

Wetland Ecology

Third Edition

Richly illustrated in full colour and packed with examples from every major continent and wetland type, this third edition has been completely rewritten to provide undergraduates with a thoroughly accessible introduction to the basic principles. It divides the world's wetlands into six principal types and presents six major causal environmental factors, arranged by importance and illustrated with clear examples, making it easy for instructors to plan tailored lectures and field trips and avoid overwhelming students with unnecessary detail. It retains its rigour for more advanced students, with sections on research methods and experiments, and over a thousand classic and contemporary references. Each chapter ends with questions that review the content covered and encourage further investigation. With expanded sections on topical issues such as sea level rise, eutrophication, facilitation and the latest approaches to restoration and conservation, the new edition of this prize-winning textbook is a vital resource for wetland ecology courses.

Paul A. Keddy is an independent researcher who was a full professor at the University of Ottawa and then the first holder of the Schlieder Endowed Chair for Environmental Studies at Southeastern Louisiana University. He has published more than 100 scholarly papers on plant ecology and wetlands, as well as serving organizations such as NSF, NSERC, World Wildlife Fund and The Nature Conservancy. His first edition of *Wetland Ecology: Principles and Conservation* won the Society of Wetland Scientists' Merit Award. He has won multiple other prizes, most recently a Meritorious Service Medal from the Governor General of Canada. His other Cambridge University Press publications include *The World's Largest Wetlands* (2005), *Plants and Vegetation* (2007), *Plant Ecology* (2017), and *A Framework for Community Ecology* (2021).

‘Keddy’s new version of *Wetland Ecology* is even more readable, not stuffy; it successfully strives for comprehension, not memorization, imbued with questions and principled hypotheses to guide experiments and syntheses. He retrieves both older and newer writings as a scientist first, and also as a citizen-scientist with affection for personal curiosity and society.’

R. Eugene Turner, Louisiana State University, USA

‘This new edition is essential reading for all those around the globe interested in wetlands. The book emphasizes general principles and causal factors responsible for shaping natural wetlands and how they apply to restoration and conservation. Dr Keddy recalls how the old foundational studies contributed to building current understandings of wetland ecology. Numerous illustrations and probing concluding questions at the end of each chapter make the book a valuable teaching resource.’

Barry G. Warner, University of Waterloo, Canada

‘In this third edition of *Wetland Ecology: Principles and Conservation*, Dr Paul Keddy has once again shown his strong understanding of how wetlands function. Rather than minor changes and edits to the second edition, this is a reorganized and rewritten expansion, with new sub-sections that delve further into the subject matter. Reference to the classical wetland literature is retained, but wetland science is brought up to date with references through 2022. New examples are included to help explain principles, and a concerted effort was made to use international examples. The effect of humans on wetland functions is prominent in many sections. Most figures are now in colour, and many excellent colour photographs have been added to assist in understanding of the text. Inclusion of insightful questions after each chapter helps to make this book an excellent text for use in undergraduate and graduate courses.’

Douglas Wilcox, SUNY Brockport, USA

‘This is the most comprehensive book in wetland ecology. It explores the diversity and complexity of wetlands, covering a wide range of topics from ecology and functioning to restoration and conservation. These topics are presented clearly, they are superbly illustrated and organized in a way that makes this textbook of equal value to both students and researchers. A must-have book for anyone interested in wetlands.’

Vasilis Louca, University of Aberdeen, UK

Wetland Ecology

Principles and Conservation

THIRD EDITION

Paul A. Keddy



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This book, and in particular this latest edition, would not have been possible without the encouragement, support and hard work of my wife, Cathy Keddy, 1953–2022. Cathy was always available to offer informed opinions on the contents of the book. She also prepared some of the original figures, handled all the figure permissions and was a proof-reading tigress. In addition to her devoted collaboration with me for some fifty years, Cathy has left her own legacy of scientific reports and published papers in the realm of botany, plant ecology and conservation. She helped protect significant areas of wetland and forest across eastern Canada.



Cathy in 2018 after she received a Meritorious Service Medal from the Governor General of Canada.

