

Ecological Studies, Vol. 207

Analysis and Synthesis

Edited by

M.M. Caldwell, Washington, USA
G. Heldmaier, Marburg, Germany
R.B. Jackson, Durham, USA
O.L. Lange, Würzburg, Germany
H.A. Mooney, Standford, USA
E.-D. Schulze, Jena, Germany
U. Sommer, Kiel, Germany

Ecological Studies

Further volumes can be found at springer.com

Volume 189

Ecology of Harmful Algae (2006)

E. Granéli and J.T. Turner (Eds.)

Volume 190

Wetlands and Natural Resource Management (2006)

J.T.A. Verhoeven, B. Beltman,
R. Bobbink, and D.F. Whigham (Eds.)

Volume 191

Wetlands: Functioning, Biodiversity Conservation, and Restoration (2006)

R. Bobbink, B. Beltman, J.T.A. Verhoeven,
and D.F. Whigham (Eds.)

Volume 192

Geological Approaches to Coral Reef Ecology (2007)

R.B. Aronson (Ed.)

Volume 193

Biological Invasions (2007)

W. Nentwig (Ed.)

Volume 194

Clusia: A Woody Neotropical Genus of Remarkable Plasticity, and Diversity (2007)

U. Lüttge (Ed.)

Volume 195

The Ecology of Browsing and, Grazing (2008)

I.J. Gordon and H.H.T. Prins (Eds.)

Volume 196

Western North American Juniperus Communities: A Dynamic Vegetation Type (2008)

O. Van Auken (Ed.)

Volume 197

Ecology of Baltic Coastal Waters (2008)

U. Schiewer (Ed.)

Volume 198

Gradients in a Tropical Mountain Ecosystem of Ecuador (2008)

E. Beck, J. Bendix, I. Kottke,
F. Makeschin, R. Mosandl (Eds.)

Volume 199

Hydrological and Biological

Responses to Forest Practices: The Alsea Watershed Study (2008)

J.D. Stednick (Ed.)

Volume 200

Arid Dune Ecosystems:

The Nizzana Sands in the Negev Desert (2008)

S.-W. Breckle, A. Yair,
and M. Veste (Eds.)

Volume 201

The Everglades Experiments: Lessons for Ecosystem Restoration (2008)

C. Richardson (Ed.)

Volume 202

Ecosystem Organization of a Complex Landscape:

Long-Term Research in the Bornhöved Lake District, Germany (2008)

O. Fränzle, L. Kappen, H.-P. Blume,
and K. Dierssen (Eds.)

Volume 203

The Continental-Scale Greenhouse Gas Balance of Europe (2008)

H. Dolman, R. Valentini, and A. Freibauer (Eds.)

Volume 204

Biological Invasions in Marine Ecosystems: Ecological, Management, and Geographic Perspectives (2009)

G. Rilov and J.A. Crooks (Eds.)

Volume 205

Coral Bleaching: Patterns, Processes, Causes, and Consequences (2009)

M.J.H van Oppen and J.M. Lough (Eds.)

Volume 206

Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change (2009)

M. Wahl (Ed.)

Volume 207

Old-Growth Forests: Function, Fate and Value (2009)

C. Wirth, G. Gleixner, and M. Heimann (Eds.)

Christian Wirth • Gerd Gleixner • Martin Heimann
Editors

Old-Growth Forests

Function, Fate and Value



Springer

Editors

Dr. Christian Wirth
Max-Planck-Institute for
Biogeochemistry
Hans-Knöll-Str. 10
07745 Jena
Germany
cwirth@bgc-jena.mpg.de

Dr. habil. Gerd Gleixner
Max-Planck-Institute for
Biogeochemistry
Hans-Knöll-Str. 10
07745 Jena
Germany
ggleix@bgc-jena.mpg.de

Prof. Dr. Martin Heimann
Max-Planck-Institute for
Biogeochemistry
Hans-Knöll-Str. 10
07745 Jena
Germany
martin.heimann@bgc-jena.mpg.de

ISBN 978-3-540-92705-1 e-ISBN 978-3-540-92706-8
DOI: 10.1007/978-3-540-92706-8

Ecological Studies ISSN 0070-8356

Library of Congress Control Number: 2009926062

© Springer-Verlag Berlin Heidelberg 2009

This work is subject to copyright. All rights are reserved, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilm or in any other way, and storage in data banks. Duplication of this publication or parts thereof is permitted only under the provisions of the German Copyright Law of September 9, 1965, in its current version, and permission for use must always be obtained from Springer. Violations are liable to prosecution under the German Copyright Law.

