
Biological Diversity

Frontiers in Measurement and Assessment

EDITED BY

Anne E. Magurran

*Professor of Ecology & Evolution,
University of St Andrews, UK*

and

Brian J. McGill

*Assistant Professor, School of Biology and Ecology
& Sustainability Solutions Initiative, University of Maine, USA*

OXFORD
UNIVERSITY PRESS

Contents

List of Contributors	xiii
Foreword	xv
<i>R. M. May</i>	
1 Challenges and opportunities in the measurement and assessment of biological diversity	1
<i>Anne E. Magurran and Brian J. McGill</i>	
1.1 Introduction	1
1.2 State of the field	1
1.3 What is in this book	2
Acknowledgements	7
Part I Basic Measurement Issues	
2 An overview of sampling issues in species diversity and abundance surveys	11
<i>Scott A. Bonar, Jeffrey S. Fehmi, and Norman Mercado-Silva</i>	
2.1 Introduction	11
2.2 State of the field	11
2.2.1 Setting objectives	12
2.2.2 An important partner: the statistician	12
2.2.3 What species to sample	12
2.2.4 Where to sample	13
2.2.5 Bias, sampling error, and precision	14
2.2.6 How to sample	17
2.2.7 Quantifying the sample	19
2.2.8 When to sample	20
2.2.9 How many samples to collect	21
2.2.10 Comparing information from different surveys	23
2.2.11 Preparing for the field	23
2.3 Prospectus	24
2.4 Key points	24
3 Biodiversity monitoring: the relevance of detectability	25
<i>Stephen T. Buckland, Angelika C. Studeny, Anne E. Magurran, and Stuart E. Newson</i>	
3.1 Introduction	25
3.2 State of the field: which biodiversity measure?	26

3.3	Detectability: are species counts relevant for monitoring biodiversity?	28
3.3.1	Individual detectability	28
3.3.2	Estimating individual detectability	28
3.3.3	Species detectability	29
3.4	Case study: the UK Breeding Bird Survey	32
3.5	Discussion	34
3.6	Prospectus	35
3.7	Key points	36
	Acknowledgements	36
Part II Diversity		
4	Estimating species richness	39
	<i>Nicholas J. Gotelli and Robert K. Colwell</i>	
4.1	Introduction	39
4.2	State of the field	39
4.2.1	Sampling models for biodiversity data	39
4.2.2	The species accumulation curve	42
4.2.3	Climbing the species accumulation curve	43
4.2.4	Species richness versus species density	43
4.2.5	Individual-based rarefaction	45
4.2.6	Sample-based rarefaction	46
4.2.7	Assumptions of rarefaction	47
4.2.8	Estimating asymptotic species richness	48
4.2.9	Comparing estimators of asymptotic species richness	52
4.2.10	Software for estimating species richness from sample data	53
4.3	Prospectus	53
4.4	Key points	53
	Acknowledgements	54
5	Measurement of species diversity	55
	<i>Brian A. Maurer and Brian J. McGill</i>	
5.1	Introduction	55
5.2	State of the art	55
5.2.1	Species diversity as variance	59
5.2.2	Species diversity as information	60
5.2.3	Traditional measures of various types of diversity	61
5.2.4	Addressing the difference between the empirical and ecological samples: estimating species diversity components using empirical samples	62
5.2.5	Testing for heterogeneity among ecological samples	63
5.3	Prospectus	64
5.4	Key points	64
6	Compositional similarity and β (beta) diversity	66
	<i>Lou Jost, Anne Chao, and Robin L. Chazdon</i>	
6.1	Introduction	66