Contents

Preface	<i>page xi</i>
1 Wetlands: An Introduction	1
1.1 Definitions and Distribution	2
1.2 Types of Wetlands	4
1.3 Wetland Soils	16
1.4 Flooding Stress: The Primary Constraint	21
1.5 The Scientific Method in Wetland Ecology: Causal Factors and Consequences	27
1.6 Secondary Constraints Produce Different Types of Wetlands	29
1.7 Wetlands Provide Valuable Services	35
1.8 Causal Factors in Wetland Ecology	39
1.9 Some More Complications for Wetland Classification	44
Conclusion	46
Questions for Review and Consideration	49
2 Flooding	51
2.1 Flood Pulses Are an Important Causal Factor	52
2.2 Some Biological Consequences of Flooding	55
2.3 A Survey of Water Level Fluctuations	63
2.4 General Relationships Between Wetlands and Water Level Fluctuations	76
2.5 Reservoirs, Dams and Floodplains	79
2.6 Predicting Wetland Responses to Flood Pulses	86
2.7 Extreme Events, Big Pulses, Megafloods and Hurricanes	90
Conclusion	91
Questions for Review and Consideration	92
3 Fertility	95
3.1 Experiments Show Effects of Nutrients on Wetlands	97
3.2 Descriptive Studies Also Show Effects of Nutrients on Wetlands	101
3.3 Nutrients Have Effects on Animals	104
3.4 A Brief Survey of Some Wetlands with Low Fertility	106
3.5 Some Other Issues Related to Fertility	109
3.6 Return to Causal Factors: A Global Model for Hydrology and Fertility	115
3.7 A Possible Global Synthesis on Fertility	116

viii **Contents**

3.8	Eutrophication: Humans Often Increase Nutrient Levels in Wetlands	117
3.9	A Global View of Nutrient Inputs to Wetlands	126
	Conclusion	127
	Questions for Review and Consideration	127
4	Natural Disturbance	131
4.1	Examples of Natural Disturbance and Its Effects on Wetlands	133
4.2	Disturbances Are Often Extreme Events	147
4.3	Disturbances Can Be Used in Wildlife Management	154
4.4	Recovery from Disturbance by Means of Seeds and Rhizomes	155
4.5	Anthropogenic Disturbances May Have Different Consequences	161
	Conclusion	166
	Questions for review and consideration	167
5	Competition	169
5.1	Some Examples of Competition in Wetlands	171
5.2	Competition Is Often One-Sided	176
5.3	Competition for Light Produces Competitive Hierarchies	177
5.4	Dominant Plants Are Often Larger than Subordinate Plants	180
5.5	Escape in Space: Competition in Patches	181
5.6	Escape in Time: Competition and Disturbance	182
5.7	Gradients Provide Another Way of Escaping in Space	182
5.8	Competition Gradients Produce Centrifugal Organization	186
5.9	Woody Plant Invasion of Wetlands: Competition for Light	189
5.10	A Rare Animal in a Rare Habitat: The Case History of the Bog Turtle	190
	Conclusion	192
	Questions for Review and Consideration	193
6	Herbivory	195
6.1	Some Herbivores Have Large Impacts on Wetlands	196
6.2	Wildlife Diets Document Which Animals Eat Which Plants	204
6.3	Plants Have Defences to Protect Them Against Herbivores	208
6.4	Today's Wetlands Have Many Missing Herbivores	211
6.5	There Are General Patterns in Herbivory	213
6.6	Humans Can Change Rates of Herbivory in Wetlands	215
6.7	Three Pieces of Relevant Theory	218
	Conclusion	224
	Questions for Review and Consideration	224
7	Burial	227
7.1	Exploring Rates of Burial	230
7.2	Plants Can Regenerate After Burial	242
7.3	Burial Has Impacts on Many Animal Species	246

