

# Contents

## Part I Introduction

<b>1</b>	<b>Old-Growth Forests: Function, Fate and Value – an Overview</b>	<b>3</b>
	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
<b>2</b>	<b>Old-Growth Forest Definitions: a Pragmatic View</b>	<b>11</b>
	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
<b>3</b>	<b>Old Trees and the Meaning of ‘Old’</b>	<b>35</b>
	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

<b>4 Ecophysiological Characteristics of Mature Trees and Stands – Consequences for Old-Growth Forest Productivity .....</b>	<b>57</b>
Werner L. Kutsch, Christian Wirth, Jens Kattge, Stefanie Nöller, 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
<b>5 The Imprint of Species Turnover on Old-Growth Forest Carbon Balances – Insights From a Trait-Based Model of Forest Dynamics ..</b>	<b>81</b>
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
<b>6 Functional Relationships Between Old-Growth Forest Canopies, Understorey Light and Vegetation Dynamics .....</b>	<b>115</b>
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
<b>7 Biosphere–Atmosphere Exchange of Old-Growth Forests: Processes and Pattern .....</b>	<b>141</b>
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
<b>8 Woody Detritus Mass and its Contribution to Carbon Dynamics of Old-Growth Forests: the Temporal Context .....</b>	<b>159</b>
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**

<b>9</b>	<b>Aboveground and Belowground Consequences of Long-Term Forest Retrogression in the Timeframe of Millennia and Beyond ...</b>	<b>193</b>
	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
<b>10</b>	<b>Rooting Patterns of Old-Growth Forests: is Aboveground Structural and Functional Diversity Mirrored Belowground? .....</b>	<b>211</b>
	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
<b>11</b>	<b>Soil Carbon Accumulation in Old-Growth Forests .....</b>	<b>231</b>
	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**

	<b>with Contrasting Approaches</b>	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?**

	Yves Bergeron and Karen A. Harper	285
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
<b>14</b>	<b>Biomass Chronosequences of United States Forests: Implications for Carbon Storage and Forest Management .....</b>	<b>301</b>
	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
<b>15</b>	<b>Temperate and Boreal Old-Growth Forests: How do Their Growth Dynamics and Biodiversity Differ from Young Stands and Managed Forests? .....</b>	<b>343</b>
	Ernst-Detlef Schulze, Dominik Hessenmoeller, Alexander Knohl, Sebastian 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
<b>16</b>	<b>Old-Growth Temperate Rainforests of South America: Conservation, Plant–Animal Interactions, and Baseline Biogeochemical Processes .....</b>	<b>367</b>
	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
<b>17</b>	<b>Tropical Rain Forests as Old-Growth Forests .....</b>	<b>391</b>
	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
 <b>Part V Human Dimensions</b>		
<b>18</b>	<b>Detecting Intact Forests from Space: Hot Spots of Loss, Deforestation and the UNFCCC .....</b>	<b>411</b>
	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
<b>19</b>	<b>Impacts of Land Use on Habitat Functions of Old-Growth Forests and their Biodiversity .....</b>	<b>429</b>
	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
<b>20</b>	<b>Old-Growth Forests in the Context of International Environmental Agreements .....</b>	<b>451</b>
	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

20.5	Conclusions .....	460
	References .....	460

## Part VI Synthesis

<b>21</b>	<b>Old-Growth Forests: Function, Fate and Value – a Synthesis .....</b>	<b>465</b>
	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
	<b>Abbreviations and Glossary .....</b>	<b>493</b>
	<b>Geographic Index .....</b>	<b>497</b>
	<b>Subject Index .....</b>	<b>499</b>
	<b>Taxonomic Index .....</b>	<b>509</b>

Old-Growth Forests

Function, Fate and Value

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

2009, XXVI, 512 p. 113 illus., Hardcover

ISBN: 978-3-540-92705-1