

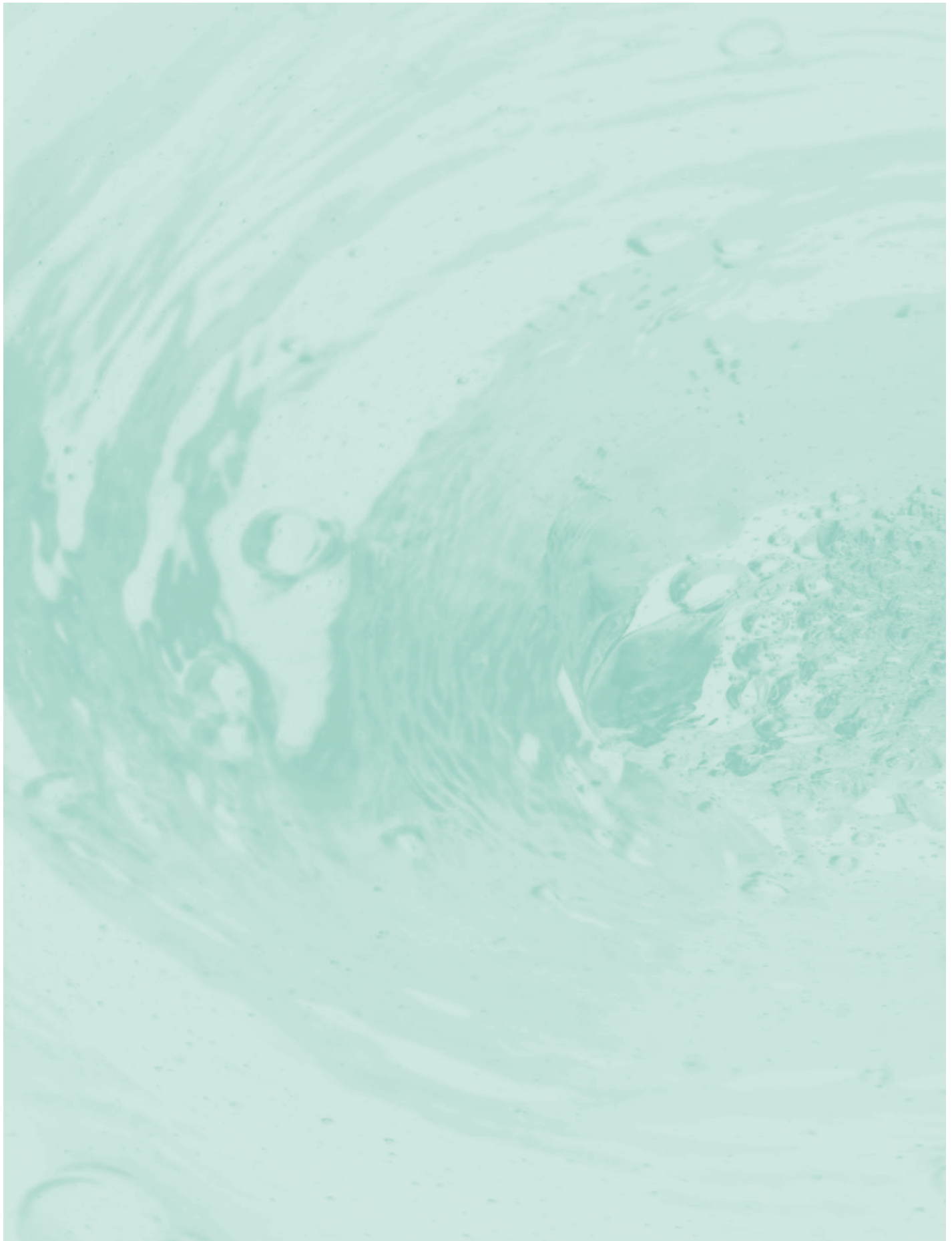
Wetland Ecology

Principles and Conservation, Second edition

Richly illustrated and packed with numerous examples, this unique global perspective introduces the fundamentals of wetland ecology from basic principles to advanced applications. Thoroughly revised and reorganized, this new two-color edition of this prize-winning textbook begins with underlying causal factors, before moving on to more advanced concepts that add depth and context.

