Contents

Part I Introduction

1	Old	Old-Growth Forests: Function, Fate and Value – an Overview			
	Chri	stian 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		
	Refe	erences			
2	Old	-Growth Forest Definitions: a Pragmatic View	11		
	Chri	stian Wirth, Christian Messier, Yves Bergeron, Dorothea			
	Fran	k, 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		
			24		
		2.4.2 Spatial Scale	27		
	2.5	•	27		
	2.6	Conclusions and Pragmatic Considerations	29		
	Refe	•	31		
3	Old	Trees and the Meaning of 'Old'	35		
		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?			
		3.3.1 Programmed Cell Death			
		3.3.2 Whole Plant Longevity – Internal Versus			
		External Factors	40		



3.4	Concluding Remarks	52
Refe	rences	53

Part II Aboveground Processes

4			ogical Characteristics of Mature Trees and	
			onsequences for Old-Growth Forest Productivity	57
			Kutsch, Christian Wirth, Jens Kattge, Stefanie Nöllert,	
	Mat		erbst, and Ludger Kappen	
	4.1		uction	57
	4.2		sed Respiratory Demand	
	4.3	Limita	ations of Photosynthesis	
		4.3.1	Hydraulic Limitation	58
		4.3.2	Reduced Sink Strength	62
	4.4	Stand-	Level Controls	63
	4.5	Comn	nunity and Ecosystem Constraints on	
		Age/S	ize-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	
			(Fagus sylvatica)	72
	4.6	Concl	usions	
	Refe			
5	The	Imprin	nt of Species Turnover on Old-Growth Forest Carbon	
	Bala	nces –	Insights From a Trait-Based Model of Forest Dynamics	. 81
	Chri	stian W	/irth and Jeremy W. Lichstein	
	5.1	Introd	uction	81
	5.2		it-Based Model of Forest Carbon Dynamics	
		5.2.1	Successional Guilds	
		5.2.2	Model Structure	84
		5.2.3		
		5.2.4	Model Setup	
	5.3	The S	pectrum of Traits	
	5.4		Performance and Lessons from the Equilibrium	
			riour	91
	5.5		pectrum of Carbon Trajectories	
	0.0		rth American Forests	94
	5.6		minants of Old-Growth Carbon Stock Changes	
	5.7		ssion	
	2.,	5.7.1	Limitations of Our Approach	
		5.7.2	• •	
		5.7.2		
		5.1.5	Why so rew December:	100

	5.8	Conclusion	
	Refe	erences	110
6		ctional Relationships Between	
		-Growth Forest Canopies, Understorey	
	Ligl	ht and Vegetation Dynamics	115
	Chri	istian 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	
	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
	Refe	erences	134
7	Bios	sphere–Atmosphere Exchange	
	of C	Old-Growth Forests: Processes and Pattern	141
	Alex	kander 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	
	7.6	Conclusions	153
	Refe	erences	154
8	Woo	ody Detritus Mass and its Contribution to Carbon	
	Dyn	amics of Old-Growth Forests: the Temporal Context	159
	Mar	k E. Harmon	
	8.1	Introduction	159
	8.2	Underlying Processes	160
		8.2.1 Disturbance	
		8.2.2 Forest Re-Establishment	161
		8.2.3 Mortality	
		8.2.4 Decomposition	164
		8.2.5 CWD Amounts in Old-Growth Forests	
	8.3	Theoretical Trends	169
	8.4	Comparison of Theoretical and Observed	
		Temporal Trends	178

	8.4.1 Studies Matching the Classic Model 1	78
	8.4.2 Studies Not Matching the Classic Model 1	80
8.5	Effect of Management	82
8.6	Consequences for Net Ecosystem Carbon Balance 1	83
8.7	Reducing Observational Uncertainties 1	85
8.8	Conclusions 1	86
Refe	rences 1	187

Part III Belowground Processes

9	Abov	reground and Belowground Consequences of Long-Term	
	Fore	st Retrogression in the Timeframe of Millennia and Beyond	193
	Davi	d 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
	Refe	ences	206
10	Roc	ting Patterns of Old-Growth Forests: is Aboveground	
	Str	ctural and Functional Diversity Mirrored Belowground?	211
	Jürg	en Bauhus	
	10.	Introduction	211
	10.2	2 What Comprises Belowground Structural Diversity?	212
	10.3		
		Density in Old-Growth Forests	213
	10.4	-	
	10.5		
	10.0	0	
		Types, Mycorrhizae, and the Vertical Patterning of	
		Root Systems	222
	10.3	Conclusions	225
	Refe	rences	225
11	Soil	Carbon Accumulation	
	in (Old-Growth Forests	231
	Ger	d Gleixner, Cindy Tefs, Albrecht Jordan,	
	Mat	thias Hammer, Christian Wirth, Angela Nueske,	
	Ale	xander Telz, Uwe E. Schmidt and Stephan Glatzel	
	11.1	Introduction	231
	11.2	2 Development of Soil Carbon Stocks in Ecosystems	231
	11.3	-	
		11.3.1 Effects of Quantity and Quality of Input Material	
		11.3.2 Effects of Organic Matter Decomposition and Soil	
		Respiration	237
		• · · · · · · · · · · · · · · · · · · ·	