The use of general descriptive names, registered names, trademarks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

Cover illustration: This book explores how ecosystem functions change with progressive forest development from young over mature to old-growth forests. The photographs by Thomas Stephan illustrate the change in canopy structure with stand age in a mixed beech forest in the Hainich National Park, Thuringia, Germany.

Cover design: WMXDesign GmbH, Heidelberg, Germany

Printed on acid-free paper

Springer-Verlag Berlin Heidelberg (www.springer.com)

This book is dedicated to Ernst-Detlef Schulze

Homage to Ernst-Detlef Schulze

During the course of a very long career I have met legions of scientists but none comparable to Ernst-Detlef Schulze. I have had the pleasure of knowing him since the beginning of his extraordinary career and he is certainly one of the most distinctive and unforgettable scientists that I have encountered. I first met him when he came to the University of California at Los Angeles for a master's degree after studying forestry in Göttingen, Germany. Unfortunately, he set a very bad example for me as to what I should expect from master's students for the rest of my academic career, which was just starting. In less than a year while he was at UCLA, he completed a successful thesis performed at 3,000 m elevation, during the wintertime, on the gas exchange of needles of bristlecone pine – the oldest-known living tree – foreshadowing his lifelong interest in old forests and long-lived trees.

But that arduous thesis was only a part of his accomplishments during that brief period. He also participated in a tropical program in Costa Rica, where he completed a publishable study on soil respiration. Then, to cap off his stay at UCLA he traveled by vehicle to the Arctic on his way home. I am sure I am forgetting many other things he did in his spare time during his short stay with us. As far I can see he has never slacked off the torrid pace to this day since that awesome start. He went on to study for his PhD with the pioneering and leading plant physiological ecologist Otto Lange at the University of Würzburg. He subsequently went on to establish a vigorous plant ecology program at the University of Bayreuth. He then became a founding director of the Max Planck Institute for Biogeochemistry in Jena, Germany.

Since those early days, I have had the privilege of working with Detlef in many parts of the world – the redwoods of California, the tropical dry forests of Mexico, the temperate forests of Argentina, and the sand dunes of the Kalahari. In all of these studies he used his unique approach to science. He dives into the system with ferocious intensity, learning about the system as he goes by probing until he finds the critical measurements needed to test his hypotheses. His desire to learn, first-hand, about the functioning of the diversity of ecosystems of the world can be appreciated by those who visit his institute, where there are displays of wonderful

pictures of all of the ecosystems where he has worked. Clearly he has been inspired, as have all ecologists, by the pioneering studies of Alexander von Humboldt seeing, doing and learning.

His deep knowledge about science and science history is phenomenal. A field trip with him is incredibly interesting since he can tell you everything about an area that you would want to know: its history, the geomorphology, and its natural history. If he is driving during his exposition, the trip can be very exciting and certainly death defying.

Detlef has published extensively. It is lucky that electronic PDF files have been developed this past two decades since without them I would have run out of file cabinet space for his prodigious contributions. He has led the way in melding process level physiological ecology with ecosystem and landscape functioning. His strong contributions and interests in the carbon cycle in recent years are reflected in the final chapters of his monumental *Plant Ecology* textbook at one level and, at another, his work with the IPCC and the Framework Convention on Climate Change.

For a long time, Detlef has been interested in bringing attention to the old-growth forests of the world and the important role they play in so many environmental and social dimensions but in particular in carbon storage. This book is a fitting tribute to Detlef's deep interest in this topic as well as to his enormous accomplishments. He should be very gratified to see all of the new and exciting insights that have been brought together in this volume. Hopefully it will provide a stimulus for greater protection of those remaining islands of a once vast sea of old-growth forests with their extraordinary storehouses, of not only carbon, but also biotic diversity.

Harold A. Mooney
Stanford University, Stanford, California, USA

Preface

How do old-growth forests function in comparison to younger and managed stands? There exists a whole suite of negative attributes that are commonly used to characterise the old-growth stage (e.g. ‘senescent’, ‘over-mature’, ‘break-up’, ‘decay’) implying that these forests are less vigorous, less productive and less stable than earlier stages of forest development. Another line of thinking that goes back to Clement’s climax concept [Clements FE (1936) Nature and structure of the climax. *J Ecol* 24:252–84] and Odum’s ecosystem theory [Odum EP (1969) Strategy of ecosystem development. *Science* 164:262–270] emphasises the notion of a compositional and biogeochemical equilibrium: The same set of species replaces itself via gap-phase regeneration, and input of carbon and nutrients equals the output. It is the latter perception, which suggests the inability of old-growth forests to sequester carbon, that led to the exclusion of non-managed old-growth forests from the carbon accounting schemes of the Kyoto-Protocol of the United Nations Framework Convention on Climate Change (UNFCCC). In the last two decades, an increasing number of ecological studies employing novel methods, improved sampling designs, and large datasets have yielded results that challenge these views of decline or neutrality.