- Examples carefully drawn from every major continent and wetland type give global context and help students see how their region fits into global patterns
- Many new illustrations and photographs increase the amount of natural history that supports the general principles
- A chapter on research methods provides useful guidance for the advanced student planning their own research
- Includes new chapters on wetland restoration and wetland services
- Clear chapter organization supports a wide variety of lecture plans, course objectives, and teaching styles

Paul A. Keddy, the first holder of the Schlieder Endowed Chair for Environmental Studies at Southeastern Louisiana University, has conducted wetland research as a professor of ecology for 35 years. He has published more than 100 scholarly papers on plant ecology and wetlands, as well as serving organizations such as the National Science Foundation, the National Science and Engineering Research Council of Canada, World Wildlife Fund, and The Nature Conservancy. His first edition of *Wetland Ecology: Principles and Conservation* won the Society of Wetland Scientists' Merit Award.



Wetland Ecology

Principles and Conservation

SECOND EDITION

PAUL A. KEDDY



Cambridge University Press
978-0-521-73967-2 - Wetland Ecology: Principles and Conservation, Second Edition
Paul A. Keddy
Frontmatter
[More information](#)

CAMBRIDGE UNIVERSITY PRESS
Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore,
São Paulo, Delhi, Dubai, Tokyo

Cambridge University Press
The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org
Information on this title: www.cambridge.org/9780521519403

© P. A. Keddy 2010

This publication is in copyright. Subject to statutory exception
and to the provisions of relevant collective licensing agreements,
no reproduction of any part may take place without
the written permission of Cambridge University Press.

First published 2010

Printed in the United Kingdom at the University Press, Cambridge

A catalog record for this publication is available from the British Library

Library of Congress Cataloging in Publication Data

Keddy, Paul A., 1953–

Wetland ecology : principles and conservation / Paul A. Keddy. – 2nd ed.

p. cm.

ISBN 978-0-521-51940-3 (Hardback)

ISBN 978-0-521-73967-2 (Pbk.)

1. Wetland ecology. 2. Wetland conservation. I. Title.

QH541.5.M3K44 2000

577.68–dc22 2010009142

ISBN 978-0-521-51940-3 Hardback

ISBN 978-0-521-73967-2 Paperback

Additional resources for this publication at www.cambridge.org/9780521519403

Cambridge University Press has no responsibility for the persistence or
accuracy of URLs for external or third-party Internet websites referred to
in this publication, and does not guarantee that any content on such
websites is, or will remain, accurate or appropriate.

Contents

Preface to the second edition *page* [ix]
Preface to the first edition [xiii]
Acknowledgments [xvii]

1 Wetlands: an overview [1]

1.1 Definitions and distribution [2]
1.2 Wetland classification [4]
1.3 Wetland soils [15]
1.4 Flood tolerance: the primary constraint [18]
1.5 Secondary constraints produce different types of wetlands [22]
1.6 Wetlands provide valuable functions and services [28]
1.7 Causal factors in wetland ecology [30]
1.8 More on definitions and classification of wetlands [34]
Conclusion [38]

2 Flooding [43]

2.1 Flooding and humans: an old story [46]
2.2 Some biological consequences of flooding [48]
2.3 A survey of water level fluctuations [54]
2.4 General relationships between wetlands and water level fluctuations [67]
2.5 Reservoirs, dams, and floodplains [68]
2.6 Predicting consequences for wetlands [74]
Conclusion [77]