Contents

	11.3.3	Drainage of Dissolved Carbon from Forest Ecosystems	239
	11.3.4	Soil Carbon Stock Changes	240
11.4	Case St	udy 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	Discussio	on of Carbon Stock Changes	258
11.6	Conclusi	ons	260
Referen	nces		261
		eoretical Limit to Soil Carbon Storage	
		h Forests? A Model Analysis	
		ing Approaches	267
Mark		stein, Göran I. Ågren, and Sebastién Fontaine	
12.1		ction	267
12.2		ations of Old-Growth Forest Carbon Balance	268
12.3	Is There	e a Theoretical Limit to Soil Carbon Storage?	
	12.3.1	Classical Carbon Pool Models	269
	12.3.2	Alternative Model Concepts of Soil Carbon Dynamics	
	12.3.3	Complicating Factors not Considered	274
12.4	Perspec	tives 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	Conclus	ions	278
	••		

Part IV Biomes

13	Old-0	Growth Forests in the Canadian Boreal: the Exception	
	Rath	er 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		
	Refer	ences	298
14		ass Chronosequences of United States Forests: ications for Carbon Storage and Forest Management	301
		y W. Lichstein, Christian Wirth, Henry S. Horn,	501
		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	
		14.2.2 Large Mortality Events	
		14.2.3 Successional Changes in Growth Conditions	
		14.2.4 Species Effects on Forest Stature	
	14.3	Aboveground Biomass Chronosequences for US Forests	
		14.3.1 Methods 14.3.2 Results	
	14.4	Discussion	
	14.4	14.4.1 Late-Successional AGB Trajectories	
		14.4.2 Summary and Validity of Results	
		14.4.3 Implications	
	Refer	rences	
15	Tem	perate and Boreal Old-Growth Forests: How do	
	Thei	r Growth Dynamics and Biodiversity Differ	
	from	Young Stands and Managed Forests?	343
		-Detlef Schulze, Dominik Hessenmoeller, Alexander Knohl,	
	Sebas	stiaan Luyssaert, Annett Boerner, and John Grace	
	15.1	Introduction	
	15.2	Global Distribution of Temperate and Boreal Forests	
	15.3	Productivity of Temperate and Boreal Forests	
	15.4	Disturbance and Forest Succession at the Regional Scale	
	15.5	Effects of Management	
	15.6 15.7	Forest Management and Forest Protection in Europe	
		Conclusions	
	Kelei	ences	304
16	Old-	Growth Temperate Rainforests of South America:	
10		ervation, Plant-Animal Interactions, and Baseline	
		eochemical Processes	367
		J. Armesto, Cecilia Smith-Ramírez, Martín R. Carmona,	201
		L. Celis-Diez, Iván A. Díaz, Aurora Gaxiola,	
		ro G. Gutiérrez, Mariela C. Núñez-Avila, Cecilia A. Pérez,	
		Ricardo Rozzi	

	16.1	Introduction	367
	16.2	Conservation Status, Values and Threats	369
		16.2.1 Main Threats	
		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
	Refer	ences	385
17	-	ical Rain Forests as Old-Growth Forests	391
17	-	Grace and Patrick Meir	
17	-	Grace and Patrick Meir Introduction	391
17	John	Grace and Patrick Meir Introduction Structure	391 392
17	John (17.1	Grace and Patrick Meir Introduction Structure Physiological Attributes	391 392 395
17	John 17.1 17.2	Grace and Patrick Meir Introduction Structure Physiological Attributes Are Rain Forests Carbon Sinks?	391 392 395
17	John 17.1 17.2 17.3	Grace and Patrick Meir Introduction Structure Physiological Attributes Are Rain Forests Carbon Sinks?	391 392 395
17	John 17.1 17.2 17.3 17.4	Grace and Patrick Meir Introduction Structure Physiological Attributes Are Rain Forests Carbon Sinks?	391 392 395 397 399
17	John 17.1 17.2 17.3 17.4 17.5	Grace and Patrick Meir Introduction Structure Physiological Attributes Are Rain Forests Carbon Sinks? Are There Recent Changes in Species Composition? How Will Rain Forests Behave in a Hotter and Drier Climate? .	391 392 395 397 399
17	John 17.1 17.2 17.3 17.4 17.5 17.6	Grace and Patrick Meir Introduction Structure Physiological Attributes Are Rain Forests Carbon Sinks? Are There Recent Changes in Species Composition? How Will Rain Forests Behave in a Hotter and Drier Climate? The Future	391 392 395 397 399 399
17	John 17.1 17.2 17.3 17.4 17.5 17.6	Grace and Patrick Meir Introduction Structure Physiological Attributes Are Rain Forests Carbon Sinks? Are There Recent Changes in Species Composition? How Will Rain Forests Behave in a Hotter and Drier Climate? The Future	391 392 395 397 399 399 402 402

