Darwin and the Founding of Ecology	14
The Wolf and the Raven	16
To What Ends? Next Steps	17
References	18
<b>3 Biomes, life forms, and ecoregions</b>	<b>19</b>
Introduction	20
Are There Animal Life Forms?	20
How Did the Concept of Biomes Arise?	22
What Determines Where Biomes Are Located?	22
What Are the Limitations of Biomes?	24
What Are Ecoregions and Are They Better Than Biomes?	24
World Wildlife Fund Designations	25
The 14 Land Biomes Recognized by WWF	25
Next Steps	25
References	31
	vii

<b>4</b>	<b>Biomes: Tundra and taiga</b>	<b>33</b>
	What Is Meant by "Tundra?"	35
	Does Antarctica Have Tundra?	35
	What Is the Vegetative Life Form for Tundra?	35
	What Are Other Characteristics of Arctic Tundra?	35
	Animal Life in Arctic Tundra	36
	Conservation Problems of Arctic Tundra	36
	What Are Characteristics of Alpine Tundra?	37
	What Is Meant by Taiga?	37
	What Is the Plant Life Form for Taiga?	38
	What Are Other Characteristics of Taiga?	38
	Conservation Problems of Taiga	38
	References	40
<b>5</b>	<b>Biomes: Grassland</b>	<b>41</b>
	What Is Meant by "Grassland?"	42
	What Are Characteristics of Temperate Grassland?	42
	What Is the Plant Life Form for Temperate Grassland?	42
	The Desert-Forest Diagonal in Temperate Grassland	43
	Animal Life in Temperate Grassland	43
	Grassland Conservation Problems	44
	The Great Plains of North America	44
	North American Grassland Not in the Great Plains	45
	Open Canopy Areas and Grassland in Eastern N. America	46
	Tropical Grassland, Savanna, and Shrubland	46
	Conservation of Tropical Grassland, Savanna, and Shrubland	47
	South American Grassland	47
	Grassland and Savanna of Africa	47
	Australian Grassland	47
	References	49
<b>6</b>	<b>Biomes: Shrubland, thickets, and desert</b>	<b>51</b>
	What Is Meant by Shrubland (Scrubland)?	52
	What Is the Plant Life Form for Shrubland?	52
	What Are Other Characteristics of Shrubland?	52
	What Animals Occur in Shrubland?	53
	Locations of Shrubland and Notable Types	53
	Mediterranean	53
	Thorn Scrub	53
	Great Basin of the U.S.	53
	Southwestern Australian	54
	Fynbos – Cape Region of South Africa	54
	Coastal Shrubland of Europe	54
	Chaparral and Chaco of the Americas	54
	Grand Choco of South America	54
	Heathland of Europe	54
	Thickets in U.S. Forests	54
	Conservation of Shrubland	54
	What Is "Desert?"	54
	What Are Other Characteristics of Desert?	55
	Desert Formation	55
	Plant Life Form in Desert	55
	Animal Life in Desert	56

	The Major Ecological Processes of Desert	56
	Deserts of N. America	56
	Conservation Problems of Desert	57
	References	58
<b>7</b>	<b>Biomes: Savanna and forest</b>	<b>59</b>
	Introduction	60
	What Is Savanna?	60
	What Are Characteristics of Savanna?	60
	Animals of Savanna?	60
	Conservation of Savanna	61
	Does N. America Have Savanna? Yes	61
	What Is Meant by Forest?	62
	What Is the Plant Life Forms of Forest?	62
	Characteristics of Temperate Deciduous Broadleaf Forest	62
	Stratification in Temperate Deciduous Broadleaf Forests	63
	Light Varies Seasonally within the Temperate Deciduous Broadleaf Forest	63
	Types of Deciduous Broadleaf Forest in Eastern N. America	64
	Temperate Evergreen Forests	64
	Other Temperate Coniferous Forests in N. America	64
	Tropical Forests	65
	Soils of Tropical Forest	66
	Humans in the Tropical Forest and Conservation	66
	Tropical Rainforest Life Forms	66
	Animals of Tropical Rainforest	66
	Tropical Seasonal Forest	66
	References	69
<b>8</b>	<b>Why are biomes where they are?</b>	<b>71</b>