6.2 State of the field	66
6.2.1 Measures of relative compositional similarity and differentiation	68
6.2.2 Diversity and compositional similarity	77
6.2.3 Statistical estimation of assemblage differentiation and similarity	83
6.3 Prospectus	83
6.4 Key points	84
7 Measuring biological diversity in time (and space)	85
<i>Anne E. Magurran</i>	
7.1 Introduction	85
7.2 State of the field: timescales of change and community boundaries	86
7.3 What is being measured?	87
7.4 Assessing change through time	89
7.4.1 Temporal turnover: species time curves	89
7.4.2 Temporal turnover: turnover indexes	89
7.4.3 Using species abundance distributions to evaluate change	90
7.4.4 Assessing change using biodiversity indexes	91
7.5 Measuring change in the rate of change	92
7.6 Using temporal change to shed light on community structure	93
7.7 Partitioning diversity in space and time	93
7.8 Prospectus	93
7.9 Key points	93
Part III Distribution	
8 Commonness and rarity	97
<i>Anne E. Magurran and Peter A. Henderson</i>	
8.1 Introduction	97
8.2 State of the field	97
8.3 Commonness and rarity: ecological context	98
8.4 Assessing commonness and rarity	102
8.5 Prospectus	103
8.6 Key points	103
9 Species abundance distributions	105
<i>Brian J. McGill</i>	
9.1 Introduction	105
9.2 State of the field	106
9.2.1 Visual approaches to SADs	106
9.2.2 Parametric approaches to SADs	110
9.2.3 Non-parametric approaches to SADs	110
9.2.4 Multivariate approaches to SADs	113
9.3 Identifying a useful, parsimonious subset of SAD metrics	113
9.3.1 Efficiency and bias	114
9.3.2 Independence of measures	115

9.3.3 Overall assessment of useful, parsimonious metrics of SADs	121
9.4 Prospectus	121
9.5 Key points	122
Acknowledgements	122
10 Fitting and empirical evaluation of models for species abundance distributions	123
<i>Sean R. Connolly and Maria Dornelas</i>	
10.1 Introduction	123
10.2 State of the field	124
10.2.1 Species abundance models	124
10.2.2 Obtaining predicted abundances	125
10.2.3 Choosing parameters	126
10.2.4 Goodness-of-fit testing	131
10.2.5 Model selection	134
10.3 Prospectus	137
10.3.1 Sampling theory for species abundance models	137
10.3.2 Parameter estimation	137
10.3.3 Goodness-of-fit testing	138
10.3.4 Model selection	139
10.3.5 Conclusions	139
10.4 Key points	140
11 Species occurrence and occupancy	141
<i>Kevin J. Gaston and Fangliang He</i>	
11.1 Introduction	141
11.2 State of the field	143
11.2.1 Occupancy–area relationships	143
11.2.2 Occupancy–abundance relationships	145
11.2.3 Species occupancy distributions	147
11.3 Prospectus	149
11.4 Key points	150
Acknowledgements	151
12 Measuring the spatial structure of biodiversity	152
<i>Brian J. McGill</i>	
12.1 Introduction	152
12.1.1 What spatial structure is of interest?	152
12.1.2 Number of variables recorded – pattern or association?	154
12.1.3 Types of data	155
12.2 State of the art	156
12.2.1 Estimating intensity (first-order effects)	157
12.2.2 Studying effects at a distance (second-order effects)	160
12.2.3 Associations between two variables	166
12.2.4 Software available	170
12.3 Prospectus	170

12.4 Key points	170
Acknowledgements	171
Part IV Alternative measures of diversity	
13 A primer of trait and functional diversity	175
<i>Evan Weiher</i>	
13.1 Introduction	175
13.1.1 General definitions	175
13.1.2 General importance	175
13.1.3 A brief history of trait and functional diversity	176
13.2 State of the field	178
13.2.1 Overview	178
13.2.2 Indices of trait and functional diversity	178
13.2.3 Partitioning the components of trait diversity	184
13.2.4 Methodological issues	185
13.2.5 Conceptual issues	188
13.3 Prospectus	191
13.3.1 Recommendations	191
13.3.2 Future directions	192
13.4 Key points	193
Acknowledgements	193
14 Measuring phylogenetic biodiversity	194
<i>Mark Vellend, William K. Cornwell, Karen Magnuson-Ford, and Arne Ø. Mooers</i>	
14.1 Introduction	194
14.1.1 Overview	194
14.1.2 Approaching the study of phylogenetic diversity	195
14.2 State of the field	197
14.2.1 Null models	198
14.2.2 Simulation analyses	200
14.2.3 Simulation results	201
14.3 Prospectus	203
14.3.1 Phylogenetic diversity in conservation	203
14.3.2 Phylogenetic diversity in community ecology	205
14.3.3 Abundance vs presence–absence data	206
14.4 Key points	207
15 Genetic methods for biodiversity assessment	208
<i>Melanie Culver, Robert Fitak, and Hans-Werner Herrmann</i>	
15.1 Introduction	208
15.2 Genetic methods in biodiversity assessment	209
15.2.1 Mitochondrial, chloroplast, and nuclear DNA	209
15.2.2 Genome technologies	209
15.3 Biodiversity assessments	209