Synthesising the new findings and integrating them into a more comprehensive picture of old-growth forest functioning was the goal of a symposium entitled “Old-growth forest: function and value of a vanishing ecosystem”, which was held at the Max-Planck-Institute for Biogeochemistry in Jena, Germany, on 12–13 September 2006. A second, equally important purpose of this symposium was to celebrate the 65th birthday of Ernst-Detlef Schulze – one of the founding directors of our institute – to whom this book is dedicated. His endless scientific curiosity in general and his long-standing fascination with old-growth forests in particular inspired a large portion of the research documented in this book.

During the production of this book it turned out that many authors were willing to go far beyond a mere review of existing studies. A large number of chapters in this book present new original data and comprehensive meta-analyses based on large datasets that have so far not been evaluated in the context of old-growth forest research. Many people have contributed to this book. In particular, we would like to

thank the main authors of this book, who have all contributed to the overall effort by providing constructively critical reviews of one or several chapters. Among them, we are specifically indebted to Jeremy Lichstein, who carried the extra load of reviewing the introduction and synthesis chapters. In addition, we would like to thank the following external reviewers: Richard Birdsey, Ivan Jansen, Jill Johnstone, Till Pistorius, and Thomas Wutzler. Two other ‘external’ reviewers, Göran Ågren and Sébastien Fontaine, got so deeply involved in the book project that they eventually became co-authors. Martina Mund, Marion Schrumpf, Anja Fankhänel, and Natalia Ungelenk provided critical comments and helped with the acquisition of literature. Annett Börner provided superb software support and Dirk Sawade took on the great task to improve and harmonize the figures and graphics presented in this volume.

Without the help of Dorothea Frank and Angela Nüske from the Organismic Biogeochemistry Group of our institute, this book would probably not exist. They helped with just about everything, from erasing typos, pre-formatting figures, critically reviewing the chapter contents, adding mark-ups for the subject indices and the glossary, to chasing up manuscripts, reviews and revisions from over-committed scientists.

Finally, we would like thank our families for their patience in enduring our absent-mindedness during the writing of this book.

Jena, February 2009

Christian Wirth
Gerd Gleixner
Martin Heimann

Contents

Part I Introduction

1 Old-Growth Forests: Function, Fate and Value – an Overview	3
Christian Wirth, Gerd Gleixner, and Martin Heimann	
1.1 Old-Growth Forest Perception	3
1.2 Old-Growth Forest Services	5
1.3 Aims and Scope	5
References	9
2 Old-Growth Forest Definitions: a Pragmatic View	11
Christian Wirth, Christian Messier, Yves Bergeron, Dorothea Frank, and Anja Fankhänel	
2.1 Introduction	11
2.2 Old-Growth Forest Definitions and their Limitations	12
2.2.1 Structural Definitions	12
2.2.2 Successional Definitions	15
2.2.3 Biogeochemical Definitions	18
2.3 Use of the Term “Old-Growth” – a Literature Survey	19
2.4 Old-Growth and the Disturbance Spectrum	24
2.4.1 Temporal Scale	24
2.4.2 Spatial Scale	27
2.5 Identifying Old-Growth – the Conservation Perspective	27
2.6 Conclusions and Pragmatic Considerations	29
References	31
3 Old Trees and the Meaning of ‘Old’	35
Fritz Hans Schweingruber and Christian Wirth	
3.1 Introduction	35
3.2 Longevity of Conifers and Angiosperms	35
3.3 What Limits the Life Span of a Tree?	39
3.3.1 Programmed Cell Death	39
3.3.2 Whole Plant Longevity – Internal Versus External Factors	40