3 Fertility [79]

3.1 Fertility and plants [80]
3.2 Infertile wetlands are constrained by low nutrient levels [84]
3.3 Other issues related to fertility [88]
3.4 Animals and fertility [94]
3.5 Eutrophication: too much of a good thing [96]
3.6 Calcium interacts with fertility in peatlands [104]
3.7 Fertility and hydrology explain a great deal about wetlands [106]
Conclusion [107]

4 Disturbance [109]

- 4.1 Disturbance has four properties [111]
- 4.2 Disturbance triggers regeneration from buried propagules [112]
- 4.3 Examples of disturbance controlling the composition of wetlands [113]
- 4.4 Disturbances can create gap dynamics [130]
- 4.5 Measuring the effects of disturbance in future studies [133]
- Conclusion [136]

5 Competition [139]

- 5.1 Some examples of competition in wetlands [141]
- 5.2 Competition is often one-sided [145]
- 5.3 Competition for light produces competitive hierarchies [146]
- 5.4 Dominant plants are often larger than subordinate plants [148]
- 5.5 Escape in space: competition in patches [148]
- 5.6 Escape in time: competition and disturbance [149]
- 5.7 Gradients provide another way of escaping in space [150]
- 5.8 Competition gradients produce centrifugal organization [153]
- 5.9 Rare animals are found in peripheral habitats: the case history of the bog turtle [156]
- Conclusion [158]

6 Herbivory [161]

- 6.1 Some herbivores have large impacts on wetlands [162]
- 6.2 Wildlife diets document which animals eat which plants [166]
- 6.3 Impacts of some other herbivores on wetlands [168]
- 6.4 Plants have defenses to protect them against herbivores [174]
- 6.5 General patterns in herbivory [179]
- 6.6 Three pieces of relevant theory [181]
- Conclusion [186]

7 Burial [189]

- 7.1 Exploring rates of burial [192]
- 7.2 Burial changes the species composition of wetlands [201]
- 7.3 Burial has impacts on many animal species [205]
- 7.4 Sedimentation, sediment cores, and plant succession [206]

- 7.5 Ecological thresholds: burial, coastlines, and sea level [207]
- 7.6 So is sediment bad or good? [210]
- Conclusion [211]

8 Other factors [213]

- 8.1 Salinity [214]
- 8.2 Roads [222]
- 8.3 Logs and coarse woody debris [225]
- 8.4 Stream type [227]
- 8.5 Human population density is becoming a key factor [229]
- Conclusion [233]

9 Diversity [235]

- 9.1 Introduction to diversity in wetlands [236]
- 9.2 Four general rules govern the number of species in wetlands [238]
- 9.3 Selected examples [242]
- 9.4 Some theory: a general model for herbaceous plant communities [255]
- 9.5 More theory: the dynamics of species pools [261]
- 9.6 Conservation of biological diversity [264]
- Conclusion [265]

10 Zonation: shorelines as a prism [269]

- 10.1 The search for fundamental principles [270]
- 10.2 Shorelines provide a model system for the study of wetlands [271]
- 10.3 Possible mechanisms of zonation [273]
- 10.4 Zonation and changing sea level [286]
- 10.5 Statistical studies of zonation [289]
- 10.6 General lessons from analysis of zonation [298]
- Conclusion [299]

11 Services and functions [301]

- 11.1 Wetlands have high production [302]
- 11.2 Wetlands regulate climate [306]
- 11.3 Wetlands regulate the global nitrogen cycle [310]
- 11.4 Wetlands support biological diversity [314]
- 11.5 Wetlands provide recreation and cultural services [317]
- 11.6 Wetlands reduce flood peaks [319]

- 11.7 Wetlands record history [323]
- 11.8 Adding up the services: WWF and MEA evaluate wetland services [325]
- Conclusion [328]

12 Research: paths forward [331]

- 12.1 Some context: the great age of explorers [332]
- 12.2 Four basic types of information [334]
- 12.3 Limitations to species-based research [337]
- 12.4 Empirical ecology [338]
- 12.5 Assembly rules driven by key factors [341]
- 12.6 Simplification through aggregation into groups [347]
- 12.7 Six tactical guidelines [360]
- Conclusion [363]