	Contents	ix
7.4 Ecological Thresholds: Burial, Coastlines and Sea Level		248
7.5 So Is Sediment Bad or Good?		251
Conclusion		251
Questions for Review and Consideration		252
8 Other Factors		255
8.1 Salinity		255
8.2 Rising Sea Levels Are Increasing Salinity in Coastal Wetlands		265
8.3 Roads Change Wetlands		268
8.4 Logs and Coarse Woody Debris		271
8.5 Facilitation		274
8.6 Overhunting Effects on Wildlife		278
8.7 Human Population Density		281
Conclusion		284
Questions for Review and Consideration		284
9 Diversity		287
9.1 Introduction to Diversity in Wetlands		287
9.2 Four General Rules That Govern the Number of Species in Wetlands		292
9.3 Selected Examples of Diversity in Wetland Animals		296
9.4 Diversity of Wetland Plants		305
9.5 Some Theory: A General Model for Herbaceous Plant Communities		312
9.6 Conservation of Biological Diversity		318
Conclusion		319
Questions for Review and Consideration		320
10 Zonation		323
10.1 Shorelines as a Prism		323
10.2 Shorelines Provide a Model System for the Study of Wetlands		325
10.3 Possible Mechanisms of Zonation		328
10.4 Some Context for Future Experiments		342
10.5 Statistical Analysis of Zonation		343
Conclusion		353
Questions for Review and Consideration		354
11 Services and Functions		357
11.1 Wetlands Have High Production		357
11.2 Wetlands Regulate Climate		362
11.3 Wetlands Regulate the Global Nitrogen Cycle		369
11.4 Wetlands Support Biological Diversity		373
11.5 Wetlands Provide Recreation and Cultural Services		377
11.6 Wetlands Reduce Flood Peaks		381
11.7 Wetlands Record History		385

x Contents

11.8 Adding Up the Services: WWF and MEA Evaluate Wetland Services	388
Conclusion	391
Questions for Review and Consideration	392
12 Research: Paths Forward	395
12.1 Some Context: The Great Age of Explorers	395
12.2 Four Basic Types of Information	397
12.3 Limitations to Species-Based Research	401
12.4 Empirical Ecology	403
12.5 Assembly Rules Driven by Key Factors	406
12.6 Simplification through Functional Groups	413
12.7 Six Tactical Guidelines	428
Conclusion	431
Questions for Review and Consideration	432
13 Restoration	435
13.1 The Importance of Understanding Wetland Restoration	435
13.2 Three Examples	437
13.3 What Is Restoration?	442
13.4 Monitoring	446
13.5 When Does Restoration Succeed?	452
13.6 More Examples	453
13.7 One Big Problem: Invasive Species	460
13.8 A Brief History of Restoration	466
Conclusion	467
Questions for Review and Consideration	469
14 Conservation and Management	471
14.1 Humans Have Greatly Changed Wetlands	471
14.2 Wetlands Naturally Change with Time	481
14.3 Two Views on Conservation Objectives	484
14.4 Creating Reserve Systems	485
14.5 Wicken Fen: An Example of a Habitat Fragment	492
14.6 Building a Global Reserve System	495
14.7 Humans as the Biggest Problem	499
14.8 Conservation Objectives for Wetland Ecology	500
14.9 Scientific Objectives for Wetland Ecology	501
Conclusion	502
Questions for Review and Consideration	504
Bibliography	505
Index	570

Preface

Welcome, everyone, to this new edition of *Wetland Ecology*.

I hope that this new version retains all the virtues of the first and second editions, as well as now including important updates, fresh new examples and more illustrations. Yes, the good news is that we are making progress in both the science and applications of wetland ecology. I am delighted to be able to share them with you.

When I began the first edition back around 1995, I admit to being most unsatisfied with the state of both the science and applications of wetland ecology. It often seemed that the field consisted of immense numbers of facts and observations about wetlands without a set of guiding principles to connect them. Consider, in contrast, physics, where a mere handful of forces provide a unified view of the universe. I set out to write a book that introduced the general principles of wetland ecology, and the importance of using the scientific method to test them and rank them in order of importance. At that time, I was chronically ill and sometimes able to write only a few sentences a day. I recall working from my bed on the third floor of our old home on Chapel Street, in downtown Ottawa. That edition appeared in 2000.

In this new edition, I have sought to place even more emphasis upon unifying principles, particularly the handful of causal factors that create and influence wetlands (Chapters 2 to 8). After a chapter of introduction to wetlands, Chapter 1, I discuss each causal factor in turn, starting with the most important one, flood duration. These seven chapters provide a shopping list of the factors likely influencing each wetland that you will encounter. This shopping list applies wherever you live, be it in the northern temperate zone, the Himalayas, or the Amazon basin – or anywhere else you find a wetland. These same chapters provide important advice about manipulating these causal factors to restore and protect the world's wetlands.