3.4 Concluding Remarks	52
References	53

Part II Aboveground Processes

4 Ecophysiological Characteristics of Mature Trees and Stands – Consequences for Old-Growth Forest Productivity	57
Werner L. Kutsch, Christian Wirth, Jens Kattge, Stefanie Nöllert, Matthias Herbst, and Ludger Kappen	
4.1 Introduction	57
4.2 Increased Respiratory Demand	57
4.3 Limitations of Photosynthesis	58
4.3.1 Hydraulic Limitation	58
4.3.2 Reduced Sink Strength	62
4.4 Stand-Level Controls	63
4.5 Community and Ecosystem Constraints on Age/Size-Productivity Relationships	65
4.5.1 Light, Water and Nutrient Availability	67
4.5.2 Shifts in Ecophysiological Traits with Changes in Community Composition	67
4.5.3 Imperfect Acclimatisation of Late-Successional to Full Sunlight: A Case Study on European Beech (<i>Fagus sylvatica</i>)	72
4.6 Conclusions	75
References	76
5 The Imprint of Species Turnover on Old-Growth Forest Carbon Balances – Insights From a Trait-Based Model of Forest Dynamics ..	81
Christian Wirth and Jeremy W. Lichstein	
5.1 Introduction	81
5.2 A Trait-Based Model of Forest Carbon Dynamics	83
5.2.1 Successional Guilds	83
5.2.2 Model Structure	84
5.2.3 Input Data	87
5.2.4 Model Setup	89
5.3 The Spectrum of Traits	89
5.4 Model Performance and Lessons from the Equilibrium Behaviour	91
5.5 The Spectrum of Carbon Trajectories in North American Forests	94
5.6 Determinants of Old-Growth Carbon Stock Changes	96
5.7 Discussion	99
5.7.1 Limitations of Our Approach	99
5.7.2 Comparison with Independent Data	99
5.7.3 Why so Few Declines?	106

5.8 Conclusion	109
References	110
6 Functional Relationships Between Old-Growth Forest Canopies, Understorey Light and Vegetation Dynamics	115
Christian Messier, Juan Posada, Isabelle Aubin, and Marilou Beaudet	
6.1 Introduction	115
6.2 Structural and Compositional Features of Old-Growth	115
6.3 Understorey Light Environments and Dynamics	117
6.4 Consequences for Understorey Vegetation	
Composition and Dynamics	125
6.4.1 Traits of the Understorey Vegetation	126
6.5 Acclimatisation of Plant Form and Function	
to Low Light Availability	126
6.6 Resource Allocation and Shade Tolerance	129
6.6.1 Comparison among Biomes and Forest Types	131
6.7 Conclusions	133
References	134
7 Biosphere–Atmosphere Exchange of Old-Growth Forests: Processes and Pattern	141
Alexander Knohl, Ernst-Detlef Schulze, and Christian Wirth	
7.1 Introduction	141
7.2 Characteristics of Old-Growth Forests Relevant for Biosphere–Atmosphere Exchange	142
7.3 Exchange of Carbon Dioxide	143
7.4 Exchange of Water and Energy	149
7.5 Effect of Diffuse Light	151
7.6 Conclusions	153
References	154
8 Woody Detritus Mass and its Contribution to Carbon Dynamics of Old-Growth Forests: the Temporal Context	159
Mark E. Harmon	
8.1 Introduction	159
8.2 Underlying Processes	160
8.2.1 Disturbance	160
8.2.2 Forest Re-Establishment	161
8.2.3 Mortality	162
8.2.4 Decomposition	164
8.2.5 CWD Amounts in Old-Growth Forests	169
8.3 Theoretical Trends	169
8.4 Comparison of Theoretical and Observed Temporal Trends	178

8.4.1	Studies Matching the Classic Model	178
8.4.2	Studies Not Matching the Classic Model	180
8.5	Effect of Management	182
8.6	Consequences for Net Ecosystem Carbon Balance	183
8.7	Reducing Observational Uncertainties	185
8.8	Conclusions	186
	References	187
Part III Belowground Processes		
9	Aboveground and Belowground Consequences of Long-Term Forest Retrogression in the Timeframe of Millennia and Beyond ...	193
	David A. Wardle	
9.1	Introduction	193
9.2	Lake Islands in Northern Sweden	195
9.3	Retrogressive Successions Elsewhere in the World	200
9.4	Conclusions	205
	References	206
10	Rooting Patterns of Old-Growth Forests: is Aboveground Structural and Functional Diversity Mirrored Belowground?	211
	Jürgen Bauhus	
10.1	Introduction	211
10.2	What Comprises Belowground Structural Diversity?	212
10.3	Root Gaps and Horizontal Variation in Rooting Density in Old-Growth Forests	213
10.4	Pit-and-Mound Topography in Old-Growth Forest	219
10.5	Old-Growth Structures Harbouring Roots	220
10.6	Influence of Stand Age on Diversity of Functional Root Types, Mycorrhizae, and the Vertical Patterning of Root Systems	222
10.7	Conclusions	225
	References	225
11	Soil Carbon Accumulation in Old-Growth Forests	231
	Gerd Gleixner, Cindy Tefs, Albrecht Jordan, Matthias Hammer, Christian Wirth, Angela Nueske, Alexander Telz, Uwe E. Schmidt and Stephan Glatzel	
11.1	Introduction	231
11.2	Development of Soil Carbon Stocks in Ecosystems	231
11.3	Soil Carbon Storage in Old-Growth Forests	234
11.3.1	Effects of Quantity and Quality of Input Material	234
11.3.2	Effects of Organic Matter Decomposition and Soil Respiration	237