13 Restoration [365]

- 13.1 The importance of understanding wetland restoration [366]
- 13.2 Three examples [367]
- 13.3 More on principles of restoration [373]
- 13.4 More examples [377]
- 13.5 One big problem: invasive species [383]
- 13.6 A brief history of restoration [385]
- Conclusion [387]

14 Conservation and management [391]

- 14.1 Humans have greatly changed wetlands [392]
- 14.2 Wetlands have changed with time [397]
- 14.3 Two views on conservation objectives [400]
- 14.4 Protection: creating reserve systems [403]
- 14.5 Problems and prospects of reserve systems [411]
- 14.6 More on restoration [415]
- 14.7 So what shall we create with restoration? [416]
- 14.8 Indicators: setting goals and measuring performance [417]
- 14.9 Humans as the biggest problem [424]
- Conclusion [425]

References [427]

Index [476]

The color plates are situated between pages 238 and 239

Preface to the second edition

Why a second edition? And how different is it from the first? These are two obvious questions that a writer must address. Overall, this is a major revision in form, but built around the same principles. Some chapters, such as Flooding and Fertility, are revised with new figures. Other chapters, including Services and functions and Restoration, are entirely new.

Having had ten years to observe reactions to the first edition, I now have a better understanding of how ecologists in general, and American students in particular, think about wetlands. I have therefore re-balanced and reorganized the book to better reflect these realities. At the same time, I have stuck to the view that a small number of general principles are needed to unify wetland ecology, and that a small set of causal factors are present in all wetlands, albeit in differing relative importance.

Over the book as a whole, I have reorganized the flow of ideas to place causal factors nearer the beginning, and in order of relative importance. Students, then, can start immediately with effects of flooding in Chapter 2 and fertility in Chapter 3. The more conceptually difficult material (such as zonation, biodiversity, and valuation of ecological services) has been moved to later in the book.

Each chapter begins with a few basic principles up front and early, usually accompanied by a few clear examples to illustrate the principle. The more difficult concepts are introduced later in each chapter. The inevitable exceptions also occur here – but only once the general principle is well established.

There is an entire new restoration chapter which draws upon practical examples from around the world, including the Everglades, coastal Louisiana, the Danube River, and the Yangtze River. As noted in the first edition, there is still an unfortunate tendency for wetland ecologists to work in geographical and taxonomic isolation, and this chapter tries to bring together a consistent worldwide perspective on restoration.

There is also a new chapter on research. I have moved certain topics to this chapter, in the view that an overview of tactics and strategies may be of most use to advanced students who are planning their own investigations.

Biodiversity conservation grows in importance with each passing year. I have rewritten the chapter on biodiversity to make the hierarchy of causation more clear. I have also introduced new information such as the IUCN *Red List* and principles for designing wetland reserve systems. I have also introduced wetland evaluation systems for land use planning.

x Preface to the second edition

I have removed examples and topics that time has taught were extraneous, and added in others, always trying to keep an international perspective, since wetland plants and animals do not recognize political borders. There are many new figures, including some drawn specifically for this book, as well as new photographs.

Names are always an issue. I have used common names for most groups where nomenclature is well established – particularly birds and mammals – but scientific names for plants and insects, owing to their diversity. In some cases, in appropriate context, I deviate from this rule. Since names continue to change (e.g. *Scirpus*, *Schoenoplectus*), I have resisted the temptation to make everything internally consistent. This sort of consistency introduces problems of its own – for example, if I were to change every incidence of *Scirpus* to *Schoenoplectus*, then students consulting the original papers could be misled. Hence, in most cases, I have used names that were current when the work was published.