	Introduction	71
	What Determines Life Form at the Global Level?	71
	What Determines Climate?	72
	Determinants of Life Form at the Global Level – Seasons	73
	Determinants of Life Form at the Global Level – Air Masses	73
	Determinants of Life Form at the Global Level – Prevailing Winds	73
	Determinants of Life Form at the Global Level – Trade Winds, ITCZ, Doldrums, Monsoons	74
	Determinants of Life Form at the Global Level – El Nino	75
	Determinants of Life Form at the Continental Level – Prevailing Westerlies in Temperate Latitudes	76
	Determinants of Life Form at the Regional Level – Altitude	76
	Why Do Vegetation Patterns Change with Altitude?	76
	Determinants of Life Form at the Regional Level – Aspect	76
	Determinants of Life Form at the Regional Level – Rain Shadow	76
	Determinants of Life Form at the Regional Level – Valley Influences	77
	Determinants of Life Form at the Regional Level – Maritime Influences	78
	Determinants of Life Form at the Local Level	78
	References	79
<b>9</b>	<b>Why are individual species where they are?</b>	<b>81</b>
	What Characterizes Species Diversity Patterns throughout the Earth?	81
	The Species Distribution Constraint Hierarchy	82
	Working through the Constraint Hierarchy at the Global Level	85
	Tolerance Limits	86
	Species Gradients	86



	The Constraint Hierarchy at the Regional Spatial Scale	86
	Dispersal	86
	Speciation	87
	The Constraint Hierarchy at the Local Spatial Scale	88
	Next Steps	88
	References	88
<b>10</b>	<b>Introduction to evolution: The modern synthesis</b>	<b>91</b>
	Three Periods for Understanding Biological Evolution	92
	What Were the Main Features of the Darwinian Synthesis?	92
	What Were the Main Features of the Modern Synthesis?	92
	Three Further Categories for Understanding the Modern Synthesis	92
	What Is Molecular Evolution?	92
	What Is Meant by Microevolution?	93
	What Are the Basics of Microevolution and Population Genetics?	93
	Why Do Changes in Allele Frequency Occur?	93
	Natural Selection in More Detail	94
	What Are Adaptations?	95
	Natural Selection Does Not Create Adaptations	96
	Specific Types of Evolution and Natural Selection	96
	Kin Selection	97
	Can Kin Selection Be Applied to Humans?	97
	The Evolution of an Idea	97
	References	98
<b>11</b>	<b>Advances in microevolution, molecular evolution, and evo-devo</b>	<b>99</b>
	The Revolution in Evolution	100
	What Are the Features of Postmodern Thinking?	101
	Postmodern Discoveries in Developmental Biology	104
	Phenotypic Plasticity within Evo-Devo	104
	How Does Phenotypic Plasticity Affect Evolution?	105
	The Emerging Paradigm	108
	References	110
<b>12</b>	<b>An autobiography of the Earth</b>	<b>111</b>
	Getting a Handle on a 4.5-Billion-Year-Old Autobiography	112
	The Most Important Events within Macroevolution	112
	The 14-Billion-Year Time Scale	112
	What Is a Fossil?	114
	The History of Life and Systematics	114
	Geologic History Since 600 mya (Lomolino et al. 2016)	116
	Tectonic Plates	116
	Geologic History Since 600 mya	116
	Evolution during the Paleozoic – Cambrian	118
	Evolution during the Paleozoic – Ordovician	118
	Evolution during the Paleozoic – Silurian	119
	Evolution during the Paleozoic – Carboniferous	119
	The Mesozoic	119
	Evolution in the Triassic, Jurassic, and Cretaceous	119
	The Cenozoic	120
	Evolution in the Cenozoic – Paleogene	120
	Evolution in the Cenozoic – Neogene	120
	Evolution in the Pleistocene on a 2-Million-Year Scale	120
	History of Humans	121

