

Contents

List of contributors	xvi
Foreword	xix
Preface	xxi
Acknowledgements	xxiii
Part one Biogeographic patterns and the driving variables S. J. Milton and W. R. J. Dean	1
1. The climate of the karoo – a functional approach P. G. Desmet and R. M. Cowling	3
1.1. Introduction	3
1.2. A general overview of the climate of the karoo	3
1.2.1. Precipitation	3
Rainfall	3
Fog	4
Dew	5
1.2.2. Reliability of sources of moisture	8
1.2.3. El Niño in southern Africa	8
1.3. Temperature	9
1.4. Cloud and light	10
1.5. Wind	10
1.5.1. Berg winds	10
1.6. The weather systems of the karoo	10
1.6.1. Fine-weather conditions	10
Subtropical anticyclones	10
Coastal lows	11
1.6.2. Tropical disturbances	11
Easterly waves and lows	11
Subtropical lows	11
1.6.3. Temperate disturbances	11
Westerly waves	11

vi	Contents	
	Cut-off flows	11
	Southerly meridional flow	11
	Ridging anticyclones	11
	West-coast troughs	11
	Cold fronts	11
1.6.4.	Other rain-producing systems	12
	Thunderstorms	12
	Development of the continuous high-pressure cell	12
1.7.	An ecological interpretation of the weather patterns of the karoo: the role of climate in understanding vegetation patterns	12
1.7.1.	The model	13
1.7.2.	Discussion: vegetation–climate relationships	13
	Succulent karoo	13
	Nama-karoo	15
	Desert	16
1.8.	Conclusions	16
2.	Soils of the arid south-western zone of Africa M. K. Watkeys	17
2.1.	Introduction	17
2.2.	Controlling factors on soil variability	17
2.2.1.	General factors	17
2.2.2.	Geology and geomorphology of the karoo	18
2.2.3.	Climate of the karoo	20
2.3.	Soils of the karoo	20
	Region 1. West coast	20
	Region 2. Namaqualand, Bushmanland and Korannaland	21
	Region 3. The Great Karoo (north)	22
	Region 4. Great Karoo (south)	23
	Region 5. Little Karoo	23
	Region 6. The Great Escarpment	23
2.4.	Discussion of the soil pattern	25
2.5.	Acknowledgements	25
3.	Palaeoenvironments M. E. Meadows and M. K. Watkeys	27
3.1.	Introduction	27
3.2.	Long-term geological and biological history	28
3.2.1.	Pre-Gondwana (3400–1000 Ma)	28
3.2.2.	Gondwana assembling (800–250 Ma)	30
3.2.3.	Gondwana assembled (250–155 Ma)	32
3.2.4.	Gondwana breaking up (155 Ma to present)	32
3.3.	Tertiary historical biogeography	33
3.3.1.	Palaeoenvironmental indications during the Tertiary	33
3.3.2.	The Banke flora	35
3.3.3.	Geomorphological development	35
3.4.	The Quaternary period including the Holocene	35
3.4.1.	Fluctuating climates of the Quaternary	35
3.4.2.	Florisbad	36
3.4.3.	Aliwal North	36
3.4.4.	Pan sites of the karoo	37