One of the most basic principles of science is to have multiple working hypotheses. I have tried to include competing points of view in this book. I would like to think that we could encourage our students to accept that there are unknowns in science, and to respect differences of opinion as healthy, and as an opportunity for designing the research that will resolve the confusion.

Some people think the only way to read a book is to start at the beginning and plow through every word until the end, which might indeed seem challenging. This is not, in my opinion, the best option for using this book, or any book. Here are some others. (1) You could start by flipping through the book for just the color plates – they tell a story of their own. (2) Next you could choose a handful of black-and-white illustrations that catch your attention – each also tells a story. (3) You could read the first chapter for an overview of wetlands – the short story. (4) You could then read Chapters 2–8 that deal with causal factors in wetlands. (5) If you are a busy manager, you could consult Chapters 13 and 14 for restoration and conservation issues. (6) I would suggest that Chapters 9–12 be left for a second reading. They deal with more advanced topics that may be of more interest to graduate students and research scientists. (7) A very short course in wetlands and conservation would consist of Chapters 1 and 14 only. A longer course in wetlands and conservation would consist of Chapters 1–8 and 13–14. (8) Each chapter could also stand alone, so if there is a particular topic that you need to learn about – say nutrients or grazing – go directly to the chapter on that topic. (9) Finally, as I still have to remind my classes, there is an index. Use it. Some time has gone into selecting these topics. It is not just generated by a machine, but by human thought. Feel free to dive into a selected topic – say dams or coarse woody debris or amphibians or fire – and then work your way outward. Overall,

the point is to make this book your own and use it in whatever way helps you grasp the material most quickly.

Although the volume of information on wetlands will always grow, I would like to think that the principles in this book are timeless, since wetlands themselves will always be organized by a few causal factors, leaving us with the task of documenting their consequences – for ecological processes, for surrounding landscapes, and for the wild species that live in wetlands.

PAUL KEDDY

Preface to the first edition

According to Bernard Shaw, writer of many a lengthy preface, the lesson intended by an author is hardly ever the lesson the world chooses to learn from his book. If Shaw is right (and who would risk disagreeing with him), why would anyone trouble to write a book? And why a book on wetlands?

In answer to the first question, the motivation of all writers includes a healthy dose of inspiration, frustration, and ego gratification. Events can conspire to feed these forces, with unfortunate consequences for both writers and the public. When Dr Birks first asked me to write this book, I therefore declined. In part, I was not convinced that a need existed.

Bringing a new book into the world requires the shouldering of parental obligations. (While one can keep one's rowdy children at home, a book is always on public display.) The world certainly has too many children, and only the most devoted reader, deep-pocketed publisher, or hardened bibliophile could believe that every author who is inclined towards writing should do so. The self-restraint that is a virtue in biological procreation, may be equally so for aspiring authors.

Events can, however, over-ride caution. Illness, like the threat of a hanging, tends to concentrate and clarify one's mind. Moreover, during the days chained to the wall before the hanging, one is inclined to dwell on shortcomings, particularly those of one's associates. But I digress. This is, after all, a preface to a book on wetlands.

The principal objective of this book is to try to provide some unity and coherence in the study of wetland ecology. To do so, I have organized this book into three sections. The first section (Chapters 1–3) emphasizes the properties of wetlands, or, in statistical terms, the dependent variables in our inquiry. The next section (Chapters 4–9) addresses the environmental factors that control these properties: in statistical terms, the independent variables. In these chapters, I freely range across wetland types and geographic regions. My self-assigned task is to illustrate the relationships among properties and environmental factors, whether they occur in an Amazonian floodplain, prairie pothole, boreal peatland or tidal marsh. The book may still tend to emphasize the types of wetlands with which I am most familiar, but this should not distract a reader from principles and scientific generalities. The final section (Chapters 10–12) illustrates some larger frameworks for studying the relationships between ecological properties and conservation biology. Assembly rules, functional groups, and restoration ecology receive particular attention.