The Overkill Hypothesis	122
Summary of Macroevolution Events	122
Evidence for Evolution	122
References	124
<b>13 Introduction to statistics</b>	<b>125</b>
Introduction	125
The Null Hypothesis	125
The Problems with Null Hypotheses	125
P value	126
Why Do We Use $P=0.05$ as the Cutoff Point?	126
An Obsession with Rejection—Statistical versus Scientific Significance	127
Means Comparisons	127
Parametric versus Non-parametric Tests	127
Which Is the Best Choice, Parametric or Non-Parametric?	128
What If the First Two Assumptions of the t-Test Are Not Met?	128
What If the Researcher Is Comparing More Than Two Means?	128
Post Hoc Tests to Compare Pairs of Means	130
How Do I Signify Pairwise Significant Differences on My Graph?	130
Tabular Comparisons: Comparing Frequencies through Chi-Square Test	131
Example Hypotheses Tested in Chi-Square	131
Correlation and Regression	132
How Are Regression and Correlation Different?	135
Some Other Differences between Regression and Correlation	135
The Strength of the Correlation Can Be Measured	135
Words of Caution about Correlation	135
References	135
<b>14 Population ecology basics</b>	<b>137</b>
Why Focus on One Species at a Time?	138
Where Should a Student Begin?	138
What Is a Population?	139
What Is Population Ecology?	139
When Did Population Ecology Arise?	139
How Is a Population “delineated?”	139
How Many Individuals Are in a Population?	139
How Are the Number of Individuals Counted?	140
What Is Relative Abundance?	140
What Is an Index?	140
What Is Noise?	140
More Difficulties: What about Counting Modular Units?	140
What about Counting Clones?	140
How Are Individuals Distributed?	141
Conclusions about the Population Concept	142
Vital Rates	142
Graphical Modeling for Animals	142
Incorporating Vital Rates to Make a Life Table	142
What Is a Life Table?	143
How to Read Life Tables	144
Life Tables in Ecology	144
What Is a Fecundity Table?	145
What Are the Different Types of Life Tables?	147
What Can We Conclude Overall about Life Tables?	147

Simple Equations for Modeling Population Growth	148
What Is Exponential and Arithmetic Growth?	148
The Equations for Exponential Growth	149
How Do We Assign Values to $r$ or $R$ ?	149
References	152
<b>15 Population ecology's profound questions</b>	<b>153</b>
What Is This Chapter About?	154
The Challenge for Students	155
The Remedy Is Clarity and Context	155
Spoiler Alert – Answers to This Chapter's Big Questions	155
Logistic Growth Models	155
The Equilibrium Theory Formalized in the 1920s	156
The Equilibrium Debate Begins in the 1930s	156
What "Regulates" Population Growth?	156
Non-equilibrium School of Thought	158
Support and Evidence for Density Independence	158
Which Side Was Right in the Equilibrium Debate?	159
Do We See the Logistic Pattern for Newly Colonized Species?	159
Why Not Logistic Growth – Abiotic Factors	161
Why Not Logistic Growth– Biotic Factors, the Allee Effect	161
Why Not Logistic Growth – Biotic Factors, Stunting	161
If the Sigmoid Curve Is Not Typical, What Is the Common Pattern?	161
Examples of Boom, Bust, and Irruptions	164
What Explains Boom and Bust– Phytoplankton Example	164
What Explains Boom and Bust– Self-Thinning in Trees	165
What Else Explains Boom and Bust – Biotic Effects, Compensatory Mortality	165
Why Do the Phytoplankton Populations Not Go Locally Extinct – The "Law" of Diminishing Returns in Hunting	166
Revisiting the Phytoplankton Case, Why the Bimodal Curve?	167
In the Equilibrium Debate, Who Was Right?	167