11.3.3	Drainage of Dissolved Carbon from Forest Ecosystems	239
11.3.4	Soil Carbon Stock Changes	240
11.4	Case Study of Soil Carbon Sequestration in a 250-Year-Old Beech Forest	250
11.4.1	Site Description and Experimental Setup	250
11.4.2	Historical Carbon Export	251
11.4.3	Soil Respiration in Hainich NP	254
11.4.4	Carbon Export to the Liquid Phase	254
11.4.5	Development of Carbon Stocks	255
11.5	Discussion of Carbon Stock Changes	258
11.6	Conclusions	260
	References	261
12	Is There a Theoretical Limit to Soil Carbon Storage in Old-Growth Forests? A Model Analysis with Contrasting Approaches	267
	Markus Reichstein, Göran I. Ågren, and Sébastien Fontaine	
12.1	Introduction	267
12.2	Observations of Old-Growth Forest Carbon Balance	268
12.3	Is There a Theoretical Limit to Soil Carbon Storage?	269
12.3.1	Classical Carbon Pool Models	269
12.3.2	Alternative Model Concepts of Soil Carbon Dynamics	270
12.3.3	Complicating Factors not Considered	274
12.4	Perspectives for a New Generation of Models	275
12.4.1	Models Connecting the Decay Rate of Soil Carbon to the Size, Activity and Functional Diversity of Microbe Populations	276
12.4.2	Determining the Mechanisms Stabilising Recalcitrant Soil Carbon	277
12.5	Conclusions	278
	References	279
Part IV	Biomes	
13	Old-Growth Forests in the Canadian Boreal: the Exception Rather than the Rule?	285
	Yves Bergeron and Karen A. Harper	
13.1	Introduction	285
13.2	Abundance of Old-Growth Forests	286
13.3	Characteristics of Old-Growth Boreal Forests	288
13.3.1	Old-Growth Black Spruce Boreal Forest	289
13.3.2	Old-Growth Mixedwood Boreal Forest	292
13.3.3	Characterisation of Old-Growth Boreal Forests	294
13.4	Implications for Forest Management	296

13.5 Conclusions	297
References	298
14 Biomass Chronosequences of United States Forests: Implications for Carbon Storage and Forest Management	301
Jeremy W. Lichstein, Christian Wirth, Henry S. Horn, and Stephen W. Pacala	
14.1 Forest Management and Carbon Sequestration	301
14.2 Mechanisms of Biomass Decline	302
14.2.1 Transition from Even- to Uneven-Aged Stand Structure	302
14.2.2 Large Mortality Events	303
14.2.3 Successional Changes in Growth Conditions	304
14.2.4 Species Effects on Forest Stature	305
14.3 Aboveground Biomass Chronosequences for US Forests	305
14.3.1 Methods	306
14.3.2 Results	312
14.4 Discussion	328
14.4.1 Late-Successional AGB Trajectories	328
14.4.2 Summary and Validity of Results	333
14.4.3 Implications	334
References	336
15 Temperate and Boreal Old-Growth Forests: How do Their Growth Dynamics and Biodiversity Differ from Young Stands and Managed Forests?	343
Ernst-Detlef Schulze, Dominik Hessenmoeller, Alexander Knohl, Sebastiaan Luyssaert, Annett Boerner, and John Grace	
15.1 Introduction	343
15.2 Global Distribution of Temperate and Boreal Forests	345
15.3 Productivity of Temperate and Boreal Forests	346
15.4 Disturbance and Forest Succession at the Regional Scale	355
15.5 Effects of Management	358
15.6 Forest Management and Forest Protection in Europe	360
15.7 Conclusions	363
References	364
16 Old-Growth Temperate Rainforests of South America: Conservation, Plant–Animal Interactions, and Baseline Biogeochemical Processes	367
Juan J. Armesto, Cecilia Smith-Ramírez, Martín R. Carmona, Juan L. Celis-Diez, Iván A. Díaz, Aurora Gaxiola, Alvaro G. Gutiérrez, Mariela C. Núñez-Avila, Cecilia A. Pérez, and Ricardo Rozzi	