xiv Preface to the first edition

The book has been prepared with several audiences in mind. It is intended as a text book for senior undergraduates, an introduction to key factors controlling wetlands for busy managers, and as general reading for any scientist intending to work in wet habitats. Further, the first chapter will, I hope, introduce the essential features of wetlands to a general reader; while superficial in places, it is less so than many popular treatises, and it will simultaneously remind more experienced readers about the salient features that make wetlands of particular interest to humanity. The main body of the book presents a general framework for the study of wetland communities. For practising wetland scientists I had an expanded purpose. The discipline of wetland ecology is currently Balkanized by habitat types, geographic regions, and study organisms. Many of the studies of particular wet habitats that I have read over the past decade have seemed blissfully unaware of nearly identical work in other habitats, wet or dry. By combining all wetland types within one book, I have tried to restore some conceptual unity to the discipline by emphasizing the essential processes that all wetlands share, and then by illustrating the ways in which some of them differ. Hence the part of the title referring to principles. I hope that specialists will be stimulated by seeing the parallel advances in habitat types and geographic regions other than their own, and that this enriched context will assist them with further progress within their own areas of specialization. In exchange, I trust they will forgive the inevitable oversights that annoy a specialist.

The final part of the title mentions conservation. Sound science is the essential foundation of good ecosystem management. Ecosystem management emphasizes ecological processes and their interconnections. This book takes exactly such a perspective: it begins with patterns present in wetlands, and then proceeds to the processes and interconnections that produce the patterns. The focus is upon communities and ecosystems themselves; implications for global biogeochemical cycles are mentioned from time to time, but they are not a primary focus. Rather, it is assumed that, in most cases, maintaining the normal processes within wetlands will ensure that their valued functions continue to occur. When, and if, it is necessary to manipulate wetlands in order to change some aspect of their global function, say, to increase wildlife production or to decrease methane production, this will always require knowledge of processes at the local community scale.

I first thought that such a book might be too personal a perspective on wetlands. Fields of enquiry are now so large that perhaps only multiauthored works are appropriate. However, my editor and advisor, Alan Crowden, has convinced me that many readers actually prefer a systematic and personal account of a field to a series of edited papers. Moreover, I have slowly convinced myself, too, that the existing literature is far too fragmented and diffuse and therefore confused. I have already written bluntly, perhaps too much so, of my views on symposium reports and festschrifts (Keddy 1991a, b, c). A number of recent symposium volumes on

wetlands appear to be little more than expensive books with a haphazard collection of people giving a haphazard collection of papers with no unifying theme whatsoever except for the fact that all work in wet areas. Surely we can aspire to do better than this. While my own community oriented perspective undoubtedly has its limitations, it at least compensates with continuity and consistency.

I have tried to emphasize several research strategies. These include (i) greater emphasis upon measurable properties of ecosystems and (ii) the relative importance of different environmental factors that produce pattern. Far too many studies in wetlands consist, it seems, of little more than drawings of transects through wetlands or autecological studies of small groups of species living in wet places. Neither of these latter styles will inspire bright young scientists to enter the field. In fact, wetland community ecology is exciting, challenging, socially significant, and worthy of our best minds.

At first I was going to include a chapter on applications. But then my continued resistance to the forced distinction between theoretical and applied ecology intervened. Throughout this book there is an interplay between theory and application. In combining them we can achieve maximum impact upon knowledge with a minimal expenditure of effort. An appeal to efficiency itself ought to be sufficient, but we are now faced, in addition, with the rapid loss of the very ecosystems we study. We must hasten if we are to solve some of the growing problems with management of wetlands. Throughout the book there are practical examples that show that wetland ecologists have a great many useful things to say to environmental managers. Altered hydrology, eutrophication, loss of species – these are fundamental environmental issues and conceptual axes in the study of wetlands. There is therefore no single chapter on conservation alone because the entire book is about conservation.