Life Histories ( $K$ Selected, $r$ Selected Species) and a Truce	168
The Iteroparity/Semeliparity Phenomenon and Its Significance	169
Problems with the $r$ and $K$ Hypothesis	169
Advances in Modeling: Time Lags, Stage Structure, Leslie Matrices	170
What Does Stage Structure Mean?	171
Matrix Projection Models	171
The Curious Phenomenon of Chaos	171
Further Theoretical Ideas – Metapopulations	172
What Are Stochastic Models?	173
Stochastic Modeling for Small Populations – Endangered Species Management	174
A Summary of Current Population Models – And a Wish List	175
Are There Any Good Models Not Based on the Logistic?	175
What Is the Current Understanding in the Equilibrium/Non-equilibrium Debate?	175
References	177
<b>16 Community ecology basics</b>	<b>181</b>
What Characterizes Community Ecology?	181
Questions Asked by Community Ecologists	182
What Are the Ways Organisms Can Interact?	182
What Is the Difference between Symbiosis, Mutualism, and Facilitation?	182
Summary of Mutualism	184
Commensalism and Amensalism	184
Predation	185



Herbivory	185
Parasitism	185
Competition	185
Competition: The Central Concept in Ecology?	186
References	187
<b>17 Theory in community ecology/competition</b>	<b>189</b>
Early Assumptions about Ecological Communities	190
Competition in a Garden	190
Predicting Winners through Lotka-Volterra Equations	190
How Do Environmental Conditions Affect Competition?	190
Does the Lotka-Volterra Model Apply Well to Natural Situations?	191
The Golden Age of Ecological Theory – Hutchinson, MacArthur, and Wilson	191
What Is a Niche?	191
The Hutchinsonian Definition of Niche	192
What Happens If Two Species Try to Occupy the Same Niche?	193
The Equilibrium Debate	193
The Theory of Island Biogeography	193
Simberloff-Diamond Debate: How to Do Science	195
Simberloff-Diamond Debate: SLOSS	195
What Is the Neutral Model in Ecology?	196
Ideas That Emerged Since 1975 in Understanding Community Structure	196
Endnotes, Updates, and Conclusions	197
References	198
<b>18 Predation</b>	<b>201</b>
Truth, Myth, and Controversy	201
The Answers Start with Definitions	202
More Definitions: Not All Predators Kill the Same Way	202
What Is Hyperpredation?	203
Ecological Theory Regarding Predation	204
Do Predator-Prey Dynamics Cycle?	204
How Can Predators and Prey Coexist?	205
The Insights of Holling	205
Plant Defenses against Herbivores	206
Modeling Predator-Prey Interactions	206
Keystone Predators	207
Keystone Species That Are Not Predators	207
Jane Lubchenco	208
Menge and Sutherland	208
References	208
<b>19 Succession</b>	<b>211</b>
Succession Overview	212
Types of Succession	212
Theoretical Questions about Succession	213
Theory of Succession	213
The Individualistic View of Succession	214
Resolution of the Debates	214
Models That Organize Ideas about What Controls Community Changes during Succession	214
Disturbance	215
Analysis of the Succession and Community Ecology Paradigm – Facilitation	215
Further Advances in Understanding and Modeling Mutualism	216
References	219

<b>20</b>	<b>Ecosystem ecology basics</b>	<b>221</b>
	What Characterizes Ecosystem Ecology?	221
	Characteristics of Ecosystem Ecology – Machine Theory	221
	Characteristics of Ecosystem Ecology – Holism	222
	Characteristics of Ecosystem Ecology – Emergent Properties	222
	Characteristics of Ecosystem Ecology – Systems Approach	222
	Characteristics of Ecosystem Ecology – Feedback Loops	222
	Characteristics of Ecosystem Ecology – Food Chains and Trophic Levels	223