16.1	Introduction	367
16.2	Conservation Status, Values and Threats	369
16.2.1	Main Threats	370
16.2.2	Values	373
16.2.3	Conservation Prospects	375
16.3	Plant–Animal Interactions	377
16.4	Biogeochemistry	380
16.4.1	Relevant Features of the Nitrogen Cycle in Unpolluted South American Forests	381
16.4.2	Human Impact on Biogeochemistry of Southern Forests	383
16.5	Conclusions	384
	References	385
17	Tropical Rain Forests as Old-Growth Forests	391
	John Grace and Patrick Meir	
17.1	Introduction	391
17.2	Structure	392
17.3	Physiological Attributes	395
17.4	Are Rain Forests Carbon Sinks?	397
17.5	Are There Recent Changes in Species Composition?	399
17.6	How Will Rain Forests Behave in a Hotter and Drier Climate? ..	399
17.7	The Future	402
17.7.1	A Pessimistic View of the Future	402
17.7.2	An Optimistic View of the Future	402
	References	403
Part V	Human Dimensions	
18	Detecting Intact Forests from Space: Hot Spots of Loss, Deforestation and the UNFCCC	411
	Frédéric Achard, Hugh Eva, Danilo Mollicone, Peter Popatov, Hans-Jürgen Stibig, Svetlana Turubanova, and Alexey Yaroshenko	
18.1	Introduction	411
18.2	Monitoring of Forest Areas from the Global to the Regional Scale using Satellite Imagery	411
18.3	Information on Global Forest Extent and Deforestation Rates	412
18.3.1	Distribution of Forest Areas at Global Scale	412
18.3.2	Distribution of ‘Intact Forests’: from Boreal Eurasia to the Global Scale	413
18.3.3	Hot Spots of Forest Loss	414
18.3.4	Estimates of Forest Conversion Rates in the Tropics ..	415

18.3.5	Monitoring of Intact Forests in Northern European Russia	417
18.3.6	Options for Future Monitoring	418
18.3.7	Processes of Deforestation and Forest Degradation	419
18.4	Tropical Forest Monitoring in the Context of the UNFCCC	421
18.4.1	Tropical Deforestation and Carbon Emissions	421
18.4.2	Use of the Concept of ‘Intact Forest’ in a Potential Mechanism for Reducing Emissions from Deforestation in Developing Countries	422
18.5	Conclusions	424
	References	425
19	Impacts of Land Use on Habitat Functions of Old-Growth Forests and their Biodiversity	429
	Dorothea Frank, Manfred Finckh, and Christian Wirth	
19.1	Introduction	429
19.2	Old-Growth Forests – Habitat Function	430
19.2.1	Structure	431
19.2.2	Stand Microclimate	432
19.2.3	Spatiotemporal Stability	432
19.3	Characteristic Human Impacts on Old-Growth Forests in Different Biomes and their Impact on Habitat Characteristics, Habitat Functions and Biodiversity	434
19.3.1	Boreal Forests	435
19.3.2	Temperate Forests	437
19.3.3	Tropical Forests	441
19.4	Conclusions	444
	References	445
20	Old-Growth Forests in the Context of International Environmental Agreements	451
	Annette Freibauer	
20.1	Introduction	451
20.2	Forests in UN Processes	452
20.2.1	UN Framework Convention on Climate Change	452
20.2.2	Convention on Biological Diversity	455
20.2.3	UN Forum on Forests (UNFF)	456
20.3	Consideration of Old-Growth Forests in UN Processes	457
20.3.1	Old-Growth Forests and the UN Framework Convention on Climate Change	457
20.3.2	Old-Growth Forests and the Convention on Biological Diversity	458
20.3.3	Old-Growth Forests and the UN Forest Focus	458
20.4	Potential Role of Old-Growth Forests in Future International Environmental Agreements	459

Contents	xix
----------	-----

20.5 Conclusions	460
References	460

Part VI Synthesis

21 Old-Growth Forests: Function, Fate and Value – a Synthesis	465
Christian Wirth	
21.1 Challenges in Functional Old-Growth Forest Research	465
21.2 Functional Consequences of Old-Growth Forest Structure: the Spatial View	467
21.2.1 Tall Stature	467
21.2.2 The Imprint of Aboveground Structural Complexity ..	468
21.2.3 The Imprint of Belowground Structural Complexity ..	469
21.2.4 Habitat Structure	470
21.3 Old-Growth Forests in the Context of Succession: the Temporal View	471
21.3.1 Long-Term Trends in Tree and Stand Productivity	472
21.3.2 Are Old-Growth Forests Carbon Neutral?	474
21.3.3 Nutrient Dynamics	477
21.3.4 Consequences of Successional Species Change	479
21.3.5 Shapes of Responses	480
21.4 The Fate of Old-Growth Forests Worldwide	482
21.4.1 Current Status of Old-Growth Forests	482
21.4.2 Politics and the Future of Old-Growth Forests	484
21.5 Research Needs	485
21.5.1 Methods	485
21.5.2 Knowledge Gaps	486
21.6 Overall summary	488
References	490
Abbreviations and Glossary	493
Geographic Index	497
Subject Index	499
Taxonomic Index	509

Contributors

Achard, Frédéric

Joint Research Centre of the European Commission, CCR/TP 440, 21027 Ispra, Italy

frederic.achard@jrc.it

Ågren, Göran

Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, PO Box 7072, 750 07 Uppsala, Sweden

Armesto, Juan J.