Were it not for the inseparability of theory and application, this book might be considered schizophrenic. It is written with both the basic researcher and the resource manager in mind. I hope that both bright, young graduate students and cynical, overworked managers can benefit from consulting it. I have made abundant use of subheadings and figures so that parts that, at least on first reading, appear of secondary importance can easily be skipped. Each chapter will, I hope, be able to stand alone. Those needing an immediate short course, or feeling too harried to deal with an entire book, can obtain an overview of essentials with Chapters 1, 4, 5, and 12. Chapters 10 and 11 are the most speculative, and can be safely omitted from a first reading since they deal more with future possibilities than established phenomena.

Some of the limitations of the book are deliberate. I have placed an emphasis upon communities and on the factors than influence them. Although nutrient cycling is an important topic, I have not dealt with it extensively except

under the heading of eutrophication. Similarly, systems models are already well covered in works such as Good *et al.* (1978), Mitsch and Gosselink (1986), and Patten (1990). Apart from eutrophication, I have left the topic of toxic contaminants to other better-qualified authors. There are also two fine compendia which already describe wetland types by region (Gore 1983; Whigham *et al.* 1992). I have not tried to duplicate their efforts. The logical structure of this book is built upon similarities in process rather than geography.

Finally (restrictions on travel are inclined to make one long-winded) this is not *just* a book on wetlands. I have tried to present not only an overview of wetland ecology, but to illustrate the general procedures with which one can dissect an ecological community to search for patterns and the mechanisms that may cause them. In this way, I hope to not only contribute to our understanding of wetlands, but to illustrate practices that will be of use in other vegetation types and ecological communities.

Since we began with Shaw, let us also close with him too. A successful book, according to Shaw, will impress the strong, intimidate the weak and tickle the connoisseur.

PAUL KEDDY

Acknowledgments

Let me start by acknowledging the many wetland ecologists whose work, cited or not, has produced the body of knowledge that allows such a book to be written. I hope I have faithfully transmitted the information and experience that they worked so hard to uncover. I have tried to give credit where it is due, but any voyage through a vast literature is bound to be personal; if you feel your work has not received the credit due, forgive me. Those who kindly contributed figures are acknowledged in the figure captions. Beyond this, I should mention some colleagues who cheerfully corresponded with me to help clarify issues. These included Barbara Bedford, Bruce Bury, Dan Campbell, Fangliang He, John Lopez, Reid Kreutswieser, Ted Mosquin, Susan Newman, Michael Redmer, Stephen Richter, Clay Rubec, Fred Sklar, Rich Seigel, Orieta Hulea, Li Bo, Eugene Turner, Aline Waterkeyn, Doug Wilcox, and Robert Zampella. Beyond this Cathy Keddy has served dutifully in every task from chasing references to discussing content. The staff of the Carleton Place Public Library have also been cheerful in tracking down technical works from universities far afield.

Artists and photographers are often overlooked. I have tried to acknowledge them in captions wherever possible. Special thanks go to Howard Coneybeare, who produced the cover – a new version of the original line drawing used in the first edition – as well as Figure 2.18. I thank Rochelle Lawson for taking the plunge many years ago and preparing figures including 6.9, 6.11, 7.12, and 9.1. Thanks too to Betsy Brigham who prepared figures including 1.14, 2.19, 5.12, and 14.11. Finally, my son Ian and my spouse Cathy have spent many hours upgrading and refining older figures so they can inspire, educate, and delight a new generation of students. Perhaps a few younger readers will even consider the career path of biological illustration.

Chapter contents

- 1.1 Definitions and distribution
- 1.2 Wetland classification
- 1.3 Wetland soils
- 1.4 Flood tolerance: the primary constraint
- 1.5 Secondary constraints produce different types of wetlands
- 1.6 Wetlands provide valuable functions and services
- 1.7 Causal factors in wetland ecology
- 1.8 More on definitions and classification of wetlands
- Conclusion