	Contents	vii
3.4.5. Valley deposits of the karoo		37
3.4.6. Other deposits		39
3.4.7. Climate change or human impact?		40
3.5. The karoo as a dynamic landscape		40
4. Plant biogeography, endemism and diversity R. M. Cowling and C. Hilton-Taylor		42
4.1. Introduction		42
4.2. Biogeographical background		42
4.2.1. Biogeographical units and delimitation		42
4.2.2. Composition and characteristics of floras		44
4.2.3. Selective regimes		45
4.3. Endemism		46
4.3.1. Patterns		46
4.3.2. Taxonomic aspects		46
4.3.3. Biological aspects		47
4.3.4. Habitat aspects		47
4.4. Local diversity		48
4.4.1. Theory		48
4.4.2. Patterns		49
4.4.3. Explanations		50
4.5. Differentiation diversity		51
4.6. Regional diversity		51
4.6.1. Theory		52
4.6.2. Patterns		52
4.6.3. Explanations		53
4.7. General discussion		54
4.7.1. Phytochoria compared		54
4.7.2. Global comparisons		55
4.7.3. Diversification in an arid world		56
4.8. Acknowledgements		56
5. Biogeography, endemism and diversity of animals in the karoo C. J. Vernon		57
5.1. Introduction		57
5.1.1. Environmental influences		57
Seasonal movements		57
5.1.2. Evolution		58
5.2. Origins of the karoo fauna		58
5.2.1. Gondwana		58
5.2.2. Palaeartic links and the mussel fauna		58
5.2.3. Drainage basins and the fish fauna		61
5.2.4. Rivers as dispersal routes		62
5.2.5. Afro-montane zone		62
5.2.6. The arid corridor and other biogeographic patterns		63
The Cradock corridor		63
The Transkei gap		64
Marine regression		64
5.2.7. Savanna–fynbos links		64
5.3. Endemicity and distribution patterns – Nama-karoo		65
5.3.1. Invertebrates		66

viii	Contents	
	5.3.2. Vertebrates	68
5.4.	Endemicy and distribution patterns – succulent karoo	72
	5.4.1. Invertebrates	72
	5.4.2. Vertebrates	74
5.5.	Anthropogenic factors influencing biogeography	77
5.6.	Conclusions	78
	Part two Form and function	87
	B. G. Lovegrove	
6.	Form and function in perennial plants G. F. Midgley and F. van der Heyden	91
6.1.	Introduction	91
6.2.	Growth form abundance, distribution and diversity	92
6.3.	Distribution and abundance of photosynthetic types	93
6.4.	Water	94
	6.4.1. Succulence	94
	6.4.2. Succulent vs. non-succulent shrubs	97
	6.4.3. Minutism	99
	6.4.4. Grasses	99
	6.4.5. Desiccation tolerance	100
	6.4.6. Root architecture	100
6.5.	Temperature	102
6.6.	Herbivory	103
	6.6.1. Comparing shrubs with grasses	103
	6.6.2. Shrub functional types	104
6.7.	Nutrient availability	105
6.8.	Conclusions	106
6.9.	Acknowledgements	106
7.	Functional aspects of short-lived plants M. W. van Rooyen	107
7.1.	Introduction	107
7.2.	Seedbanks	108
	7.2.1. Mechanisms for seed longevity	108
	7.2.2. Spatial and temporal distribution of seed	108
7.3.	Germination	110
	7.3.1. After-ripening	110
	7.3.2. Polymorphism	110
	7.3.3. Selective response mechanisms to specific environments	111
	7.3.4. Endogenous rhythm	112
	7.3.5. Parental effects	112
7.4.	Vegetative growth	113
	7.4.1. Establishment	113
	7.4.2. Growth rate	113
	7.4.3. Photosynthetic pathway	114
7.5.	Reproductive growth	114
	7.5.1. Timing of reproduction	114