15.3.1	Phylogenies for biodiversity assessment using mtDNA and nuclear DNA	209
15.3.2	Non-invasively monitoring for biodiversity	211
15.3.3	DNA barcoding for biodiversity assessment	212
15.3.4	Genome technologies for biodiversity assessment	216
15.4	Prospectus	217
15.5	Key points	217
Part V Applications		
16	Microbial diversity and ecology	221
	<i>Lise Øvreås and Thomas P. Curtis</i>	
16.1	Introduction	221
16.2	The diversity concept	222
16.3	Phylogeny	223
16.4	rRNA as an evolutionary chronometer	223
16.5	Methods for assessing diversity	223
16.5.1	PCR-based methods	223
16.5.2	Pyrosequencing	225
16.5.3	Metagenomics	228
16.6	Sampling, scale, and thresholds	229
16.7	Mathematical tools for estimating diversity	231
16.7.1	Collectors curves	231
16.7.2	Chao's non-parametric estimators	231
16.7.3	Parametric estimators that assume a distribution	232
16.7.4	Estimating diversity by inferring a distribution from the data	233
16.8	Estimation of required sample size	234
16.9	In-depth metagenome analyses	234
16.10	Prospectus	234
16.11	Key points	236
17	Biodiversity and disturbance	237
	<i>Maria Dornelas, Candan U. Soykan, and Karl Inne Ugland</i>	
17.1	Introduction	237
17.2	What is a disturbance?	237
17.2.1	Source of the disturbance	238
17.2.2	Timescale	238
17.2.3	Spatial scale	238
17.2.4	Intensity	239
17.2.5	Specificity	239
17.2.6	Summary	239
17.3	State of the field: measuring the effects of disturbance on biodiversity	239
17.3.1	Univariate metrics	239
17.3.2	Species abundance distribution based metrics	243
17.3.3	Multivariate analysis	247
17.4	Prospectus	250

17.5 Key points	251
Acknowledgements	251
18 Measuring biodiversity in managed landscapes	252
<i>Steven L. Chown and Melodie A. McGeoch</i>	
18.1 Introduction	252
18.2 State of the field	253
18.2.1 Variation in biodiversity measurement goals	253
18.2.2 Bioindicators and monitoring	255
18.2.3 Measuring biodiversity for management	258
18.2.4 Matrices for measurement	261
18.3 Prospectus	263
18.4 Key points	264
Acknowledgements	264
19 Estimating extinction with the fossil record	265
<i>Peter J. Wagner and S. Kathleen Lyons</i>	
19.1 Introduction	265
19.2 State of the field	265
19.2.1 Basic metrics	265
19.2.2 Survivorship curves	267
19.2.3 The importance of sampling	267
19.2.4 Relevant studies	269
19.2.5 Occurrence-based diversity estimates	269
19.2.6 Gap analyses	271
19.3 Prospectus	274
19.4 Key points	275
20 Estimating species density	276
<i>Michael L. Rosenzweig, John Donoghue II, Yue M. Li, and Chi Yuan</i>	
20.1 Introduction	276
20.1.1 The problem: what is the density of species?	276
20.1.2 Defining the density of species	276
20.1.3 Species density takes on new importance in an era of environmental concern	278
20.2 Data set	278
20.2.1 Data description	278
20.2.2 Data manipulation	280
20.2.3 NP : our surrogate for A	280
20.3 Density estimates	280
20.3.1 First density estimate	280
20.3.2 Density estimates for subsets with a uniform plot size	280
20.4 Curvature in SPARs	282
20.5 Reducing the bias	282
20.5.1 Extrapolation	283
20.5.2 Estimators based on the frequency of scarce species	284

20.6	Applying bias reduction	284
20.7	Checking our results on the scale of all of Virginia	285
20.8	Why species density?	286
20.8.1	Species density as an environmental indicator	286
20.8.2	Species density as a topic of study	287
20.9	Key points	287
	Acknowledgements	287
Part VI Conclusions		
21	Conclusions	291
	<i>Brian J. McGill and Anne E. Magurran</i>	
	References	295
	Index	337