	Characteristics of Ecosystem Ecology – Adaptive Management	223
	The Aquatic Ecology Legacy	223
	Legacy of Birge and Juday	223
	Raymond Lindeman	223
	The Odums	224
	The Savannah River Project in South Carolina	224
	Ecosystem Ecology after 1960 – Big Biology	224
	The IBP	225
	The Environmental Movement and Environmental Studies	225
	References	226
<b>21</b>	<b>Energy</b>	<b>227</b>
	The Ecosystem Machine	227
	What Is Energy?	228
	What Are Photons?	228
	Wavelengths or Frequencies?	228
	What Is Sound, MRI, CT, and Ultrasound?	229
	Back to the Ecosystem Machine – Energy Can Change Form	230
	Sun Energy and Its Effect on Earth's Atmosphere	230
	The Ocean Energy Budget	232
	El Nino Phenomena	232
	References	234
<b>22</b>	<b>Matter</b>	<b>235</b>
	What Is Nutrient Recycling	236
	Organizing Categories in Biogeochemistry – Compartments	236
	Organizing Categories in Biogeochemistry – State and Carbon Condition	236
	Nutrient Cycles	236
	Hydrologic Cycle	237
	Carbon Cycle	237
	Carbon in Water and Its Effect on pH	238
	Carbon Decomposition in Lakes	240
	Carbon Cycle Dynamics in General	240
	Nitrogen Cycle	240
	Final Analysis	242
	References	243
<b>23</b>	<b>Ecosystem regulation</b>	<b>245</b>
	Introductory Principles	245
	Why Is the World Green?	245
	Eutrophication in Lakes	246
	David Schindler	246
	More Lake Studies – Lake Michigan	248
	Solutions for Lake Michigan and the Great Lakes	248
	Whole Lake Experiments – Steve Carpenter	248
	What Does This Tell Us about the Regulation of Lakes?	249

	Trophic Cascades in Benthic Ecosystems?	250
	Nutrient Cycles in Terrestrial Ecosystems – Hubbard Brook	250
	What Regulates Ecosystems?	250
	Alternative Stable States	251
	Ecosystem Summary	251
	References	252
<b>24</b>	<b>Landscape ecology</b>	<b>253</b>
	Introduction	253
	Major Themes	253
	Vocabulary in Landscape Ecology	256
	Progression of Theory in Landscape Ecology	256
	1960s	256
	1970s	256
	1980s	257
	1990s	257
	Recent and Future Models	257
	Top Five Uses for Landscape Ecology	257
	Synthesis	258
	References	259
<b>25</b>	<b>Wildlife management and habitat ecology</b>	<b>261</b>
	Why Wildlife Management?	262
	The Leopoldian Basics of Wildlife Management	263
	Food Found in Edge	264
	Food Types	264
	Digestion – Birds	264
	Digestion – Mammals	265
	Are Salt Licks Useful? What about Other Supplements?	266
	Water	266
	Cover	266
	Space	267
	What Are Edge Effects?	267
	Is Edge the Villain?	267
	Is Clear-Cutting Detrimental to Songbirds?	268
	References	269
<b>26</b>	<b>Wildlife management for temperate farms and ranches</b>	<b>271</b>
	What Is the Goal of This Chapter?	272
	Four Management Priorities	272
	Applying Management Priorities to Farms and Ranches	272
	Treat Water Like Gold	272
	Provide a Mosaic	273
	Protect Unique and Important Habitat Features	273
	Minimize Invasive and Introduced Species	274
	Government Programs	274
	Conservation of Grassland at Airports	275
	References	276
<b>27</b>	<b>Wildlife management in temperate forests</b>	<b>277</b>
	What Type of Forest Has Optimal Conservation Value?	277
	Highest Priorities	277
	Treat Water Like Gold	280
	What Is the Ideal Width of a Riparian Zone?	281
	Provide a Mosaic	281

	Protect Unique and Important Habitat Features	285
	Shrubby Thickets in Eastern N. America	285
	Minimize Invasive Introduced Species	286
	Minimize Human Interference	286
	Ready to Write a Forest Management Plan?	287
	References	288
<b>28</b>	<b>Conservation biology</b>	<b>289</b>