Instituto de Ecología y Biodiversidad, Universidad de Chile, Santiago, Chile
jarmesto@bib.puc.cl

Aubin, Isabelle

Centre d'Étude de la Forêt (CEF), Université du Québec à Montréal (UQAM), Montréal, Canada, CP 8888, Succ. Centre-Ville, Montréal, H3C 3P8, Canada

Bauhus, Jürgen

Institute of Silviculture, Freiburg University, Tennenbacherstr. 4, 79106 Freiburg, Germany

juergen.bauhus@waldbau.uni-freiburg.de

Beaudet, Marilou

Centre d'Étude de la Forêt (CEF), Université du Québec à Montréal (UQAM), Montréal, Canada, CP 8888, Succ. Centre-Ville, Montréal, H3C 3P8, Canada

Bergeron, Yves

Chaire Industrielle CRSNG-UQAT-UQAM en Aménagement Forestier Durable, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, C.P. 700, Rouyn-Noranda, Québec, J9X 5E4, Canada

Yves.bergeron@uqat.ca

Boerner, Annett
Max-Planck Institute for Biogeochemistry, 07701 Jena, Germany

Carmona, Martin R.
Instituto de Ecología y Biodiversidad, Universidad de Chile, Santiago, Chile

Celis-Diez, Juan L.
Instituto de Ecología y Biodiversidad, Universidad de Chile, Santiago, Chile

Diaz, Ivan A.
Instituto de Ecología y Biodiversidad, Universidad de Chile, Santiago, Chile

Eva, Hugh
Joint Research Centre of the European Commission, CCR / TP 440, 21027 Ispra, Italy

Fankhänel, Anja
Organismic Biogeochemistry Group, Max-Planck-Institute for Biogeochemistry, Hans-Knöll-Straße 10, 07745 Jena, Germany

Finckh, Manfred
University of Hamburg, Biocentre Klein Flottbek, Ohnhorststr. 18, 22609 Hamburg, Germany

Fontaine, Sébastien
Unité d’Agronomie, INRA de Clermont-Ferrand, France

Frank, Dorothea
Max-Planck-Institute for Biogeochemistry, Hans-Knöll-Straße 10, 07745 Jena, Germany
dfrank@bgc-jena.mpg.de

Freibauer, Annette
Johann Heinrich von Thünen-Institute, Institute for Agricultural Climate Research, Bundesallee 50, 38116 Braunschweig, Germany
annette.freibauer@vti.bund.de

Gaxiola, Aurora
Instituto de Ecología y Biodiversidad, Universidad de Chile, Santiago, Chile

Glatzel, Stephan
University of Rostock, Faculty for Agricultural and Environmental Sciences, Landscape Ecology and Site Evaluation, Justus von Liebig Weg 6, 18059 Rostock, Germany

Gleixner, Gerd

Max-Planck-Institute for Biogeochemistry, Hans-Knöll-Straße 10, 07745 Jena,
Germany

gleix@bgc-jena.mpg.de

Grace, John

School of GeoSciences, University of Edinburgh, Edinburgh, EH9 3JN, UK

jgrace@ed.ac.uk

Gutierrez, Alvaro G.

Department of Ecological Modelling, Helmholtz Centre for Environmental
Research (UFZ), Leipzig, Germany

Hammer, Matthias

Albert-Ludwigs-University of Freiburg, Institute of Forest and Environmental
Policy, Section Forest History, Tennenbacher Str. 4, 79106 Freiburg i. Br.,
Germany

Harmon, Mark E.

Department of Forest Ecosystems and Society, Oregon State University, 321
Richardson Hall, Corvallis, OR 97331, USA

mark.harmon@oregonstate.edu

Harper, Karen A.

School of Resource and Environmental Studies, Kenneth C. Rowe Management
Building, 6100 University Avenue, Suite 5010, Dalhousie University, Halifax, NS,
B3H 3J5, Canada

Heimann, Martin

Max-Planck-Institute for Biogeochemistry, Hans-Knöll-Straße 10, 07745 Jena,
Germany

Herbst, Matthias

Department of Geography and Geology, University of Copenhagen, Øster
Voldgade 10, 1350 Copenhagen, Denmark

Hessenmoeller, Dominik

Max-Planck Institute for Biogeochemistry, 07701 Jena, Germany

Horn, Henry S.