Part V Human Dimensions

18		cting Intact Forests from Space: Hot Spots of Loss,	
	Defor	restation and the UNFCCC 4	11
	Frédé	éric Achard, Hugh Eva, Danilo Mollicone, Peter Popatov,	
	Hans-	-Jürgen Stibig, Svetlana Turubanova, and Alexey Yaroshenko	
	18.1	Introduction 4	11
	18.2	Monitoring of Forest Areas from the Global to the	
		Regional Scale using Satellite Imagery 4	11
	18.3	Information on Global Forest Extent	
		and Deforestation Rates 4	12
		18.3.1 Distribution of Forest Areas at Global Scale 4	12
		18.3.2 Distribution of 'Intact Forests': from	
		Boreal Eurasia to the Global Scale 4	13
		18.3.3 Hot Spots of Forest Loss 4	14
		18.3.4 Estimates of Forest Conversion Rates in the Tropics 4	
		Boreal Eurasia to the Global Scale 4 18.3.3 Hot Spots of Forest Loss 4	ļ

		18.3.5 Monitoring of Intact Forests in	Northern
		European Russia	
		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 Conte	
		18.4.1 Tropical Deforestation and Car	
		18.4.2 Use of the Concept of 'Intact F	
		Mechanism for Reducing Emis	
		in Developing Countries	
	18.5		
		rences	
	10101		
19	Impa	acts of Land Use on Habitat Functions of	of Old-Growth
		sts and their Biodiversity	
		thea Frank, Manfred Finckh, and Christia	
	19.1	Introduction	
	19.2	Old-Growth Forests – Habitat Function	
		19.2.1 Structure	
		19.2.2 Stand Microclimate	
		19.2.3 Spatiotemporal Stability	
	19.3	Characteristic Human Impacts on Old-C	
		in Different Biomes and their Impact or	
		Characteristics, Habitat Functions and I	
		19.3.1 Boreal Forests	
		19.3.2 Temperate Forests	
		19.3.3 Tropical Forests	
	19.4	Conclusions	
	Refer	rences	
20	Old-	Growth Forests in the Context of Inter-	national
	Envi	ronmental Agreements	
		ette Freibauer	
	20.1	Introduction	
	20.2	Forests in UN Processes	
		20.2.1 UN Framework Convention on	Climate Change 452
		20.2.2 Convention on Biological Dive	
		20.2.3 UN Forum on Forests (UNFF)	
	20.3		
		20.3.1 Old-Growth Forests and the U	
		Convention on Climate Change	
		20.3.2 Old-Growth Forests and the Co	
		on Biological Diversity	
		20.3.3 Old-Growth Forests and the U	
	20.4		
		International Environmental Agreement	

20.5	Conc	lusions	••••	 	 	•••••	460
Refere	ences			 	 		460

Part VI Synthesis

21	Old-Growth Forests: Function, Fate and Value – a Synthesis Christian Wirth								
	21.1	Challenges in Functional Old-Growth Forest Research							
	21.2	Functional Consequences of Old-Growth Forest Structure:							
		the Spatial View 46	57						
		21.2.1 Tall Stature 46	57						
		21.2.2 The Imprint of Aboveground Structural Complexity 46	58						
		21.2.3 The Imprint of Belowground Structural Complexity 46	<u>;9</u>						
		21.2.4 Habitat Structure 47	0						
	21.3	Old-Growth Forests in the Context of Succession:							
		the Temporal View 47	/1						
		21.3.1 Long-Term Trends in Tree and Stand Productivity 47	12						
		21.3.2 Are Old-Growth Forests Carbon Neutral? 47	14						
		21.3.3 Nutrient Dynamics 47	17						
		21.3.4 Consequences of Successional Species Change 47	19						
		21.3.5 Shapes of Responses 48	30						
	21.4	The Fate of Old-Growth Forests Worldwide 48	32						
		21.4.1 Current Status of Old-Growth Forests 48	32						
		21.4.2 Politics and the Future of Old-Growth Forests 48	34						
	21.5	Research Needs 48	35						
		21.5.1 Methods	35						
		21.5.2 Knowledge Gaps 48	36						
	21.6	Overall summary	38						
	Refer	ences)()						

Abbreviations and Glossary	493
Geographic Index	497
Subject Index	499
Taxonomic Index	509