	What Is Conservation Biology?	289
	Characteristics of Conservation Biology	290
	Conserving Species Diversity	290
	The Gap between the Number Named and the Number Existing	291
	Extinction Rates	291
	Population Decline	291
	IUCN Red List	291
	The Sixth Great Extinction Event	292
	What Are the Causes of the Current Extinction Crisis?	292
	Habitat Loss	292
	Overexploitation – Hunting and Overharvesting	293
	Global Climate Change	293
	Introduction of Non-Native Species	293
	Understanding Extinction – The Most Extinction-Prone Species?	294
	What Are the Most Extinction-Prone Habitats?	294
	Managing Land for Protection of Biodiversity	295
	Irreplaceability Approach to Managing Land – Hotspots	295
	Comprehensiveness Approach to Managing Land – Gap Analysis	295
	Representative Approach to Managing Land – Biosphere Reserves	296
	Connectivity Approach to Managing Land – Wildlands Network (Originally Known as Wildlands Project)	297
	Beyond Managing Land – Other Solutions for Conserving Biodiversity	297
	Conclusions	297
	References	299
<b>29</b>	<b>Restoration ecology</b>	<b>301</b>
	Restoration Approaches	301
	What Is Next After Identifying Spatial Scale and Place on the Spectrum?	302
	Values of the Stakeholders	303
	Setting Goals for the Restoration Effort	303
	The Diagnosis and Treatment Plan?	304
	Reference Ecosystems for the Project	304
	The Restoration Execution	304
	Hydrology (Apfelbaum and Haney 2010)	304
	Pollutants	305
	Biological Techniques	305
	What Are the Indicators of Success?	305
	Example: A Landscape Ecology Understanding of Restoration	306
	References	306
<b>30</b>	<b>Aquatic ecology</b>	<b>309</b>
	Introduction	310
	Without Biomes, How Are Waterways Classified?	310
	Waterway Classifications – Salt Content	310
	Classification of Freshwaters	311
	Classification of Wetlands	311

Ecology of Streams and Rivers	311
Characteristics of Streams from Source to Mouth	312
What Are the Food Sources for Animals in Streams?	314
Habitat Classification within Lakes	314
Stratification within Lakes	314
Is the Epilimnion Well Oxygenated?	316
Is the Hypolimnion Well Oxygenated?	316
The World Experienced by Plankton – Reynolds Number	316
Nutrient Content Classification of Lakes	317
What Characterizes Saltwater Ecosystems?	317
Tides	318
Major Ecological Communities in Oceans	318
References	319
<b>31 New perspectives in biogeography</b>	<b>321</b>
The Relevance of Biogeography	321
Subsections of Biogeography	321
The Constraint Hierarchy in Chapter 9	322
The Niche Concept	322
Large Spatial Scales	322
Regional Spatial Scales	323
Local Special Scales – Interspecific Interactions	323
How Biogeography Can Fundamentally Change Our Ideas about Communities and Ecosystems	324
The Future of Biogeography	324
References	324
<b>32 Wicked problems</b>	<b>325</b>
Introductory Principles	325
Essential Vocabulary	326
The Super Wicked	326
What Is Adaptation?	326
Resilience	326
References	328
<b>33 Epilogue – the evolution of an idea</b>	<b>329</b>
Historical Overview	329
Existing Organizational Ideas in Theoretical Concepts	329
Toward a New Understanding	329
A Simplified Organizational Scheme	330
Does Ecology Have Laws?	330
A Summary of Ecological Understanding – Narrative	330
Ideas Specific to Ecology – Global Scale	330
Ideas Specific to Ecology – Regional Scale	335
Ideas Specific to Ecology – Local Scale	336
The Present and Future	337
What Can We Do?	338
What Ecology Is and Is Not	338
References	340
<b>Index</b>	<b>341</b>