Princeton University, Ecology and Evolutionary Biology Department, Princeton,
NJ 08544, USA

Jordan, Albrecht

University of Rostock, Faculty for Agricultural and Environmental Sciences,
Landscape Ecology and Site Evaluation, Justus von Liebig Weg 6, 18059 Rostock,
Germany

Kappen, Ludger

Neue Strasse 14, 37586 Dassel, Germany

Kattge, Jens

Organismic Biogeochemistry Group, Max-Planck-Institute for Biogeochemistry,
Hans-Knöll-Straße 10, 07745 Jena, Germany

Knohl, Alexander

ETH Zürich, Institute of Plant Sciences, Universitätstr. 2, LFW C38, 8092 Zürich,
Switzerland

alexander.knohl@ipw.agrl.ethz.ch

Kutsch, Werner L.

Max-Planck-Institute for Biogeochemistry, Hans-Knöll-Straße 10, 07745 Jena,
Germany

wkutsch@bgc-jena.mpg.de

Lichstein, Jeremy W.

Princeton University, Ecology and Evolutionary Biology Department, Princeton,
NJ 08544, USA

jwl@princeton.edu

Luyssaert, Sebastiaan

Department of Biology, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk,
Belgium

Meir, Patrick

Institute of Geography, School of GeoSciences, The University of Edinburgh,
Drummond Street, Edinburgh, EH8 9XP, UK

Messier, Christian

Centre d'Étude de la Forêt (CEF), Université du Québec à Montréal (UQAM),
Montréal, Canada, CP 8888, Succ. Centre-Ville, Montréal, H3C 3P8, Canada
messier.christian@uqam.ca

Mollicone, Danilo

University of Alcalá, 28801 Alcalá de Henares, Spain

Nöllert, Stefani

Organismic Biogeochemistry Group, Max-Planck-Institute for Biogeochemistry,
Hans-Knöll-Straße 10, 07745 Jena, Germany

Nueske, Angela

Organismic Biogeochemistry Group, Max-Planck-Institute for Biogeochemistry,
Hans-Knöll-Straße 10, 07745 Jena, Germany

Núñez-Avila Mariela C.

Instituto de Ecología y Biodiversidad, Universidad de Chile, Santiago, Chile

Pacala, Stephen W.

Princeton University, Ecology and Evolutionary Biology Department, Princeton,
NJ 08544, USA

Perez, Cecilia A.

Instituto de Ecología y Biodiversidad, Universidad de Chile, Santiago, Chile

Popatov, Peter

South Dakota State University, Brookings, SD 57007-3510, USA

Posada, Juan

Centre d'Étude de la Forêt (CEF), Université du Québec à Montréal (UQAM),
Montréal, Canada, CP 8888, Succ. Centre-Ville, Montréal, H3C 3P8, Canada

Reichstein, Markus

Biogeochemical Model-Data Integration Group, Max-Planck-Institute for Biogeochemistry,
Hans-Knöll-Straße 10, 07745 Jena, Germany

markus.reichstein@bgc-jena.mpg.de

Rozzi, Ricardo

Universidad de Magallanes, Parque Etnobotánico Omora, Magallanes, Chile

Schmidt, Uwe E.

Albert-Ludwigs-University of Freiburg, Institute of Forest and Environmental Policy,
Section Forest History, Tennenbacher Str. 4, 79106 Freiburg i. Br.,
Germany

Schulze, Ernst-Detlef

Max Planck Institute for Biogeochemistry, Hans-Knöll-Str. 10, 07745 Jena,
Germany
detlef.schulze@bgc-jena.mpg.de

Schweingruber, Fritz Hans

Swiss Federal Research Institute WSL, 8903 Birmensdorf, Switzerland

fritz.schweingruber@wsl.ch

Smith-Ramirez, Cecilia

Instituto de Ecología y Biodiversidad, Universidad de Chile, Santiago, Chile

Stibig, Hans-Jürgen

Joint Research Centre of the European Commission, CCR / TP 440, 21027 Ispra, Italy

Tefs, Cindy

Max Planck Institute for Biogeochemistry, PO Box 100164, 07701 Jena, Germany

Telz, Alexander

Max Planck Institute for Biogeochemistry, PO Box 100164, 07701 Jena, Germany

Turubanova, Svetlana

Greenpeace Russia, 6 Novaya Bashilovka St., Moscow 101428, Russia

Wardle, David A.

Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, 901-83 Umeå, Sweden

david.wardle@svek.slu.se

Wirth, Christian

Organismic Biogeochemistry Group, Max-Planck-Institute for Biogeochemistry, Hans-Knöll-Straße 10, 07745 Jena, Germany

cwirth@bgc-jena.mpg.de

Yaroshenko, Alexey

Greenpeace Russia, 6 Novaya Bashilovka St., Moscow 101428, Russia