7.5.2.	Phenotypic plasticity	115
7.6.	Seed dispersal	116
7.7.	Biotic interactions	117
7.7.1.	Disturbance	117
7.7.2.	Competition	118
7.7.3.	Functional classification into guilds	120
7.8.	Conclusions	122
7.9.	Acknowledgements	122
8.	Plant reproductive ecology K. J. Esler	123
8.1.	Introduction	123
8.2.	General phenology	124
8.2.1.	Phenology	124
8.3.	Flowering phenology	124
8.3.1.	Timing of flowering	124
8.3.2.	Triggers for flowering	125
8.3.3.	Landscape patterns of flowering	126
8.4.	Pollination biology	127
8.4.1.	Flowering phenology and competition for pollinators	127
8.4.2.	Insect pollination	128
8.4.3.	Other forms of pollination	129
8.4.4.	Pollinator abundance and seed set	129
8.4.5.	Associations among modes of pollination, seed dispersal and establishment	129
8.5.	Pre-dispersal hazards	130
8.5.1.	Pollen loss	130
8.5.2.	Florivory	130
8.5.3.	Resource availability	130
8.6.	Seed production	131
8.6.1.	Seed numbers (per plant)	131
8.6.2.	Seed numbers (landscape level)	131
8.7.	Dispersal	132
8.7.1.	Dispersal mechanisms and habitat	132
8.7.2.	Short-distance dispersal and seed retention	132
8.7.3.	Dispersal in Mesembryanthema	133
8.7.4.	Dispersal distances	133
8.7.5.	Dispersal and seed polymorphism	135
8.7.6.	Other forms of dispersal	135
8.8.	Seedbanks	135
8.8.1.	Soil seedbanks	135
8.8.2.	Canopy seedbanks	135
8.8.3.	Spatial distribution of seeds in seedbanks	135
8.8.4.	Correspondence between the seedbank and vegetation	136
8.9.	Post-dispersal hazards	136
8.10.	Germination	137
8.10.1.	Germination and life-histories	137
8.10.2.	Germination and intrinsic factors	138
8.10.3.	Germination and extrinsic factors	139
8.11.	Seedling establishment	139
8.11.1.	Timing of recruitment	139
8.11.2.	Size of recruitment events	140
8.11.3.	Microsites and recruitment	140

x	Contents	
	8.11.4. Disturbance and recruitment	141
	8.11.5. Mycorrhizal status and recruitment	142
8.12.	Seedling mortality	142
8.13.	Seed vs. vegetative reproduction	143
8.14.	Concluding remarks and future research	143
8.15.	Acknowledgements	144
9.	Animal form and function B. G. Lovegrove	145
9.1.	Introduction	145
9.2.	Water balance	145
	9.2.1. Water loss	146
	9.2.2. Water gain	147
9.3.	Thermal balance	148
	9.3.1. Thermal tolerance	148
	9.3.2. Heat gain	149
	9.3.3. Heat loss	151
9.4.	Energy balance	152
	9.4.1. Basal metabolic rates	152
	9.4.2. Circadian metabolic rhythms	152
	9.4.3. Torpor	153
9.5.	Retreat	153
	9.5.1. Short-term retreat	154
	9.5.2. Burrowing adaptations	154
	9.5.3. Circadian rhythms of retreat	155
	9.5.4. Nest shelter retreats	155
	9.5.5. Long-term retreat (diapause, migration and nomadism)	156
9.6.	Sociality and co-operative breeding	156
9.7.	Predator-prey adaptations	158
	9.7.1. Behaviour	158
	9.7.2. Crypsis and colouration	159
	9.7.3. Mimicry	159
	9.7.4. Morphology and body shape	160
9.8.	Reproduction	160
	9.8.1. Cues and Zeitgeber for reproduction	160
	9.8.2. The brown locust	162
10.	Animal foraging and food W. R. J. Dean and S. J. Milton	164
10.1.	Introduction	164
10.2.	Dependable resources	164
	10.2.1. Below-ground foragers	165
	Herbivores	165
	Carnivores	165
	10.2.2. Above-ground foragers	165
	Detritivores	165
	Herbivores	166
	Termitivores	167
	Formicivores	169
	Other insectivores	169
	10.2.3. Parasitoids and parasites	169