In the earlier editions, I was a strong advocate of experimental testing of hypotheses about causal factors. I still am. But I have noted that even experiments can be carried out carelessly and routinely. I see more and more experiments that simply repeat previous work, often with little context, or without a serious attempt to properly connect the results with earlier studies. We could easily end up with a list of published experiments that still do not reveal general principles. So, if you are thinking about experiments in wetlands, this new edition also guides you gently toward causal factors that are important to include in future experiments.

This third edition has been written under trying circumstances, while I was seriously ill, in and out of hospital, and enduring a pandemic lockdown, but otherwise living deep in the country surrounded by a protected complex of wetlands and forests. My spouse Cathy Keddy and I began purchasing this land decades ago, managed to acquire nearly a square mile, and have now ensured long-term protection by donating an easement to the Mississippi Madawaska Land Trust (these properties are known as the Keddy Nature Sanctuary and Salamander Forest). My

xii Preface

wife Cathy was here caring for me every step of the way in preparing this new edition, and even worked diligently on getting permissions for each figure in this book while sitting at my bedside in the hospital. Alas, Cathy did not herself live to see this edition completed. One of her last emails to me was a reminder to find higher-resolution images for two *Wetland Ecology* figures. So, Cathy's diligence and devotion to this book, along with her love of wetlands and wild places, lives on in this edition. In addition, she herself helped protect a significant number of other wetlands in Ontario, including Byrne Big Creek Nature Preserve and Marble Woodlands. She also did original research on rare wetland plants in both Nova Scotia and Ontario ... but that is another story. Her dedication to *Wetland Ecology* was inspiring, and she was truly a proof-reading tigress.

I wrote the first edition in the belief that all of us could improve our approach to studying wetlands and teaching wetland ecology to the next generation. That same motivation carried me through this latest edition. In a few places you will read that I remain dissatisfied at the current state of knowledge and have left suggestions for future work. For example, I was really quite surprised at how rudimentary our numbers are for carbon storage in wetlands, and for species diversity in wetlands. In trying to fill such gaps, however, I wish to remind you that we still need to focus on the broad general principles that organize wetlands. And then, we need the wise application of these principles to restoration and conservation. The last two chapters of this book focus on wise application, and even include an original and cheerful figure that Cathy prepared showing the rate of expansion of protected natural areas around the world (Figure 14.15). This figure shows that we have made real advances in land protection within a single generation. I sometimes remind my audiences that the first textbook in ecology, Eugene Odum's *Fundamentals of Ecology*, was written the year I was born, 1953. So, in my lifetime we have made great progress in the understanding of ecology, and in the protection of wild places. It is now time for new students and younger scientists to take the field forward.

There is one final virtue of this new edition. At the last few conferences Cathy and I attended, I was struck by how much important work, already published, seems to have been forgotten. I have even heard that some professors now tell students not to read work more than five years old. This is a big mistake. We have enjoyed some decades of important accomplishments in ecology by hard-working scientists, and we cannot simply ignore that work because it is old. Good science is not "old", it is "foundational"! You cannot practise a scientific discipline without understanding its foundations. Getting back to physics, we still teach classic research in physics, and there is every reason to do the same in wetland ecology. So, to the best of my ability, I have retained and even expanded older work that I consider to be foundational. And, I have reproduced some classic illustrations too. If you do not read this older work, and do not teach it, there is every reason to fear that some unfortunate person will not only be unaware of it but will repeat it when it is quite unnecessary. As but one example, the capacity of large flocks of waterfowl to turn marshes into open water was documented back in 1932 – yet this work is routinely overlooked in modern studies of goose ecology in particular and herbivory in general (Chapter 6). I hope that this book will provide a collection of such foundational examples for the next generation of scientists and conservationists to build upon.

Enjoy the book, and please do your best to apply it to protecting the world's wild places. And, if, a few years from now, you are inspired to think it is time for a fourth edition, then I invite you to step forward and get to work.



Figure 1.1 The cover of the second edition of this book comes from a painting prepared by wildlife artist Howard Coneybeare to illustrate some important aspects of wetland ecology. Here are a few of them. The water line creates a clear difference in habitat conditions. Wetlands are important for wading birds. Reeds and aquatic plants are abundant, but most are rooted in the sediment, and their leaves must transport oxygen to roots. The abundance of fish illustrates the high primary production of wetlands. And the turtle illustrates a more subtle point: that much of what we know about wetlands is hidden below the surface of the water.