10.3.	Seasonal resources	170
	10.3.1. Opportunism and diet switching	170
	10.3.2. Storage and caching of food	172
	10.3.3. Seasonally active and short-lived animals	173
10.4.	Unpredictable resources scattered in time and space	175
	Granivores	175
	Herbivores	176
10.5.	Food webs	176
 Part three Dynamics		179
P. A. Novellie		
 11.	Population level dynamics S. J. Milton, R. A. G. Davies and G. I. H. Kerley	183
11.1.	Introduction	183
11.2.	Structure and dynamics of plant populations	183
	11.2.1. Ephemerals and annuals	183
	11.2.2. Grasses	184
	11.2.3. Succulents	186
	11.2.4. Non-succulent dwarf shrubs	187
	11.2.5. Shrubs and trees	190
	11.2.6. Principal drivers of karoo plant populations	191
11.3.	Invertebrates	191
	11.3.1. Brown locust <i>Locustana pardalina</i>	191
	11.3.2. Other insects	193
	11.3.3. General patterns in invertebrate populations	193
11.4.	Reptiles and birds	194
	11.4.1. Tortoises	194
	11.4.2. Spatial and temporal patterns in bird abundance	194
	11.4.3. Resident, raptorial birds	196
	11.4.4. Resident, omnivorous birds	196
	11.4.5. Local migrants and nomads	198
11.5.	Mammals	198
	11.5.1. Lagomorphs, rodents and shrews	198
	11.5.2. Rock hyrax <i>Procavia capensis</i>	199
	Additions to rock hyrax populations	200
	Losses to rock hyrax populations	202
	Key factors affecting rock hyrax populations	203
	11.5.3. Large herbivores	204
	11.5.4. Primates and carnivores	205
11.6.	Conclusions	206
 12.	Community patterns and dynamics A. R. Palmer, P. A. Novellie and J. W. Lloyd	208
12.1.	Introduction	208
12.2.	Vegetation patterns: landscape scale	209
	12.2.1. Topo-moisture gradients, rainfall seasonality and uncertainty	209
	12.2.2. Soil types, depth, stoniness, texture and chemistry	210

xii	Contents	
12.3.	Vegetation patterns: local scale	211
12.3.1.	Nutrient enrichment patterns	211
12.3.2.	Nutrient transport patterns	214
12.3.3.	Photosynthetic patterns	214
12.3.4.	Diversity patterns in the landscape	215
12.4.	Plant community dynamics	215
12.4.1.	Rainfall variability	215
12.4.2.	Fire	215
12.4.3.	Grazing	215
	Mechanisms for grazing-induced change	215
	Implications of grazing-induced change	219
	Reversal of grazing-induced changes	219
12.4.4.	Time scales in plant community dynamics	220
12.5.	Animal community dynamics	220
12.5.1.	Indigenous ungulates	220
12.5.2.	Invertebrates	221
	Termites and ants	222
12.6.	Conclusions	222
13.	Modelling populations and community dynamics in karoo ecosystems	224
	K. Kellner and J. Booysen	
13.1.	Introduction	224
13.2.	Models to predict the outbreak of problem animals	224
13.3.	Models to study animal population dynamics	225
13.4.	Production and drought prediction models	227
13.5.	Models for vegetation dynamics and sustainable rangeland management	228
13.6.	Conclusions	230
14.	Spatially explicit computer simulation models – tools for understanding vegetation dynamics and supporting rangeland management	231
	F. Jeltsch, T. Wiegand and C. Wissel	
14.1.	Introduction	231
14.2.	Simulation models	232
14.2.1.	Vegetation dynamics of a shrub ecosystem in the karoo	232
14.2.2.	Shrub encroachment in the north-western karoo/southern Kalahari	233
14.2.3.	Analysing a sophisticated grazing strategy at a ranch level	235
14.3.	How do the models contribute to the understanding and management of karoo vegetation?	236
	Part four Human impacts	
	W. R. Siegfried	239
	The environment	239
	The people	240
	Impacts	240

15.	Hunters and herders in the karoo landscape A. B. Smith	243
15.1.	Introduction	243
15.2.	Human adaptation to arid lands	243
15.3.	Early humans in the karoo	245
15.4.	The later Stone Age	248
15.4.1.	The Cape west coast	248
15.4.2.	Namaqualand	249
15.4.3.	Northern Namaqualand and the Namib	250
15.4.4.	Bushmanland and the Middle Orange River	251
15.4.5.	Cape Fold Belt (west) and Tanqua Karoo	251
15.4.6.	Cape Fold Belt (south) and Little Karoo	253
15.4.7.	The Great Karoo	253
15.5.	Rock art	255
15.6.	Khoisan/settler interactions	255
15.7.	Conclusions	256
16.	Historical and contemporary land use and the desertification of the karoo M. T. Hoffman, B. Cousins, T. Meyer, A. Petersen and H. Hendricks	257
16.1.	Introduction	257
16.2.	Communal lands	257
16.2.1.	Historical background	257
16.2.2.	Current land use practices and their determinants	260
16.3.	Commercial agriculture	263
16.3.1.	Settlement and historical land use practices	263
16.3.2.	Current land use practices	265
16.4.	Desertification of the karoo	270
16.4.1.	A brief history of the karoo desertification debate	270
16.4.2.	Hypothesis 1: The precolonial eastern karoo was a stable and extensive 'sweet' grassland	271
16.4.3.	Hypothesis 2: An altered and less-productive karoo vegetation is expanding into more productive grassland environments	272
16.5.	Conclusions	272
17.	Alien plant invaders of the karoo: attributes, impacts and control S. J. Milton, H. G. Zimmermann and J. H. Hoffmann	274
17.1.	Introduction	274
17.2.	Invasibility of karoo vegetation types	274
17.3.	Attributes of plants invasive in the karoo	276
17.3.1.	General trends	276
17.3.2.	Moist habitats	278
17.3.3.	Dryland habitats	278
	South-western areas: succulent karoo and Little Karoo	278
	Northern and central areas: Kalahari and Bushmanland	279
	Eastern areas: Great, Lower and Eastern Nama-karoo	279
17.4.	Impacts on the karoo ecosystem and economy	280
17.4.1.	Woody plants	280
17.4.2.	Cactaceae	281
17.4.3.	Herbaceous plants	282
17.5.	Control	283

xiv	Contents	
	17.5.1. <i>Prosopis</i>	283
	17.5.2. Cactaceae	283
17.6	Comparison with other arid and semi-arid systems	284
	17.6.1. Invasive taxa and life forms	285
	17.6.2. Karoo species as invaders elsewhere	285
17.7.	Future scenarios and research needs	286
17.8.	Acknowledgements	287
	Part five Comparisons	289
18.	Comparison of ecosystem processes in the Nama-karoo and other deserts W. G. Whitford	291
18.1.	Introduction	291
18.2.	Physical environment and primary productivity	291
	18.2.1. Precipitation patterns	291
	18.2.2. Topographic similarities	292
	18.2.3. Water redistribution	292
	18.2.4. Primary productivity	292
	18.2.5. Shrub morphology	293
18.3.	Decomposition and nutrient cycling	294
	18.3.1. Soil organisms and soil processes	294
	Termites	295
	Buried litter and roots	296
	Role of soil biota	296
	Mineralization and immobilization	297
	Rhizosphere processes	298
	Soil aggregates	298
	Soil perturbation	299
	18.3.2. Granivory and herbivory	299
18.4.	Historical changes and desertification	300
18.5.	Acknowledgements	302
19.	The succulent karoo in a global context: plant structural and functional comparison with North American winter-rainfall deserts K. J. Esler, P. W. Rundel and R. M. Cowling	303
19.1.	Introduction	303
19.2.	Selective regime	304
19.3.	Plant form and community structure	306
19.4.	Community phenology	307
19.5.	A Namaqualand–Namib domain (succulent karoo) model	309
19.6.	Plant function	310
19.7.	Population structure and turnover	313
19.8.	Conclusions	313
20.	The karoo: past and future S. J. Milton and W. R. J. Dean	314
20.1.	Current perceptions	314

	Contents	xv
20.1.1. Patterns		314
20.1.2. Processes		315
20.2. Uncertainties and contradictions		316
20.3. Directions for future research		317
References		319
Index		369